Handbook of Fish Biology and Fisheries

VOLUME 2

FISHERIES

EDITED BY
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Volume 2

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Volume 1 Fish Biology

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BLACKWELL PUBLISHING
350 Main Street, Malden, MA 02148-5020, USA
108 Cowley Road, Oxford OX4 1JF, UK
550 Swanston Street, Carlton, Victoria 3053, Australia

First published 2002
Reprinted 2004

Library of Congress Cataloging-in-Publication Data has been applied for.

Volume 1 ISBN 0-632-05412-3 (hbk)
Volume 2 ISBN 0-632-06482-X (hbk)
2-volume set ISBN 0-632-06483-8

A catalogue record for this title is available from the British Library.

Set in 9/11.5 pt Trump Mediaeval
by SNP Best-set Typesetter Ltd, Hong Kong
Printed and bound in the United Kingdom
by TJ International Ltd, Padstow, Cornwall.

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Blackwell Publishing, visit our website:
http://www.blackwellpublishing.com

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Preface

The goal of the two volumes of the *Handbook of Fish Biology and Fisheries* is to help integrate the study of fish biology with the study of fisheries. One might not expect these two subjects to need further integration. However, strong declines in many fish stocks around the globe, combined with growing concerns about the impact of fisheries on marine and freshwater biodiversity, are raising new questions about aspects of fish biology that have traditionally dwelt outside mainstream fisheries research. Thus, fisheries biologists and managers are increasingly asking about aspects of ecology, behaviour, evolution and biodiversity that had traditionally been studied by different people who attend different conferences and publish in different journals. By bringing these people and their subjects together in the two volumes of this *Handbook*, we hope to foster a better two-way flow of information between the studies of fish biology and fisheries.

A tradition runs through the prefaces of the other volumes in this series whereby the editors distance themselves from a literal translation of the word 'Handbook'. In keeping with this tradition, we wish to make clear that this is not a cookbook of recipes for how to study and manage fish populations. Instead, we have tried to produce a pair of reference books that summarize what is known about fish biology and ecology, much of which is relevant to assessment and management of fish populations and ecosystems. Of course, much of the material in the first volume may never find applications in fisheries, and that is fine with us. We encouraged our authors to provide a wide coverage of fish biology simply because the topics are interesting in their own right, and because the borders between pure and applied research are fuzzy. We therefore decided not to restrict information according to its direct relevance to fisheries as this subject is understood today. We hope the result will be of value to undergraduates and graduates looking for information on a wide variety of topics in fisheries science. The books are also aimed at researchers who need up-to-date reviews of topics that impinge on their research field but may not be central to it. The information should also be useful to managers and decision makers who need to appreciate the scientific background to the resources they are trying to manage and conserve.

In the first volume, subtitled *Fish Biology*, our introductory chapter explores the underpinnings of fisheries biology and management by basic research on fish biology. Part 1 then examines systematics and biogeography of fishes, including methods for determining phylogenetic relationships and understanding spatial patterns of diversity. Part 2 examines production and population structures of fishes, beginning with chapters on physiology and growth, followed by recruitment, life histories, migration, population structure and reproductive ecology. Part 3 considers fishes as predators and as prey, making use of conceptual advances in behavioural ecology to link predator–prey interactions to the environment. In Part 4 we scale up from individual interactions to communities and ecosystems. The chapters include comparisons of freshwater and marine communities, as well as interactions between fishes and parasites.

In the second volume, subtitled *Fisheries*, we begin with a chapter that considers the human dimension of fisheries management. Part 1 then gives background information for fisheries, including fishing technology, marketing, history of fisheries, and methods of collecting and presenting data. Part 2 provides fundamental methods of stock assessment, including surplus production models, virtual population analyses, methods for forecasting, length-based assessments, individual-based models and economics. We have also tried to consolidate this information by reviewing the various options available for modelling fisheries, including the pros and cons of each. Part 3 explores wider issues in fisheries biology and management, including the use of marine protected areas, conservation threats to fishes, ecosystem impacts and recreational fishing.

We are very grateful to our 54 authors from 10 countries for their hard work and patience while we attempted to herd them all in the same general direction. We also thank Susan Sternberg who first suggested that we take on this project, and Delia Sandford at Blackwell Sicence who has overseen it. The final stages of production have been greatly helped by two people. Valery Rose of Longworth Editorial Services worked patiently and efficiently to shepherd the book through the copy editing stages, and Monica Trigg, did an excellent job with the gargantuan task of constructing the two indices. Paul Hart would like to thank the University of Bergen, Department of Fisheries and Marine Biology, for providing him with space and support during the final editing of the manuscript. John Reynolds would like to thank his many colleagues at the University of East Anglia and at the Centre for Environment, Fisheries, and Aquaculture Science (Lowestoft) who have helped build bridges between pure and applied research.

The editors and publisher would like to thank copyright-holders for permission to reproduce copyright material. They apologize for any errors or omissions, and would be grateful to be notified of any corrections that should be incorporated in the next edition or reprint of this book.

Paul J.B. Hart and John D. Reynolds
Leicester and Norwich

Abbreviations

ANN	artificial neural network
BPR	biomass per recruit
CPUE	catch per unit of effort
EEZ	Exclusive Economic Zone
ELEFAN	electronic length–frequency analysis
FAO	Food and Agriculture Organization
GOF	goodness of fit
IBM	individual based models
ICES	International Council for the Exploration of the Sea
ICLARM	International Center for Living Aquatic Resources Management
ITQ	individual transferable quota
JAM	judicious averaging method
MBA	Mariue Biological Association
MEY	maximum economic yield
MIX	statistical mixture analysis
MPA	marine protected area
MSC	Marine Stewardship Council
MSVPA	multispecies virtual population analysis
MSY	maximum sustainable yield
NAFO	North Atlantic Fisheries Organization
SDP	stochastic dynamic programming
SFIA	Sea Fish Industry Authority
SLCA	Shepherd's length–composition analysis
SRR	stock–recruitment relationship
SSB	spawning stock biomass
TAC	total allowable catch
UNCLOS	United Nations Convention on the Law of the Sea
USDA	US Department of Agriculture
XSA	extended survivors analysis
VPA	virtual population analysis
YPR	yield per recruit

1 The Human Dimension of Fisheries Science

PAUL J.B. HART AND JOHN D. REYNOLDS

1.1 INTRODUCTION

Fisheries science and fisheries management are not the same thing. Fisheries science is a multidisciplinary subject that integrates animal behaviour, ecology and population dynamics with environmental processes to predict how animal populations respond to fishing mortality. The results of fisheries science inform fisheries management, whereby policies are implemented to meet specific objectives set by various stakeholders ranging from fishers to consumers to conservationists. The focus on science in the two volumes of this *Handbook* reflects our own backgrounds but is also a consequence of the way in which fishery science and management have developed. In this chapter we try to outline some of the fisheries management issues that are not dealt with elsewhere in any detail, but that need to be considered to put into context the state of fisheries science.

Most of the chapters in this second volume concentrate on the technical issues of either assessing a fish stock or assessing the effects that the fishery has on the ecosystem – in other words, fishery science (Hutchings et al. 1997a). However, various aspects of management are found throughout this book. For example, Misund et al. (Chapter 2) discuss the interaction between fisheries management and the type of gear used, particularly in artisanal fisheries. Gear types dictate the kinds of management measures that can be taken. Shepherd and Pope (Chapters 7 and 8) provide methods for determining how many fish are in a stock and how their abundance is likely to change in the short to medium term. In this context they discuss reference points for management. Hannesson's chapter (Chapter 12) deals extensively with fisheries management methods, particularly from an economic point of view. Clearly, economics plays a key role in every aspect of commercial fisheries, from the intensity of fishing and kinds of gear used, to the short-term costs and long-term benefits to be derived from conserving stocks. Young and Muir (Chapter 3) describe the attempt by the Marine Stewardship Council to employ accreditation of fisheries and labelling of their products to use consumer pressure to improve the standard of fisheries management. This chapter also points out that the fishing industry is almost entirely supply driven with little regard for what the consumer wants. Finally Evans and Grainger (Chapter 5) outline how management policy is integrated with data collection for fishery monitoring and assessment.

1.2 THE ORIGINS OF FISHERIES SCIENCE

Biologists, or more properly zoologists, were the first to draw attention to the problem of overfishing (Smith, Chapter 4, this volume). According to Graham (1956), fisheries science took its characteristic form from around 1890 onwards with a blend of zoology and statistics but each with a new form and function: 'The form was knowledge like that of a fisherman, and function was guidance to better use of the stocks of fish.' This foreshadows the division already pointed to between fisheries science and management. In the same book, Beverton and Holt (1956) wrote that fisheries management should aim to adjust the fishing activity to obtain the best results. They defined 'best' as being 'the greatest sustained yield'. The search for this single, biologically based objective for fisheries management came to dominate fisheries science. In the early days most biologists seemed to operate on the principle that if they could make sure that the supply of fish could be sustained, the commercial side would look after itself. This is reminiscent of the views of some fisheries biologists today when confronted with questions about biodiversity: if the supply of fish is maintained, extinction risk will be minimal (reviewed by Reynolds et al., Chapter 15, this volume).

1.3 THE OBJECTIVES OF FISHERIES MANAGEMENT

It is now recognized that there are many reasons for managing fisheries and that most of them are not to do with yield maximization. The issue of the objectives of fisheries management is critical. The early view that we should aim to sustain the highest catch possible no longer holds. It is not sufficiently precautionary (Punt and Smith 2001) and it ignores other objectives. Hilborn and Walters (1992) organize the objectives into four categories: (1) biological, (2) economic, (3) recreational and (4) social. In most cases the objectives for a particular management regime will be a mixture of the four. For example, the Norwegian government subsidizes small communities in the north to keep people living in the region and one of the main economic activities is fishing. It would not do, though, to wreck this resource base by fishing unsustainably. So we have two objectives working in parallel: to maintain the communities by supporting their infrastructure at the taxpayers' expense and to manage the fisheries sustainably.

The objectives of some management systems are simple on the surface but have wider implications. Off the south coast of Devon, UK, the inshore waters around Start Point midway between Plymouth in the west and Brixham in the east are partitioned (Hart 1998). Certain areas are closed to all mobile gears such as trawlers or scallop dredgers and are intended for the exclusive use of crab potters. Other areas are open to mobile gear for parts of the year when crab fishing is at its seasonal nadir. The principal objective of this agreement is to keep mobile and fixed gear apart. Otherwise the crab potters would constantly be having their gear destroyed by trawlers or scallop dredgers. Although this is the principal objective, there are wider consequences both for the fishing community and for the biological community. Without the agreement the potters would not be able to make a living. As there is little alternative employment, many people would have to move away, destroying the structure of small local villages such as Beesands and Hallsands and removing secondary jobs from the wholesale and transport business. From a biological perspective, the areas closed to mobile gear meet another objective by enabling a more complex benthic community, which includes larger individuals than in the areas that are trawled regularly (Kaiser et al. 2000, Kaiser and Jennings, Chapter 16, this volume). Although the conservation of biodiversity was not an original objective of the partitioning system, this has been a fortunate by-product.

The past preoccupation with maximizing sustainable yield was thought sufficient for many years even though fisheries economists were already commenting in the 1950s that fisheries management was not about biology but about fishers' behaviour (Smith, Chapter 4, this volume). The same point was made by Wilen (1979) but this thinking has not penetrated many of the institutions that assess exploited stocks (but see Hilborn et al. 1993). A focus restricted to the biological aspects of fisheries science did not grow to fully embrace the wider issues of economics and social structure. Why not?

1.4 THE DEVELOPMENT OF THE INSTITUTIONS OF FISHERIES SCIENCE

Part of the answer must come from the way in which fisheries science has become institutionalized. In Great Britain those who first drew attention to the problems of overfishing were often employed most of the time elsewhere. One of the most famous was Thomas Henry Huxley, who had wide interests in science and earned much of his income from writing and from taking various jobs such as Inspector for Salmon Fisheries (Lankester 1895; Clark 1968). Walter Garstang was primarily an academic zoologist who interested himself in the fisheries question only as a sideline. The activities of these people led eventually to the establishment of bodies such as the Marine Biological Association of the UK (MBA) whose original purpose was: 'To establish and maintain laboratories on the coast of the United Kingdom, where accurate researches may be carried on, leading to improvement of zoological and botanical science, and to an increase of our knowledge as regards the food, life-conditions, and habits of British food-fishes and molluscs' (Lankester 1895; Lee 1992). Early workers employed by the MBA, such as Ernest Holt, worked very closely with the fishing industry and spent time on trawlers and at the fish market sampling fish. As institutions became larger and employed more people, they evolved their own ethos and traditions. This led to subtle changes in the objectives of employees. In the end the MBA, for example, became a much more academic research institution focusing on the 'zoological and botanical science' part of its brief, while its fisheries function was taken over by the nascent Fisheries Laboratory at Lowestoft, now called the Centre for Environment, Fisheries and Aquaculture Science (Graham 1956; Lee 1992).

Once established as institutions charged with carrying out stock assessments and giving advice to politicians about implications of management measures, government-operated fisheries laboratories were easy targets for people in the fishing industry, who see scientists as at best a bunch of boffins and at worst as agents of the government. This put distance between the people who assess fish stocks and those exploiting the stocks. Once this gulf had developed it was easy for each side to argue that the other did not really appreciate what the problem was. Today, attempts to bridge this gulf are an important element in the drive to create suitable management measures.

Although early workers appreciated that economic questions were important to understanding fisheries (Smith, Chapter 4, this volume), it somehow took a long time for people with expertise in economics or sociology to be employed by the institutions that assessed the stocks. Even now, institutions such as the International Council for the Exploration of the Sea (ICES) have little input from economists and sociologists. Fish stock assessment has usually stopped at the assessment of the biological productivity of the stock when really it would be a good idea to also have people who could evaluate the economic or social benefits of proposed management policies. This point is taken up again later when we discuss methods for dealing with uncertainty.

Within fisheries laboratories the emphasis is often on scientific research. Assessment work is regarded as routine and not conducive to career advancement (Finlayson 1994). While fundamental research that leads to high-quality refereed publications is obviously very satisfying and important in many contexts, institutions with stock assessment responsibilities need to develop career appraisal criteria which reward people for doing good stock assessments and generating sound advice. There is a parallel here with engineering. When designers and engineers set to work to construct the bridge between Malmö (Sweden) and Copenhagen (Denmark) over the Öresund they would have depended heavily on a wide range of scientific laws and principles. But no one would have been happy if the bridge engineers were rewarded more for a general theory of bridge collapse than for choosing the correct equations to tell them how thick the suspension wires should be.

1.5 WHO OWNS THE FISHERY AND FOR WHOM IS IT MANAGED?

The separation of fishery scientists and managers into institutions, and their alienation from the fishing industry, has resulted in the two groups having very different objectives. Fishery scientists want to control and regulate the industry while fishers want to earn at least enough money to pay their costs and make a living. Who are fisheries scientists working for? If we take the view that they are working for fishers, perhaps we would expect their perspectives to coincide. But of course this is unrealistic, because fishers compete with other fishers, and scientists are often asked for advice that can be used to referee the competition. This competition often takes on nationalistic fervour: 'Why should we struggle to make ends meet under reduced quotas when fishers from another country take our fish?'

Another view is that society owns the fishery, and fishers are given permission to exploit the resource and should be grateful for this chance. In a legal sense fish in coastal waters are indeed typically the property of the state (Charles 1998a; Walters 1998). From this Walters (1998) argues that fishers have no rights, and that exploitation should only occur if this benefits society. The same argument is made about forestry companies when conservationists question the rights of loggers to exploit a common resource. When we contrast this view with the fishers' viewpoint, we see a recipe for failure of many standard management measures. The fisher borrows money from the bank to buy a boat and has to catch enough fish to pay off his loan and to maintain his crew and his family during the life of the boat. Taking account of the fisher's perspective therefore requires that management measures manipulate the costs and benefits that direct the actions of the fisher. Regulations based on total allowable catches and minimum landing sizes will be forever compromised because they require fishers to throw away money (dead fish) for the good of society or their competitors. Few individuals in any walk of life are happy doing that.

So far we have considered the fisher as the sole stakeholder, although perhaps operating on behalf of society. What do we mean by 'society'? Just as different fishers often have competing perspectives, different members of society have different views. Consumers want to be able to buy fish to eat, and in many developing countries they have few or no dietary alternatives. Members of society are also increasingly concerned about biodiversity and ecosystem structure in aquatic habitats (Reynolds et al., Chapter 15, this volume). The entry of conservationists into the sustainable use dialogue has put new demands on fisheries science and management (Reynolds et al. 2001). Whatever rights fishers may have to make a living from the sea, conservationists argue that these rights do not extend to the decimation of populations for profit. According to this viewpoint, if fishers cannot meet conservation objectives, they should stop fishing.

1.6 THE PROBLEM OF UNCERTAINTY

We began Chapter 1 in Volume 1 with Charles's (1998b) categorization of uncertainty in fisheries science. These were (i) random fluctuations, (ii) uncertainty in parameters and states of nature, and (iii) structural uncertainty. It is becoming increasingly evident that one of the biggest challenges for the future is to devise institutional systems that are able to take account of uncertainty and to take decisions in the face of it. A number of fisheries have collapsed, probably because uncertainty about their state was either ignored or played down. We outline two examples.

Between 1920 and 1945 the California sardine (*Sardinops sagax*) formed the basis of an important fishmeal and canning industry centred on Monterey, USA (McEvoy 1986; Mangelsdorf 1986). Factory owners soon realized that converting the whole fish into meal and abandoning the canning process could earn them more money. As the fishery increased, evidence for impacts on the stock was evaluated by both the California Fish and Game (CFG) Fisheries Laboratory and the US

Bureau of Fisheries' Laboratory (USBF). The former was dedicated to the conservation of Californian resources and one of the measures taken to control fishing effort was to stipulate that a certain proportion of the sardines had to be canned. To avoid this law some manufacturers bought up old factory ships abandoned by the defunct whaling industry and converted them into floating fishmeal plants. These were moored just seaward of California's three-mile state boundary, allowing the producers to ignore the CFG ruling about canning a proportion of the fish.

In the late 1930s scientists at the CFG were becoming increasingly concerned by the effect the fishery was having on the stock. In the 1936–7 season the fishery took around 40% of the estimated adult stock; by the end of the fishery, in the 1944–5 season, it took 74% (McEvoy 1986). A Congressional hearing was set up in 1936 to decide whether the stock was being overfished. The two groups of scientists used very similar data to argue different things because of their uncertainty in how to interpret events. The CFG scientists argued that there was clear evidence that the stock was being overfished. The USBF scientists, who had a brief not only to conserve stocks but also to promote the fishing industry, argued that the evidence on overfishing was equivocal and that environmental changes had brought down the sardine stock. This allowed the industry representatives to drive a wedge between the scientists at the Congressional hearing, which concluded that more evidence needed to be gathered. Soon thereafter, the Second World War stimulated demand for canned sardines for troops. This stimulated fishing, which continued until 1945 when the sardine stock collapsed and the fishery disappeared.

This sad story illustrates how Charles's (1998b) second category of uncertainty, involving the state of nature, prevented scientists from giving a clear message that the sardine stock was being overfished. At the time there was no procedure that CFG or USBF biologists could use to present to the Congressional hearing a set of possible states with possible outcomes if a range of actions could be taken. The result was a stalemate followed by the loss of a resource that has never really reappeared.

The collapse of the cod fishery off Newfoundland is our second example. We will keep the details to a minimum because much has already been written about this (Hilborn et al. 1993; Hutchings and Myers 1994; Walters and Maguire 1996; Doubleday et al. 1997; Healey 1997; Hutchings et al. 1997a,b). Conflicting evidence was available to Canadian Department of Fisheries and Oceans (DFO) scientists on the state of the cod stocks at the end of the 1980s. CPUE (catch per unit of effort) data from the commercial fishery remained high and indicated an expanded stock while the DFO's own survey data showed the stock to be at a steady level. Data from the inshore sector had shown a decline since the 1970s but these data were ignored (Finlayson 1994). The general opinion is that, at best, the institutional structure of DFO and of the ways in which the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) worked were not able to accommodate uncertainty in the assessments of the cod stock. Some have argued that the bureaucratic procedures of the DFO suppressed the expression of uncertainty by DFO scientists (Hutchings et al. 1997a). At the scientific level, the assessment work was done using the best possible methods but these are always going to produce results that have considerable uncertainty (Walters and Maguire 1996). If people at both the scientific and the management level had been better able to communicate this uncertainty and handle it, the collapse might have been lessened or averted.

Both examples show that fisheries science is not yet able to provide stock assessments with well-defined statistical precision. It probably never will (Walters and Maguire 1996; Walters 1998). This means that institutional structures must be created that can make decisions in the face of uncertainty. Suggestions have been made by Hilborn and Walters (1992) and Hilborn et al. (1993). One could use a two-phase approach to assessing stocks and deciding on which action to take. First stock assessment scientists would evaluate the possible states of the stock and propose how the state will change as a consequence of a range of actions that might be possible. The evaluation of stock states (the state of nature) would also include an estimate

Table 1.1 The form proposed by Hilborn et al. (1993) for inspecting the possible outcomes and their values for a range of policy decisions and states of nature. P_n = policy option n, S_1 = state of nature m, p_m = probability with which S_m exists, Y_{nm} = the yield expected from the particular combination of policy and state, $E(P_n)$ = the expected value of each policy option calculated, as shown in the text.

Policy	State of nature			Expected value
	$S_1(p_1)$	$S_2(p_2)$	$S_3(p_3) \ldots S_m(p_m)$	
P_1	Y_{11}	Y_{12}	$Y_{13} \ldots Y_{1m}$	$E(P_1)$
P_2	Y_{21}	Y_{22}	$Y_{23} \ldots Y_{2m}$	$E(P_2)$
P_3	Y_{31}	Y_{32}	$Y_{33} \ldots Y_{3m}$	$E(P_3)$
.	.	.	. .	.
.	.	.	. .	.
.	.	.	. .	.
.	.	.	. .	.
P_n	Y_{n1}	Y_{n2}	$Y_{n3} \ldots Y_{nm}$	$E(P_n)$

of their probability. The possible outcomes that depend upon each state would be presented in the form of a table (Table 1.1) or, in more complex situations, a series of computer models, which would then be presented to the decision makers. This group would then evaluate the costs and benefits of each alternative and determine the risk associated with each. The expected value of each possible policy in Table 1.1 is calculated from:

$$E(P_n) = \sum_{m=1}^{m} Y_{nm} p_m, \qquad (1.1)$$

where Y_{nm} is the expected yield from a particular combination of policy n and state of nature m, p_m is the probability of the mth state of nature and $E(P_n)$ is the expected value of choosing policy n. Part of the evaluation process would involve simulating the results of policy changes that the decision group might come up with ('what if' questions). These evaluations would take into account the benefit that would accrue to the fishery in all its forms. For this to be done the decision-making body would have to include representatives of all the major stakeholders and, as a group, they would have to be clear on the objectives they wanted to achieve.

The second phase of the process would be for the fisheries managers to review and evaluate the output from the first phase and decide on which option to take. At this stage, imponderables that could not be built into the assessment and evaluation phase would be taken into account.

1.7 DEVELOPMENT TO INCREASE ECONOMIC EFFICIENCY OR FREEDOM?

Much of the argument about who owns the resource and how it should be exploited derives from one particular economic viewpoint. This puts efficiency, productivity and maximization of wealth as the main objectives of economic activity. Evaluated in this context, fisheries are like firms and the management problem is to structure the industry so that the rental stream is maximized. Developing a fishery is seen as equivalent to making it more efficient. Hannesson's chapter (Chapter 12, this volume) outlines this approach, which has led to the industrialization of fisheries as fishers strive to keep costs down through economies of scale. An alternative view of development is provided by Sen (1999) who argues that 'development [is] a process of expanding real freedoms that people enjoy'. The freedom so gained allows people to live more fulfilled lives through access to improved education, health care and a clean and undamaged environment. This concept does not depend on the wealth of a society. Artisanal fishers on Lake Victoria, for example, have lost freedoms through the rise in importance of the introduced Nile perch (*Lates niloticus*) (Harris et al. 1995). The fishery for this species has become a capital-intensive enterprise catching fish for export. Artisanal fishers, who catch fish for their own consumption, have had their prospects diminished as the cichlid species on which they depend have become rarer (see Reynolds et al. Chapter 15, this volume), and because they cannot afford to enter the Nile perch fishery. This has reduced their freedom to choose how to develop their lives and has deprived them of potential improvements in health, better education and the chance to free themselves from the constraints imposed by poverty.

Economic efficiency and accumulation of wealth are often means to greater freedom but they are not goals in themselves. With greater freedom, people can choose the lifestyle they want although not without regard to the rest of society. In many senses modern economic activity, with its focus on efficiency and profit, has left out the human dimension, a point eloquently put by Hoskins (1954) in a discussion of the changes seen in the south Devon, UK, fishing industry. He points out how small fishing communities in south Devon have gradually decayed as the fishing industry has become more and more industrialized, and one of the consequences has been that it is no longer possible 'for the small man [to] find a living and work on his own account, in his own way and at his own pace'. In other words, many people lose freedom of action as a result of improved economic efficiency.

1.8 ACHIEVING SUSTAINABLE DEVELOPMENT

It is now well established that the management objectives of the early fishery scientists were too narrow. It is not enough to aim for maximum sustainable yield, and this is rarely done any more (Punt and Smith 2001). In a sense the argument has come full circle in that the modern objective in resource management is sustainable development. This concept was the centrepiece of the Brundtland Commission's report (Brundtland 1987) and the idea was accepted as a goal for most countries at the 1992 conference on the environment in Rio de Janeiro, Brazil. Anand and Sen (1996) have discussed the concept in detail. The key issue is that we should not do anything in the present which would deprive future generations of having the same opportunities as we have (the same freedoms, see Section 1.7). In fisheries terms this could mean that we should not destroy or diminish fish stocks to such a degree that future generations would not have the opportunity to gain a living from them in the way we do now or to benefit from the maintenance of biodiversity.

The economic argument is set in more general terms. Deriving from an original analysis by Ramsey (1928), the problem is to schedule consumption so as to maximize utility over time modelled by the equation:

$$u_T = \int_{t=0}^{t=T} u(c_t)e^{-\delta t} \tag{1.2}$$

where u_T is the utility over an infinite time period T, c_t is consumption at time t, $u(c_t)$ is utility as a function of consumption at time t and δ is the discount rate. The object is to maximize u_T given the level of consumption and the discount rate. This approach has been used by Clark (1990) to examine the effects of the discount rate on exploitation of a fish population. He pointed out that if the interest rate of money in the bank was greater than the rate of growth of the exploited fish population, it makes rational sense to fish the stock to extinction and invest the money earned in the bank. From the point of view of sustainable development, this means that the present value of the future of the fish stock is too low to preserve. Anand and Sen (1996) argue that such action still qualifies as sustainable development, so long as the money invested in the bank would give future generations the capacity to live a life comparable in opportunities (freedoms) to ours in the present even though those opportunities would not be identical. Under this view, sustainable development would obviously not mean that the world would remain unchanged. The freedoms would be achieved by converting living resources and biodiversity into money. In this vein, Solow (1991) has argued that '[i]f you don't eat one species of fish, you can eat another species of fish . . .' from which the conclusion is drawn that 'we do not owe to the future any particular thing. There is no specific object that the goal of sustainability, the obligation of sustainability, requires us to leave untouched'.

This conclusion is predicated on the assumption that the structure and diversity of the environment are unimportant to our continued welfare. It stems from the human-centric view of life, which separates human activity from the rest of nature as if the two had little of importance to connect them. But many people feel that biodiversity has a strong inherent value above our immediate practical needs. Furthermore, the two volumes of this book have set out to demonstrate how fisheries are embedded in an ecological framework and that we cannot have one without the other. Chapters 11 to 16 in Volume 1 and Chapters 10, 14, 15 and 16 in Volume 2 illustrate how modern knowledge forces us to recognize the critical importance of ecosystems and biodiversity to the sustainability of fisheries. It is not true that one fish species is equally as good as another, as argued by Solow (1991). Species have different roles and removing one from the system can have complex and unexpected consequences. If we damage ecosystems irreparably, then the opportunities for future generations will be severely reduced. At the simplest level, people will not be able to eat cod and chips, but, more significantly, the changed balance in the oceans, combined with continued production of CO_2 into the atmosphere, could alter our environment so radically that life as we know it could not continue. Solow (1991) argues that our ancestors consumed less than they had a right to, thereby leaving us with the means to a better life than we perhaps deserve. We are now redressing the balance and consuming more than we should, thereby leaving our inheritors with less than they will need to live a good life.

1.9 CONCLUSIONS

It is very difficult to evaluate the importance of saving fish resources and biodiversity for the future. In terms of food alone, we may imagine that aquaculture could replace all the fish we presently capture from the wild. From a wider perspective, as we have outlined in Section 1.8, diminished populations and damaged ecosystems will alter the prospects of many aspects of our lives for the future. As it is likely that many fishers choose their activity because it suits their lifestyle needs (Hart and Pitcher 1998), catching all the fish now would not allow future generations to enjoy the same lifestyle opportunities as the present. Other stakeholders would also suffer from the reduced diversity and changed function of aquatic ecosystems. In addition, as discussed by Young and Muir (Chapter 3, this volume), each fish species has its own value as a product and one cannot assume that once all the cod have been fished, people will happily convert to eating farmed salmon. As is so often the case, economic analysis leaves out the intangibles that motivate people.

The potential future benefits of biodiversity, apart from the aspect of ecosystem function, are hard to assess. It is often argued that reducing the stock of biodiversity reduces the chances of discovering new substances that might be of benefit in medicine or the food industry (Reaka-Kudla et al. 1997). Because we do not know what those substances might be and what the relation is between their existence and biodiversity, we cannot assess in an objective way what we might miss if we destroy fish stocks now. We are back to the structural uncertainty that started the first chapter of the first volume. In the final analysis we probably have to accept that there will always be a limit to our knowledge and that what we do today will have important consequences for the present as well as for our legacy for future generations.

ACKNOWLEDGEMENTS

We thank Tony Pitcher and Chuck Hollingworth for valuable comments on an earlier draft of this chapter.

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Part 1

Background to Fisheries

2 Fish Capture Devices in Industrial and Artisanal Fisheries and their Influence on Management

OLE ARVE MISUND, JEPPE KOLDING
AND PIERRE FRÉON

2.1 INTRODUCTION

Modern fishing has grown out of the methods and systems still used in artisanal fisheries. A 120-metre pelagic trawler operating out of Killybegs, Ireland, is different from its predecessors by virtue of the technology that has been applied to increase the ship's catching power and to reduce the number of people required to run it. In reality there is a continuum between the most primitive and most advanced fishing equipment and this chapter will illustrate this development. The elaboration of fishing gear from early times is outlined by Smith (Chapter 4, this volume), and this development through time is paralleled by the spatial changes observed between fleets using a large technological input and those using almost none. The new technology has clearly introduced new problems to be coped with by fisheries managers and we will spend some time in this chapter outlining the particular management problems attached to industrialized and artisanal fisheries. Along the way we will describe the equipment used in the various fisheries and how it is used.

In this chapter we focus on the main fishing techniques operated by industrialized fleets taking the bulk of the catch in oceanic fisheries, and on the techniques employed by artisanal fishermen in lakes and coastal waters in Third World countries. The basic principles for these methods is generally the same whether they are operated by industrialized fleets or artisanal fishermen, but the size of the gear, of the tools for gear handling, of the vessels, equipment for navigation and fish finding, of the catches taken and the costs involved are so different that separate considerations are necessary.

2.2 MAIN FISH CAPTURE TECHNIQUES

2.2.1 Introduction

The main fishing gears have distinct constructions and methods of operation (Fig. 2.1). Purse seines capture fish shoals by surrounding them with a huge net. Trawls filter water masses at a speed higher than the fish's sustainable swimming speed. In long lining fish are attracted by the odour of baits that they swallow and get hooked. Gillnets form invisible net walls that fish swim into and get gilled or become entangled.

The fishing vessels from which the respective gears are operated generally differ in their construction and equipment with respect to size, engine power and gear handling devices. Gill-netters haul the gear over a roller at the rail (Fig. 2.2). Behind the net hauler that is mounted to the deck, fish are removed from the net by hand, and the net is cleared and stacked in a net bin manually or by automatic net clearers, ready to be set again over the stern. The principle for handling long lines is much the same – hauling over a roller at the rail – but the fish are removed before the line goes around the line hauler (Fig. 2.2). The line is then passed through a tube and back to a room with stor-

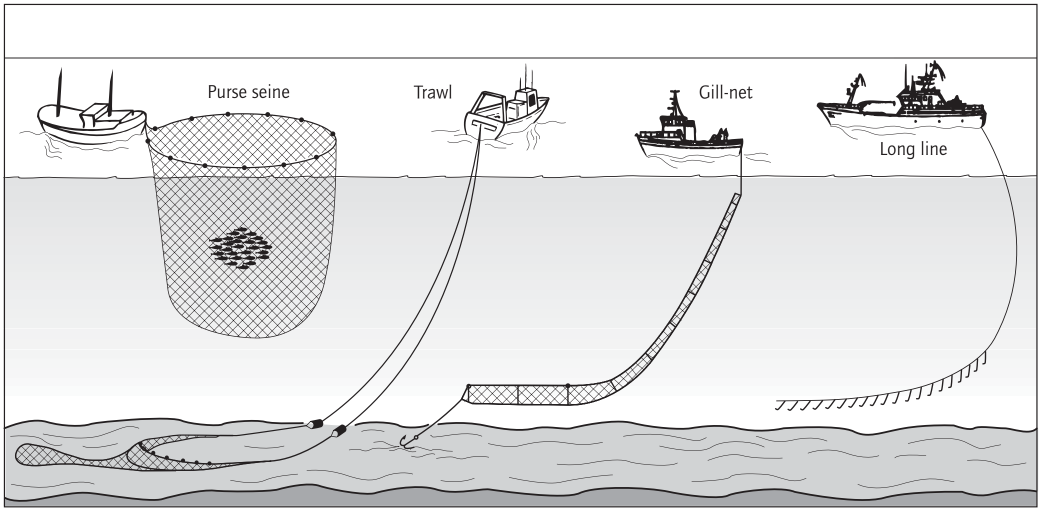


Fig. 2.1 Main fishing capture techniques. From left to right: surrounding of fish shoals by purse seine; filtration of water masses by trawl at a higher speed than the fish are able to endure; gilling of fish that move into a net; attraction and hooking of fish by baited long line.

ing magazines or onto a storing drum. The line is set over the stern through a machine that automatically baits the hooks, or else branch lines with baited hooks are clipped on manually. Large long liners have refrigerated and/or freezer holds for the bait and the catch, and also fish processing machines for heading, splitting and fillet production (Sainsbury 1986; Bjordal and Løkkeborg 1996; Bach et al. 1999a). A purse seiner has two powerful winches to pull in the purse line and thereby close the net up along the side of the vessel (Fig. 2.2). The net is then hauled on board by the net winch, pulled backwards through a net tube or slide by the net crane that also stacks the net in the bin at the stern of the vessel. The catch will finally be concentrated along the side of the vessel in the bag of the purse seine and pumped or brailed onboard with a scoop made of net and into tanks with refrigerated sea water (RSW) at −1.5 °C. This preserves the catch at the best quality. A bottom trawler has two powerful winches for towing and hauling the trawl gear with 5–50 tonnes pulling capacity, and the trawl warp passes through towing blocks at the stern where the trawl doors hang when not in use (Fig. 2.2). The trawl is hauled and shot through the stern ramp, and hauling and shooting are controlled by the sweep winches in the bow. The bottom gear is hauled into a set of trawl lanes (there are usually two such sets on modern vessels) and the trawl net and the bag are pulled in by aid of the gilson winches on the boat deck. A pelagic trawler has no gilson or sweep winches: the trawl net is therefore wound up onto a powerful net drum with 5–50 tonnes pulling capacity.

Modern industrialized fisheries are very effective. Strict regulations through the setting of Total Allowable Catches (TACs) and technical measures like minimum mesh size and closed areas, as well as effort limitations and control of catches and landings, are therefore needed to prevent the collapses of many economically important stocks. A generally important technical measure for fishing gears is the size selectivity, which is defined as the proportion of fish retained related to the length of the fish (Anon. 1996). A selection curve for trawl gears is mostly sigmoid (see Sparre and Hart,

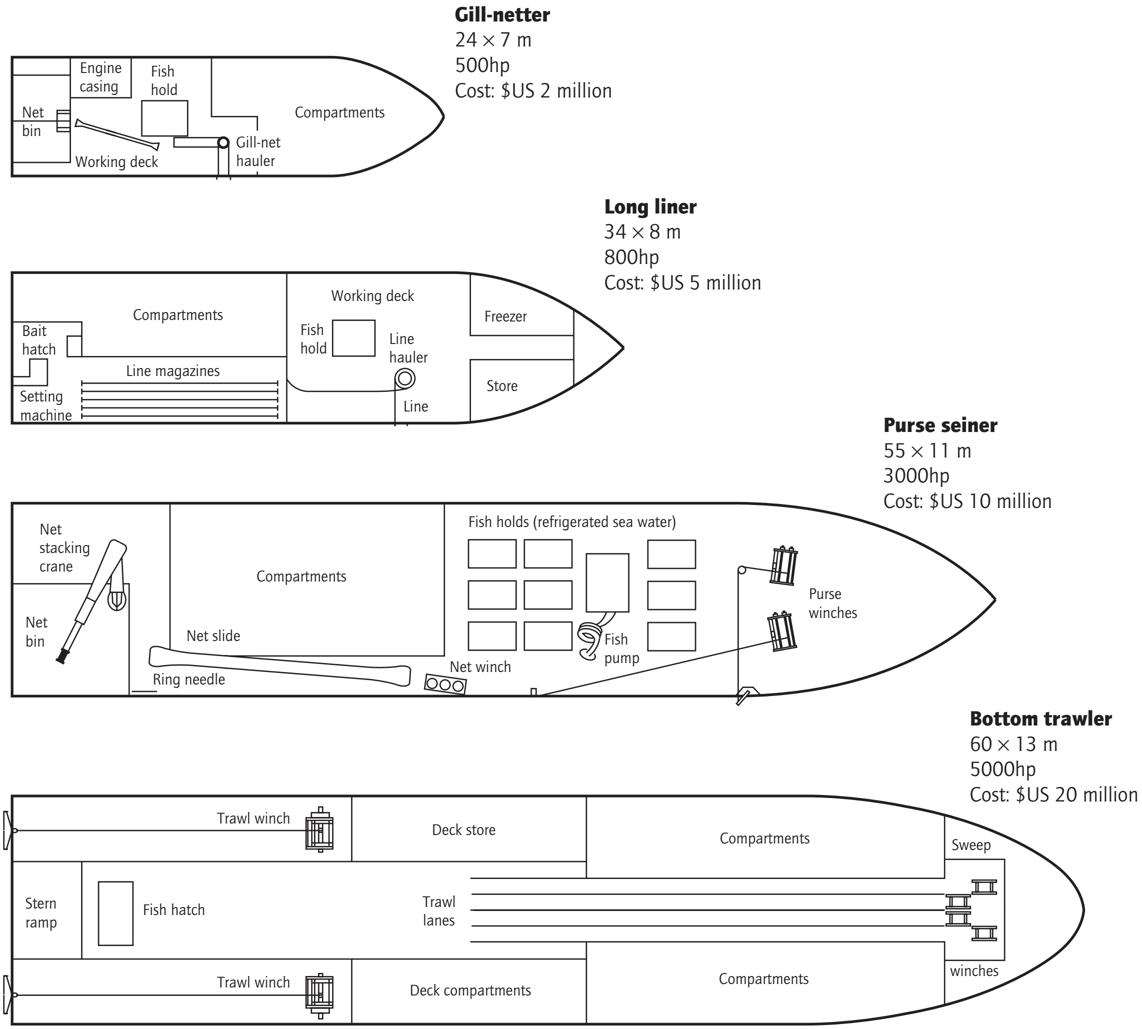


Fig. 2.2 Principal deck layout of main types of fishing vessels (provisional vessel size, engine power and building costs are indicated).

Chapter 13, this volume, equation 13.11), but bell-shaped curves can be the case for gill-nets and hooking gears. Important selectivity measures are L_{50}, defined as the fish length where 50% of the fish is retained by the gear, and the selection factor defined as L_{50} divided by mesh size in centimetres. In addition to the selection range which is defined as $L_{75} - L_{25}$ (L_{75} is fish length where 75% of the fish is retained, and L_{25} is fish length where 25% of the fish is retained), these parametres describe the size selection characteristics of fishing gears.

2.2.2 *Purse seining*

The principle of purse seining is to surround fish shoals by a large net that can be closed so that the fish cannot escape (Ben Yami 1990). When the net is hauled back, the fish will become concentrated in a bag ready for brailing or pumping onboard. The first purse seines were developed by Rhode Island fishermen in the USA for catching menhaden (*Brevoortia patronus*) in the 1860s.

The purse seine is kept floating by a line of floats at the surface, and the lower part of the net sinks by the force of a heavy leadline. The net will thus be stretched out as a circular wall surrounding the fish shoal (Fig. 2.1). The mesh size is so small that the net wall acts as an impenetrable fence preventing escape. When the purse seine has been set out and allowed to sink for some minutes, so that it reaches deeper than the depth of the target fish shoals, it can be closed by hauling the purse line. The lower part of the purse seine will be confined and pulled to the surface. When this operation is finished it is impossible for fish shoals to escape, as long as the net is not torn. However, flying fishes (Exocoetidae) or mullets (Mugilidae) can still jump over the floatline.

The size of the purse seine depends upon the behaviour of the fish to be captured and the size of the vessel from which it is operated. For catching fast-swimming fish shoals at depth, purse seines must be long, deep, have a high hanging ratio and be heavily leaded. The hanging ratio is defined as the length of the stretched net divided by the length of the line on which it is mounted. For catching slower-swimming fish shoals distributed near the surface, purse seines can be shorter, shallower, and have a low hanging ratio. The relationships between fish species, vessel size and purse seine characteristics are given in Fig. 2.3.

Modern purse seining is mostly dependent on detection and location of fish shoals by hydroacoustic instruments (Misund 1997). Larger purse seiners (>40 m) have a low-frequency, low-resolution sonar (18–34 kHz) for detecting fish shoals at long range, and a high-frequency, high-resolution sonar (120–180 kHz) for more detailed mapping of shoal size and fish behaviour in relation to the vessel and the net.

Purse seining is conducted on fish aggregated in dense shoals (Pitcher 1983), or on fish occurring in distinct schools, in which the density is much higher than in shoals. Normally, purse seining on shoals takes place in darkness during night-time, while fishing on schools is limited to the daylight hours. In some fisheries, the fish are available to profitable purse seining both when schooling during daytime and when shoaling at night. For example, this is usually the case during the winter fishery for capelin (*Mallotus villosus*) off the coast of northern Norway, and on the spawning grounds of Norwegian spring-spawning herring off the coast of western Norway in winter. Other purse seine fisheries are profitable only when the fish is shoaling at night or when schooling during daytime. An example of the former is the once-large Chilean fishery for Chilean jack mackerel (*Trachurus murphyi*), which normally is conducted when the fish occur in dense shoals near the surface at night (Hancock et al. 1995). Most of the purse seine fisheries for herring and mackerel in the North Sea in summertime are conducted when the fish are schooling during the daylight hours.

The fishing capacity of purse seiners is normally proportional to vessel size. In the Chilean jack mackerel fishery where there were no limitations set by fishing quotas in the mid-1990s, the total annual catch of purse seiners was related to the hold capacity of the vessel through the equation: total annual catch (tonnes) = 33.3 × hold capacity (m^3) + 18.2 (Hancock et al. 1995). In the 1992 season, a purse seiner with a hold capacity of 1350 m^3 was able to land about 65 000 tonnes of Chilean jack mackerel!

In some regions, artificial light is used to attract fish at night. When sufficient fish have aggregated near the light source, they are caught by purse seining (Ben-Yami 1971). This technique is probably of greatest importance for purse seine fisheries in Asian countries, where it is used offshore. The technique is also common in the Mediterranean, the Black Sea, and in the Russian and African lakes. In other regions, the technique is mostly used inshore, as during the sprat (*sprattus sprattus*), herring (*Clupea harengus*) and saithe (*Pollachius virens*) fisheries in the fjords of southern Norway.

Tuna purse seining is conducted by large vessels (mostly > 60 m) with large nets (Fig. 2.3) in

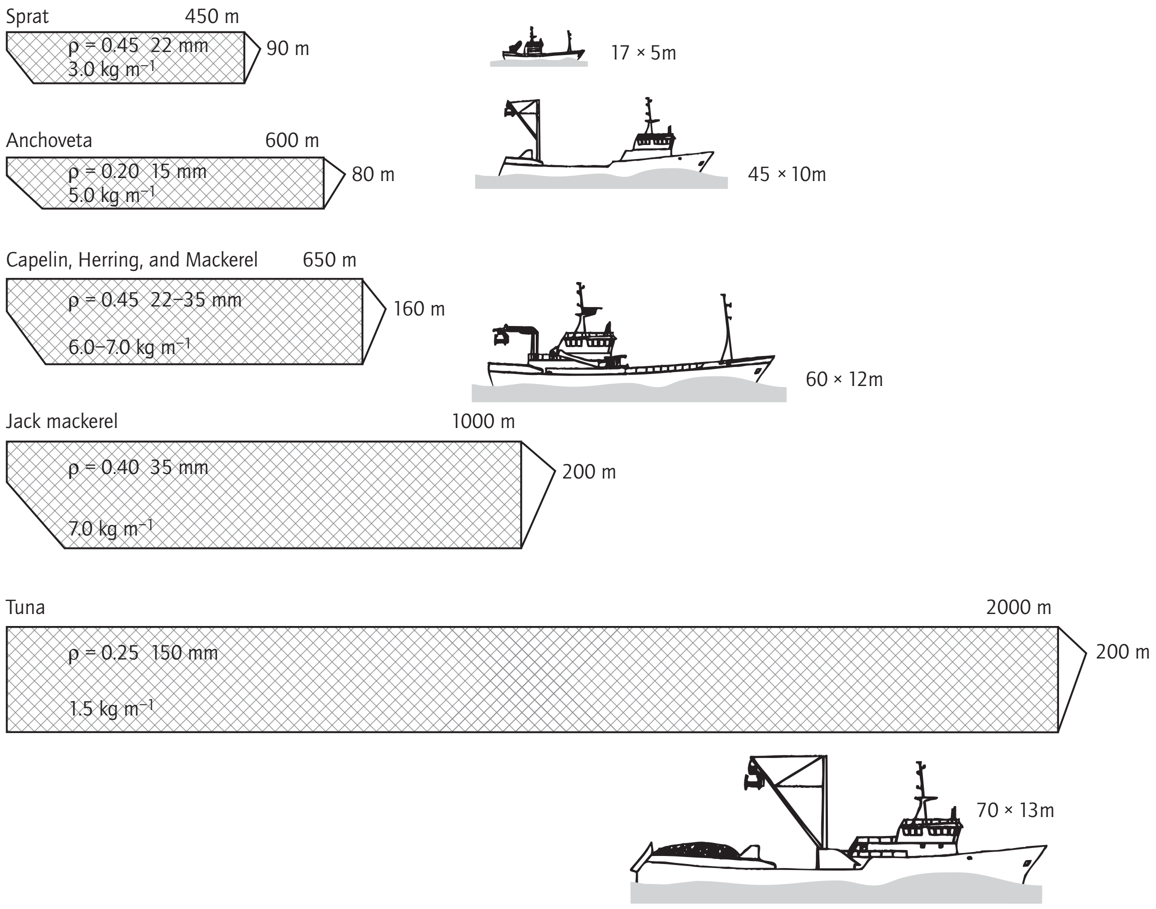


Fig. 2.3 Relationships between fish species, vessel size and purse seine characteristics (length, depth, hanging ratio (ρ), mesh size in mm and lead weight on ground rope are indicated).

tropical/subtropical regions in the Atlantic, Indian Ocean, particularly in the Mozambique Channel, and around the Seychelles, off Australia, and in the western and eastern Pacific (Fonteneau 1997). In the three oceans, the tuna is caught by sets made on free-swimming schools or by sets made on fish associated with floating objects of natural or artificial origin, which are mostly trees and branches. In the eastern Pacific, tuna are also caught by sets made on dolphin herds with which the tuna is associated (Anon. 1992; Hall 1998). The dolphin herds are visible on the surface, and rather easy to encircle by the fast-going tuna seiners (see also Kaiser and Jennings, Chapter 16, this volume). Usually, large tuna are present underneath the dolpins. When the purse seine is closed around the encircled dolpins and tuna, the fishers attempt to release the dolphin by the backdown procedure. This causes the floatline of the distant part of the purse seine to submerge so that the dolphins can swim and jump over. However, dolphin frequently become entangled in the purse seine and drown. In total, this amounted to about 60 000 killed dolphins due to the tuna purse seine fishery in the eastern Pacific in 1992 (Anon. 1992). The tuna pursers operating in this region have been under pressure to change the fishing strategy or fishing operation to eliminate the accidental killing of dolphins (Kaiser and Jennings, Chapter 16, this volume).

2.2.3 Trawling

In principle, trawling is filtration of water masses inhabited by fish at a higher speed than the target fish species are able to swim sustainably. The filtration is done by towing a net bag horizontally through the water masses, either in the pelagic zone (pelagic trawling) or along the bottom (bottom trawling).

Bottom trawling

A bottom trawl is usually rather heavy, with two steel doors to open the trawl and with enough weight to keep the trawl in contact with the bottom during towing (Fig. 2.1). The doors, which can be up to 2 m high and 4 m long and weigh up to 7 tonnes, are connected to the vessel by the trawl warp, usually a wire up to 32 mm in diameter on the largest trawlers. The trawl bag is connected to the doors by a set of one to three bridles on each side, and in the mouth of the trawl there is a ground gear with steel or rubber bobbins or rollers that enable the gear to be operated on rough and stony grounds without being torn or hooked. The first proper bottom trawls, with wooden otter boards and rollers on the ground line, were constructed in Scotland in the 1890s (Smith, Chapter 4, this volume). A long time before that, however, fishermen on sailing ships in the North Sea and in the English Channel had been towing a trawl bag on soft or sandy bottom that was kept open by a wooden boom.

Bottom trawling is conducted in depths as shallow as about 20 m when trawling for industrial species such as the sand lance (*Ammodytes* sp.) in the North Sea, at intermediate depths of about 250 m when trawling for cod and haddock (*Melanogrammus aeglefinus*) in the Barents Sea, in deep waters from 400 m to 800 m for Arctic shrimps (*Pandalus borealis*) and orange roughy (*Hoplostethus atlanticus*) off Namibia, and in depths from 1000 to 2000 m for deep-water species such as grenadier (Macrouridae) in the slopes of the deep-water basin of the Atlantic and hoki (*Macruronus novaezelandiae*) and orange roughy in New Zealand and Australian waters. The ratio of warp length-to-bottom depth decreases from about 10 : 1 in shallow waters to 3 : 1 at intermediate depths, and further down to 1.8 : 1 when towing at great depths.

The construction of bottom trawls reflects the type of species targeted and the bottom type to be operated on. Trawls used on sandy bottoms or soft sediments, such as industrial trawling in the North Sea or shrimp trawling in Arctic waters, often have no rollers on the ground gear. On such trawls the ground gear is just a wire wound with rope. On the other hand, trawls to be operated on hard bottoms with stones, sponges and hard corals are equipped with heavy ground gear with steel or rubber bobbins. During the last decades heavy rock-hopper gear with rubber discs have become popular in the fleets of white-fish trawlers operating in North Atlantic waters. With this ground gear trawlers are able to fish on hard bottom substrates with obstacles such as stones and rocks without damaging the gear or suffering snags on bottom obstacles.

In the southern North Sea beam trawls are commonly used for catching flatfishes such as sole (*Solea solea*) and plaice (*Pleuronectes platessa*). These trawls are kept open by an iron boom up to about 10 m wide that runs on iron shoes on each side so that the boom is kept about 60 cm above the bottom during towing. The beamers can operate one trawl on each side of the vessel. A beam connected to the bow mast, which can be turned at 90 ° to the side of the vessel, is used to handle the boom and the attached trawl net. The beamers are usually powerful vessels with up to 4500 hp available, and can be up to 50 m in length. They can tow the gear at a speed up to 6 knots.

With an otter trawl, fish entering between the trawl doors tend to be guided by the bridles towards the mouth of the trawl, where they turn and try to swim in front of the rolling ground gear. Small fish and species with poor swimming capacity like plaice are less herded than larger and faster fish. As fish get exhausted they turn back and enter into the trawl bag, but in the net section leading to the bag or in the bag itself, the optomotoric response causes the fish to turn forward and try to swim along with the moving mesh wall. Fish finally panic when in the bag and swim towards, and try to escape through, the meshes. The selectivity of the trawl bag then occurs as small fish pass through the meshes while a greater proportion of the larger fish are physically unable to do so.

In most bottom trawl fisheries there are regulations on minimum mesh size in the bag of the trawl, also called the cod-end, to enable proper selectivity of target species. Trawl selectivity is also affected by the number of meshes in the circumference of the trawl bag, the length of the extension, the length of selvage ropes relative to trawl bag and extension, twine thickness, catch size, and mesh geometry. In the North Sea whitefish fishery trawl selectivity can be enhanced by changing the geometry of the meshes in the cod-end from rhombic to square (Robertson and Stewart 1988; van Marlen 2000), while in other areas use of such a mesh configuration did not improve selectivity because of clogging by redfish (*Sebastes* spp.) (Isaksen and Valdemarsen 1989) or catch size-dependent selectivity (Suuronen et al. 1991). Use of rigid sorting grids, made of steel or aluminium, inserted into the net, gives a sharper and more efficient selection than mesh selection alone (Larsen and Isaksen 1993). Fishers in the Barents Sea whitefish trawl fishery have been required by regulation to use grids since 1997.

In the relatively fine-meshed shrimp trawls, bycatch has been a substantial problem. There are estimates of bycatch to shrimp catch ratios of 5 : 1 in temperate waters and up to about 20 : 1 in tropical waters (Pender et al. 1992; Alverson and Hughes 1996; Ye et al. 2000). To reduce bycatch in shrimp trawls, the Nordmore grid was made mandatory in the Barents Sea in 1990 (Isaksen et al. 1992). The name 'Nordmore' derives from Nordmøre, a northern district in Norway where the idea for the sorting grid originated. Other bycatch reduction devices (mesh or grid constructions) have been developed for tropical shrimp trawling, such as in the northern prawn fishery off Australia (Broadhurst et al. 1997; Brewer et al. 1998; Salini et al. 2000).

In recent years considerable focus has been given to the physical impact of bottom trawl gears on the bottom fauna and topography (Kaiser and Jennings, Chapter 16, this volume). On sandy bottoms, tracks of heavy beam trawls were shown to have faded completely after 37 hours (Fonteyne 2000). On other bottom types with more fragile fauna the impact can be more permanent. In the southern North Sea several benthic species have decreased in abundance and even disappeared from certain regions (Bergman and van Santbrink 2000). Some regions of deep-water coral reefs (*Lophelia* sp.) off western Norway have been 'clear cut' with heavy rock-hopper trawl gears (Fosså et al. 2000).

Pelagic trawling

Pelagic species are also caught in large quantities by pelagic trawling, both with single boats and by pair trawling. In the Atlantic, capelin (*Mallotus villosus*), herring, horse mackerel, mackerel, sardines and sprat are caught by pelagic trawling. Off Ireland there is a large pelagic trawl fishery for blue whiting (*Micromesistius poutassou*), which aggregate for spawning during winter and spring. In the northern Pacific, there is a large pelagic trawl fishery for Alaska pollock (*Theragra challcogramma*).

Single-boat pelagic trawling was mainly developed after the Second World War, and is one of the most sophisticated fishing techniques, which sets specific demands for the size, power, equipment and operation of the vessels. In the Netherlands, there has been the development of a fleet of supertrawlers of up to about 125 m in length, and with a carrying capacity of up to 7000 tonnes of frozen pelagic fish. These vessels are operated both in the northern and southern Atlantic, fishing a variety of species such as horse mackerel, mackerel, herring and sardine. During the last decade a substantial fleet of pelagic trawlers, which are often also rigged for purse seining, has been built in Northern Europe (Ireland, Norway, Scotland). These vessels are 60–80 m long, with main engines from 5000 to 12 000 hp, and a carrying capacity of 1500–2500 tonnes of fish in refrigerated seawater (RSW) tanks.

In principle, a pelagic trawl is a net bag, towed behind a single vessel or between two vessels operating together. During pair trawling, the two boats both pull the trawl, and open it horizontally by going parallel to each other, but some distance apart (500–1000 m). A single-boat trawl is kept open by the lateral forces of two large trawl doors (5–15 m^2) in front of the trawl. The doors are attached to the warps from the vessel, and the trawl is connected to the doors via a pair of two or more sweeps. The length of the sweeps depends on the vertical opening of the trawl, and is about 180 m for a 30 m high trawl. A pair of weights (50–2000 kg) attached to the lower wings and the weight of the doors pull the trawl downwards. The fishing depth of the trawl is adjusted by the warp length, the towing speed and the vertical inclination of the doors. At a towing speed of about 6 $m\,s^{-1}$ (3.5 knots), a warp length of about 500 m gives a fishing depth of about 200 m for a trawl with 30 m vertical opening, 1000 kg weights on the lower wings, and with the doors weighting about 3300 kg (Valdemarsen and Misund 1995). In most cases there are also floats or kites attached to the headline to give the trawl an upward pull. On single boats, using pelagic trawls designed to catch small pelagic fish such as capelin, which are about 15 cm in length, there can be a pair of extra doors attached to the upper wings to give the trawl a proper opening. Such trawls are towed at a low speed of about 3 $m\,s^{-1}$, and the lateral pull of just two doors will be too little to give the trawl the intended opening. According to the size, the vertical opening of a pelagic trawl varies by about an order of magnitude, from about 15 to 150 m. The horizontal opening is usually about equal to the vertical, and the total area of the opening of pelagic trawls thus varies by about two orders of magnitude, from about 200 to 20 000 m^2.

Pelagic trawls are constructed according to specific combinations of mesh size, twine, tapering and panel depth. Normally, the trawls are constructed of two or four panels that are joined in the selvage or laced together. The size of the trawl is given as the circumference of the trawl opening. This is calculated as the number of meshes in the trawl opening, minus the number of meshes in the selvage, multiplied by the stretched mesh size. The mesh size of pelagic trawls can be up to tens of metres in the front part, but decreases gradually to a few centimetres in the bag. The meshes in the front part of the trawl must herd the target fish into the centre of the trawl opening. If these meshes are too large, the target fish can escape, and the catching efficiency of the trawl decreases. The meshes in the cod-end must be so small that it is physically impossible for the target fish to escape.

Pelagic trawling is conducted mainly on fish occurring in large shoals, extended aggregations and layers. The fish can be recorded by sonar or acoustically, and the trawl opening is normally monitored by a cable-connected net sonde or a trawl sonar. These instruments provide information on the opening of the trawl, and the presence of fish inside or outside the trawl opening. There are also acoustic sensors to monitor the door spread, the headline height and depth, and catch sensors that are activated when there is catch in the cod-end.

2.2.4 Long lining

A longline is made up of a mainline to which branch lines with baited hooks are attached at regular intervals (Fig. 2.1). The mainline can be anchored to the bottom, and is sustained by vertical float lines equipped with instrumented buoys with light, radar reflector and radio beacon. The total extended length of the gear varies from a few hundred metres to more than 150 km and is made of several subunits called skates or baskets (Yamaguchi 1989a; Bjordal and Løkkeborg 1996). Three main types of longline can be identified (see Table 2.1), according to their position in the water column, the type of filament used in the mainline, hook spacing and the shape of the hook, which can be J-, wide gape, circle or EZ baiter (which has an intermediate shape between the circle hook and the J-hook and the name implies the ease with which the bait can be attached):

- bottom longline, which is subdivided into demersal and semipelagic;
- pelagic or drifting longline.

The rigging of longlines varies according to the target species, fishing conditions and countries. A de-

Table 2.1 Main characteristics of the different types of longlines.

Gear category	Mainline	Hook spacing (m)	Hook type
Bottom			
Demersal	Multifilament	1.2 to 1.8	EZ baiter
Semipelagic	Monofilament	2 to 3	J- or wide gap
Pelagic	Multifilament then monofilament	30 to 100	J- or circle hook

mersal longline is usually made of a multifilament mainline of 4–11 mm in diameter, more resistant to chafing than the monofilament lines. The line lays on the sea bed with an anchor. The branches, which are also called snoods, are made either from multifilament or monofilament, and are sometimes ended with steel wire or chain to prevent cutting by predators such as sharks. Semipelagic longlines are also anchored but the mainline is maintained above the bottom by alternate floats and sinkers set at regular intervals. Modern pelagic longlines are usually made of a synthetic, monofilament mainline of 3–4 mm in diameter. For tuna fishing, monofilament branch lines of about 20 m length and 2 mm diameter are attached to the mainline by metallic snaps. The rigging of the branches can be made more sophisticated by the use of swivels, aimed to limit twisting and chafing, and a combination of monofilament, multifilament and coated steel wires (Cook 1989; Yamaguchi 1989a,b; Bach et al. 1999a).

Catch distribution

Demersal long lining occurs mainly in the north Atlantic, targeting cod (*Gadus morhua*), haddock, tusk (*Brosme brosme*) and hake *(Merluccius* sp.) and in the northeastern Pacific where it targets essentially cod (*G. macrocephalus*) and halibut (*Hippoglossus stenolepis*). The common depth of exploited ground varies from 100 to 800 m, but can be deeper as in the case of the Patagonian toothfish (*Dissostichus eleginoides*), exploited up to 2500 m depth in Antarctic waters (Bjordal and Løkkeborg 1996).

Pelagic long lining targets tunas world wide (Fonteneau 1997). Bigeye (*Thunnus obesus*) and yellowfin (*T. albacares*) tuna are mainly caught along the whole intertropical areas of all oceans plus in the northern part (from 20° to 40° N) of the Pacific Ocean for bigeye only. Albacore (*T. alalunga*) is primarily caught in the northern (25° to 35° N) and southern (10° to 40° S) part of the oceans while bluefin tuna (*T. thynnus*) are mainly exploited in the southern hemisphere (20° to 50°) on each side of the African continent and around Australia and New Zealand (Yamaguchi 1989c; Fonteneau 1997; Carocci and Majkowski 1998). Subsurface longlines target swordfish (*Xiphias gladius*) in warm waters.

Bait and baiting

A variety of bait types are used by demersal long lining, such as small pelagic fish, saithe, shrimp, crab, octopus, mussels, whelks and lugworms. In pelagic long lining only the thawed saury (*Cololabis saira*) was used until recent years, but the bait tends nowadays to be more diversified (sardine, squid, etc.). The bait is usually dead, whole or cut in pieces. Artificial bait are currently being tested but are not commonly used at present. Chemical light sticks are sometimes added to the gear in the swordfish fishery. Baiting is done manually before setting, either onshore or on board, or by a baiting machine during the setting process. Automated baiting can be subdivided into precise baiting, where a piece of bait fish is automatically cut and hooked, and random baiting where the longline passes through a container with a mixture of precut bait and water. In tuna long lining, prebaited branch lines are stored in tubs or boxes and are attached to the mainline during setting. The use of baiting machines is common on board bottom long liners larger than 30 m as these require the baiting of up to several tens of thousands of hooks. Manual baiting is common in coastal and artisanal fisheries.

Setting and hauling

Setting the longline is normally done from the stern of the vessel. The time of setting depends on the target species but also on the feeding habits of bait scavengers. The end marker buoy and floats are dropped first at low speed, followed by the buoy line and the anchor in the case of bottom longlines. Then the vessel speeds up for setting the rest of the gear. Pre-baited bottom lines can be set at speeds of up to 10 knots since only the different skates need to be linked. When snoods are snapped on the line, a timer secures an even hook spacing. Three to five men are employed during the shooting.

Hauling is usually performed from the side of the vessel, starting by the marked buoy and the anchor for bottom longlines. When intermediate buoys and sinkers are used, they must be detached from the mainline. In tuna long lining, snoods are also detached when they arrive on board.

The importance of fish behaviour

The capture process of long lining is based on the feeding behaviour of the fish (see Juanes et al., Chapter 12, Volume 1). The bait is regarded by the fish as a food item, detected at long distance by the odour trail that is dispersed by the water current. The chemical senses of olfaction and taste are therefore essential and allow detection from several hundred metres. Vision can only detect objects from a few metres. Fish are able to locate the bait by swimming upstream. The current intensity and direction play a major role in the shape and extension of the so-called odour plume released by the bait. The rate of release of attractants, which are amino acids, in the water decreases rapidly with time so that strength has been reduced to one half after one hour, and therefore fishing time usually ranges from 10 to a maximum of 24 hours and can be reduced to only 2–3 hours when hooked fish can be attacked by large predators. Vision is an important sense at short range, especially in midwater, and explains why some species attack the bait mainly during the phase of deployment or hauling of the gear. Vision also explains the higher catching rate of monofilament lines, which are less visible than multifilament ones, and the attraction of some species, such as swordfish, to light sticks (Boggs 1992; Bjordal and Løkkeborg 1996; Bach et al. 1999b).

The success of long lining largely depends on fish behavioural aspects: level of hunger, diel foraging habits, prey attack, abundance and patchiness of the natural prey in the habitat. In French Polynesia, for instance, bigeye tuna catch rate is, as expected, positively correlated to the large-scale abundance of the micronekton. Nevertheless within relatively rich areas this correlation is negative at the much smaller scale of the longline where the micronekton distribution is patchy. This is interpreted by a competition between natural prey and baits (Bertrand 1999).

Species and size selectivity

More than 30 pelagic species can be caught by pelagic longlines and the question of untargeted species mortality by hooking is a major concern, mostly for shark species. Selectivity of longlines depends first on the match between the fish habitat and the place where the gear operates, both in the horizontal and vertical plane. Second, the type of bait used favours some species or sizes over others due to preference for food items (Juanes et al., Chapter 12, Volume 1). Finally, the size and type of hook affects the species composition, because of differences in feeding behaviour. The bait size, and to a lesser extent the hook size, are positively correlated with the fish size (Bjordal and Løkkeborg 1996), as expected from typical predator–prey size correlations (Juanes et al., Chapter 12, Volume 1). However, bottom longlines seem to catch about the same size range of cod as bottom trawls with 135 mm mesh size, and smaller fish than those caught by gill-nets (Huse et al. 2000). For Greenland halibut (*Reinhardtius hippoglossoides*), longlines catch a size range larger than that caught by bottom trawls, but smaller than by gill-nets (Huse et al. 1999).

Impact on sea birds

Impacts of fisheries on sea birds are reviewed by

Kaiser and Jenings (Chapter 16, this volume). We therefore do not go into the details here, except to reiterate the scale of the problem and methods of reducing mortality. Up to 70% of the baits can be taken by birds during longline setting. Estimated values of the number of birds killed per 1000 hooks range from 0.36 to 0.44 depending on both longline area and bird species, which results in the killing of several thousands of birds per year (Ryan and Boix-Hinzen 1998). Moloney et al. (1994) used an age-structured model to simulate population trends of albatross (*Diomedea exulans*). The simulation results portray a population decreasing at a rate of 2.3% per year, presumed to be a result of deaths caused by longline fishing vessels on this long-lived species.

To limit bird mortality, different methods are used such as shooting lines during the night, which mainly reduces the capture of albatross but is less effective for petrel. It is also possible to fit lines with lead weights, aimed to obtain a faster sinking, or to scare the bird away from the line. The two most efficient methods consist in either using a setting tunnel or trailing a 'bird scarer' made of a line with pendants parallel to the longline (Løkkeborg 1998).

Commercial aspects

Longlines mostly target highly priced species like tuna and demersal species (Table 2.2), which are very important economically and a significant source of food (Bjordal and Løkkeborg 1996; Nambiar and Sudari Pawiro 1998). In Japan, some tuna species like bluefin and bigeye are traditionally eaten raw ('sashimi' and 'sushi') and regarded as a delicacy. The wholesale price paid at landing for top sashimi-quality tuna can reach more than US$200 per kilogram. However, only very small quantities sell at these high prices and tuna used for canning can be sold for less than US$1 per kilogram (Carocci and Majkowski 1998).

Long lining is a cost-effective way of catching fish because it does not require a lot of energy, nor a large crew. This is especially so in coastal fishing that does not involve long travel distances. Nevertheless the gear is relatively expensive, as is the bait and the baiting process, which is either labour-intensive when manual or needs costly investment in baiting machines. The advantages of longlines over other fishing gears are: the quality of the fish which are often alive when caught; no or little impact on the sea bed; little 'ghost fishing' by lost equipment; little fish dumping; a relatively good size selectivity, limiting juvenile catches and the possibility to reduce unexpected mortality by using an adapted fishing strategy (Bjordal and Løkkeborg 1996; Bach et al. 1999c).

2.2.5 Gill-netting

Hand-knitted nets of natural fibres like cotton are among the oldest and most widespread fishing gears. Gill-netting is still amongst the most impor-

Table 2.2 Characteristics of the main longline fisheries.

Gear category	Common range of boat size (m)	Main target species	Yearly catches during the 1990s (million tonnes)	Main fishing countries
Bottom	8–55	Cod, hake, haddock, tusk, halibut, Patagonian toothfish	0.5	Norway, Iceland, Russia, Spain, Argentina
Pelagic	25–60	Bigeye, yellowfin and bluefin tuna, albacore	0.4	Japan, Taiwan, South Korea

tant fishing methods, and is used to harvest a variety of species worldwide. The nets are now made of synthetic fibres like polyamide forming monofilament or multifilament twines of which the net is knitted. There are several types of twine: twisted multifilament, monofilament, monotwine and multimono. The webbing of gill-nets should be as transparent and invisible as possible because gill-nets are passive gears, the fish itself moving into the net webbing head on, and trying to push through the mesh opening. Small fish pass through, but the larger ones with a maximum circumference just bigger than the girth of the mesh opening become gilled. The very large fish can entangle themselves or escape capture.

To keep it standing as a rectangular net wall in the sea, the net is mounted under a floatline with positive buoyancy and a groundline with negative buoyancy. The floatline can be made of a floating material like polypropylene, and may have synthetic floats embedded in it or solid floats formed as rings or rectangular pieces can be mounted on it. The groundline can have solid lead pieces mounted externally, or small lead pieces can be embedded in the groundline itself. For pelagic drifting gill-nets the positive buoyancy of the floatline is larger than the negative buoyancy of the groundline, while the opposite is the case for bottom-set gill-nets. At each end the gill-net webbing is mounted to a breast line joining the float and groundline. Gill-nets are normally joined together to form fleets that can consist of 10–100 units. Important parametres determining the size of fish to be captured are the mesh size and the hanging ratio of the gill-net webbing. Gill-nets are usually rather selective, but bycatch of sea birds and marine mammals can be substantial in some fisheries. Trammel nets, which have two large-meshed and a small-meshed net webbing in between have low selectivity. This is because such nets capture fish by entangling.

The visual stimulus of the net is a key factor determining whether or not fish detect the net (Cui et al. 1991), and at a certain light threshold gill-nets become invisible, depending on colour, net material and turbidity (Dickson 1989b). Gill-nets are therefore normally set to operate when the fish are actively moving around, either searching for food or migrating, and they function best at night when the fish do not see the webbing. Multifilament nets are less efficient than monofilament nets (Washington 1973; Hylen and Jackobsen 1979). Experiments have shown that attaching baits to gill-nets may increase catches of gadoids such as tusk and ling (*Molva molva*) (Engås et al. 2000). In areas with a high density of gill-nets, such as during spawning aggregations of cod in Lofoten, Norway, in winter, a satiation effect can occur so that there will be a decreasing catch rate with an increasing number of nets (Angelsen and Olsen 1987). Currents can reduce net height and change the shape of the webbing and thereby affect the efficiency substantially (Stewart and Ferro 1985). A model of how various factors influence catch rates of bottom-set gill-nets for cod has been developed (Dickson 1989a).

Fish caught in gill-nets can be gilled, wedged or entangled. In hard and stiff monofilament nets cod are mainly gilled, while in soft multifilament nets cod are mainly entangled (Stewart 1987). Despite this, gill-nets are very size-selective; few fish are caught differing from optimum length by more than 20% (Hamley 1975). The optimum girth for capture is about 1.25 times the mesh perimeter and the optimum length for capture increase approximately in proportion to mesh size (Engås and Løkkeborg 1994). A loosely hung net catches fish over a much wider size range than a more tightly hung net.

In recent years there has been much focus on 'ghost fishing' by lost gill-nets. (Kaiser and Jennings, Chapter 16, this volume). This is because synthetic gill-nets can continue to fish for several years after the nets have been lost. In Norway there is an official programme to dredge for lost gill-nets in areas where fishermen report loss of nets or where it is known that there is much gill-netting. Also, bycatch of sea mammals such as dolphins, harbour porpoise or seals take place in gill-nets (Tregenza 2000; Kaiser and Jennings, Chapter 16, this volume).

2.3 ARTISANAL FISHERIES

There is no standard, or even clear definition of small-scale artisanal fisheries (Panayotou 1982; Ben Yami 1989; Bâcle and Cecil 1989; Durand et al. 1991) other than perhaps 'scale' and 'artisanal', where the latter means a craftsman relying on his skill by himself, or with the help of family members or a few companions. Generally, artisanal fisheries can be seen as an integrated informal way of living within a geographically limited community and intrinsically dependent on local resources, rather than a formal occupation with a broad spectrum of options in terms of fishing grounds, markets and alternative investment opportunities (Thomson 1980; Panayotou 1982; Bâcle and Cecil 1989).

2.3.1 Diversity of methods

The modern large-scale fishing techniques that have been described so far have all developed from small-scale equivalents, and given the evolution in power, mobility and technical solutions of fishing vessels, the congruent evolution in commercial capture techniques have mainly been in terms of size, refinement and power requirements, with an ensuing increasing dependency on modern port facilities. Thus, small-scale artisanal capture techniques comprise all the categories and combinations of fishing methods already described (von Brandt 1959, 1984; Nédélec 1975; Nédélec and Prado 1990) but are different by being less capital-, vessel-, and fuel-intensive than modern industrialized fishing methods (Fig. 2.4). Many do not require vessels or energy-consuming accessories at all but can be operated from the shore, and many have remained virtually unchanged for centuries. Others are in rapid technological development, like the Senegalese pelagic canoe fisheries (WWF 1998), and may only be distinguished as 'artisanal' by the scale of the fishing units, and their still limited range. As a consequence a further distinction between commercial- and subsistence-artisanal fisheries has therefore sometimes been used (Kesteven 1976; Smith 1979). An important characteristic, however, of small-scale artisanal fisheries are their numerous actors (Fig. 2.4), resulting in an extraordinary variety in terms of specialized capture solutions to different resources, environments and seasons, with many being only seasonal in combination with agriculture, still small-scale fisheries are highly dynamic and diverse in terms of fishing techniques within each exploited ecosystem (e.g. Gerlotto and Stéquert 1978).

Apart from the purely technical classification of capture devices (see von Brandt 1959, 1984; Nédélec 1975; Nédélec and Prado 1990), small-scale fishing gear can be grouped into appliance or development categories (Ben-Yami 1989):

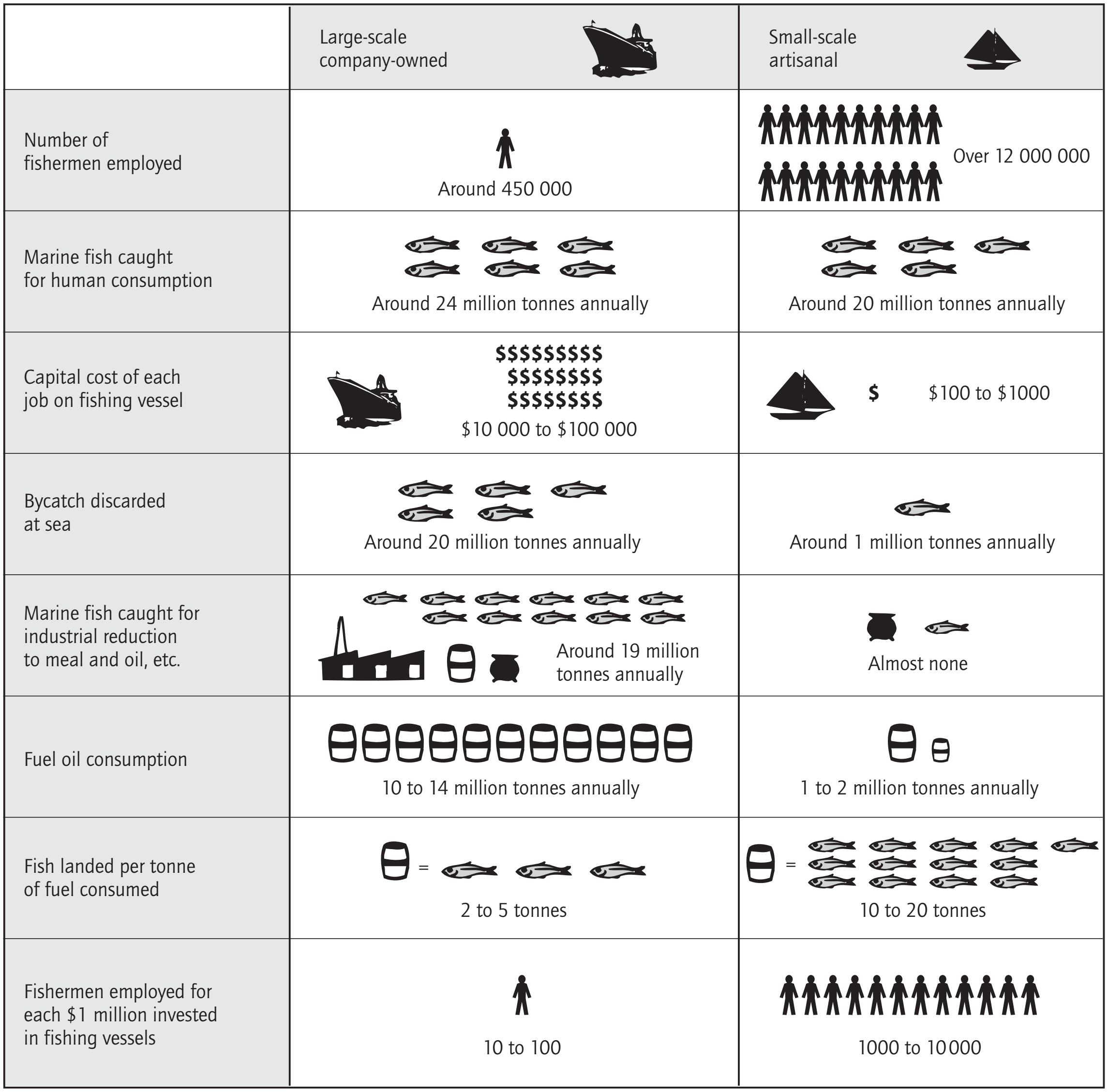
1 Traditional, 'primitive' fishing implements and installations characteristic for artisanal subsistence fisheries in developing countries. These are locally produced and operated from small canoes and rafts, and by wading or diving fishers. Barriers, weirs, traps, pots, spears, tongs, harpoons, gill-nets, dip-nets, small beach seines, and simple hook-and-line gear are included in this group.

2 Modern, 'sophisticated' equipment used almost exclusively in industrialized countries. For example dredges, automated haulers and jiggers, hydroacoustic and electronic equipment, and various auxiliary labour-saving devices.

3 Intermediate equipment used by small-scale fishermen in both industrialized and developing countries. This group consists of most fishing nets such as gill-nets, seines, and lift nets and much of the hook-and-line gear, almost all of which are factory produced and made of synthetic materials. Modern accessories, however, such as mechanized net and line haulers, light lures, and echo sounders are increasingly used in developing countries, and particularly by the small-scale enterprises which expand into harvesting previously underutilized pelagic species in lakes, reservoirs and coastal fisheries.

2.3.2 Research problems in artisanal fisheries

One of the first striking problems in artisanal fisheries is the lack of data and scientific literature. About 25–30% of the world total output of fish, or



	Large-scale company-owned	Small-scale artisanal
Number of fishermen employed	Around 450 000	Over 12 000 000
Marine fish caught for human consumption	Around 24 million tonnes annually	Around 20 million tonnes annually
Capital cost of each job on fishing vessel	$$$$$$$$$ $$$$$$$$ $$$$$$$$ $10 000 to $100 000	$ $100 to $1000
Bycatch discarded at sea	Around 20 million tonnes annually	Around 1 million tonnes annually
Marine fish caught for industrial reduction to meal and oil, etc.	Around 19 million tonnes annually	Almost none
Fuel oil consumption	10 to 14 million tonnes annually	1 to 2 million tonnes annually
Fish landed per tonne of fuel consumed	= 2 to 5 tonnes	= 10 to 20 tonnes
Fishermen employed for each $1 million invested in fishing vessels	10 to 100	1000 to 10 000

Fig. 2.4 Comparison of large-scale commercial fisheries with small-scale artisanal fisheries. (Source: modified from Thomson 1980.)

nearly half of the landings for consumption (Panayotou 1982; Fitzpatrick 1989; Allsopp 1989), come from small-scale fisheries, which engage 80–90% of all fishermen, estimated at between 12 and 15 million people (Smith 1979; Alsopp 1989; Platteau 1989). Considering the magnitude of this sector, the relative dearth of literature compared with industrial fisheries is astounding and severe. Moreover, most literature on artisanal fisheries is (semi)-anthropological or socioeconomic and gives, if anything, only descriptive accounts of capture devices and species compositions (e.g. Durand et al. 1991). The lack of quantitative data is a particularly acute problem for making meaningful suggestions for research and management (Larkin 1982), but this may also be one of the reasons for the many unsolicited notions that exist around artisanal fisheries. It may be fair to state that small-scale fisheries have received only scant attention during the past few decades of national and international development, with the exception of some agencies specialized in research in developed countries, such as the Institute of Research for Development (IRD, formerly ORSTOM), the International Center for Living Aquatic Resources Management (ICLARM), and Food and Agriculture Organization (FAO).

Many aquatic ecosystems are exploited by artisanal fisheries only. Coastal lagoons, tidal flats, shallow shores, estuaries and coral reefs on the marine side, as well as most freshwater fisheries such as lakes, reservoirs, rivers and floodplains, are by their size, depth, topography or inaccessibility only suited for small-scale enterprises and are exploited in a wide variety of ways. Other coastal areas, except for uninhabited coastlines such as those found off Namibia, are mostly exploited by both artisanal fisheries inshore and industrial fisheries offshore. In many of these there is persistent competition and conflicts between the two types and, with few exceptions, the artisanal fisheries are struggling to survive against the pressures of modernized capture techniques and overexploitation (Crean and Symes 1996).

In Senegal, the artisanal pelagic fishery has been landing over 200 000 tonnes of fish per year since the beginning of the 1990s and competes seriously with the industrial fishery (Fréon et al. 1978; Samb and Samb 1995). The bulk of the catch is made up of sardines (*Sardinella aurita* and *S. maderensis*) caught by small purse seines which are typically 250 × 30 m and surrounding gillnets of 200 m × 9 m. (Sech 1980); 14–16 m length wooden canoes, motorized with outboard engines, transport these gears. All the fishing operations are performed manually by a crew of 12 to 18 people. In the case of the purse seine fishery, a second canoe, often up to 20 m length, is used to carry the catch (Fréon and Weber 1983). Similar artisanal fisheries occur along the coast of West Africa (Bard and Koranteg 1995), particularly in Ghana and Côte d'Ivoire. The Ghanaian canoe fleet has over 8000 units, of which more than 2000 are purse-seining, but the yield is lower than in Senegal (around 70 000 tonnes per year) due to lower fish density.

In Venezuela the pelagic artisanal fishery is also well developed and targets mainly *S. aurita* using encircling nets operated by up to five canoes. In contrast with the conventional purse seine, which was commonly used until recently, this net does not close at the bottom. The fish school is encircled and then the net is pulled to the shore where its bottom part is in contact with the sea floor. The net is then secured by anchors and buoys, and left for up to a week for a larger vessel to extract the fish still alive and transport them to canneries and fishmeal plants. The landings commonly reach 140 000 tonnes per year in recent years (Fréon and Mendoza, in press).

The common limitation of artisanal fisheries is the range of operation. In Senegal two new ways of exploiting resources located far from the landing sites have developed from the 1970s. The first one, called 'marée pirgoque', consists in using large canoes loaded with ice and food that travel up to 800 km from their landing site for a period of 10 to 30 days. The second consists of loading up to 45 open canoes on board a large vessel that transports them to the fishing grounds where they are released for line fishing over several days. The mother vessel provides them with food and water and stores the catches. This mode of exploitation resembles the 'Dory' fishery for cod in the northwest Atlantic during of the nineteenth and early twentieth centuries (Charles-Dominique and Mbaye 1999).

These fisheries are all based on traditional wooden canoes that have been modified by the addition of an outboard engine, a synthetic hull, storage and conservation of the fish, and for the use of modern gear. This shows the high potential for adaptation and evolution of this traditional fishing vessel. Nevertheless the design of the canoes themselves, which dates back many hundreds of years in response to local constraints imposed by the sea and by the coastline where they are built and stored, tends to remain the same and often fishermen resist changes in design. In most of these fisheries, a large part of the catch is processed to fishmeal, the price of which is largely dependent on the global market of soya and fishmeal (Durand 1995). Therefore some crises observed in the artisanal fishery can find their origin on the global market (Fréon and Weber 1983).

For coral reef fisheries the main gears used are nets, hook and line, and spearing or traps for finfish (Medley et al. 1993). Nets are usually set just off the reef and fish are driven to them. Hooks and spearing are more effective for larger teleost predators. Traps are the least selective, taking a variety of fish and crustaceans depending on their construction. An important form of exploitation is gathering, often combined with diving, for the more sedentary organisms. Unfortunately, a number of reef-destroying fishing methods are in increasing use worldwide, often stimulated by the aquarium trade (Rubec 1986). Many poisons, such as bleach or sodium cyanide, as well as explosives, used mainly on schooling species, not only kill the target fish, but also the corals (McManus et al. 1997). Muro-ami is another destructive method where boulders are dropped on the corals to scare and drive fish out of the reef crevices and into nets. Such methods are giving rise to much international concern and inevitably create a negative impression of the whole artisanal sector.

Freshwater fisheries, which account for about 10% of the world total capture, are predominantly artisanal and these are as diverse as the freshwater habitats. Gill-nets, seines, traps, hooks and lines are generally used in most lakes and reservoirs all over the world for inshore and demersal species. However, in most freshwater fisheries of the Western world the traditional methods are slowly phasing out in favour of recreational fisheries for economic and social-political reasons. Important artisanal freshwater fisheries are therefore mainly found in the tropical and subtropical hemisphere, which produce at least 90% of the inland fisheries' yield. Africa is the only continent with large natural tropical lakes. The reported inland fish production south of the Sahel was about 1.3 million tonnes in 1987 (Vanden Bossche and Bernacsek 1990), which constituted a bit more than 40% of the total world production. Still, the reported inland production may only be about half the estimated potential. The three largest lakes, Victoria, Tanganyika and Malawi, alone cover a combined area of 132 500 km^2 and give an annual yield of more than 300 000 tonnes of fish (Kolding 1994). The traditional artisanal inshore fisheries of these and other lakes or reservoirs have over the past three decades mainly expanded and evolved towards the productive offshore resources, consisting of small barbus and clupeid species with a very high biological overturn. With the subsequent technological development of a highly specialized night fishery using larger vessels, light attraction and various encircling seine techniques or large winch-operated dip-nets, some of these fisheries are now rapidly crossing the border between subsistence fishing and small-scale commercial, or even semi-industrial, enterprises.

Rivers and floodplain fisheries are among the most diverse in the world and may still be categorized as belonging mainly within the subsistence sector of artisanal fisheries. In Bangladesh, Indonesia and Thailand, for example, each river may commonly be fished by 20 or more different gears (MRAG 1994; Hoggarth et al. 1999a,b). In the Mekong Delta, producing around 1.2 million tonnes annually, at least 62 different fishing techniques have been classified (Claridge et al. 1997), under 19 general headings ranging from scoop-, cast-, lift- and gill-nets, over a variety of traps, baskets, enclosures, fences and weirs, to spears, guns, poison and explosives. A similar diversity is found in Africa and Latin America. This general picture of a wide variety in fishing gears enables the capture of the many different fish species and sizes, in the many different habitats and during the various changing seasons. As a result floodplain fisheries are in general highly productive, where yields may reach more than 100 $\text{kg}\,\text{ha}^{-1}\,\text{yr}^{-1}$ without signs of biological overfishing (Kolding et al. 1996; Hoggarth et al. 1999a).

2.3.3 Myths and misconceptions related to artisanal fisheries

Due to the increased marginalization of small-scale fisheries in the industrial world, or their conversion into semi-industrial or recreational activities, artisanal fisheries are more and more associated with developing countries, and are often perceived as a traditional or even antiquated, poorly equipped subsidence activity (Dioury 1985; Bâcle and Cecil 1989; Platteau 1989). By their informal, free and liberal position they are habitually looked upon as unruly members of a society, which are difficult to manage. Moreover, many of the attempts to 'modernize' these fisheries have failed due to the very fact that the desired changes from 'traditional' practices have encountered formidable obstacles because such changes also affect the social structures which are entrenched in a community (Allsopp 1989; Durand et al. 1991). Africa, for example, is 'littered' with scrambled trawlers and abandoned ice plants/cold stores (Bataille Benguigui 1989; Bernascek 1989) as a result of well-meant, but poorly planned development programmes and the lack of clearly defined government policies and commitments. However, improving the standard of living of small-scale fishermen is but one of the objectives in fisheries policy. Competing, and often more important, objectives are employment creation, and increased production for consumption, export and, not least, national revenue (Smith 1979; Panayotou 1982; Dioury 1985; Chauveau and Samba 1989; Platteau 1989). Consequently, as other economic sectors are 'advancing', many small-scale fisheries are left behind with an increasingly negative image of being persistently poor, ignorant, ancestral, and often resource-depleting or ecosystem-destructive (Panayotou 1982; Bâcle and Cecil 1989; Amar et al. 1996), although the latter may be a direct consequence of the unfair competition they are exposed to (Thomson 1980). This picture, however, is not uniform and there is an increasing attention to the importance of this sector and a growing awareness of the need to conserve these communities. Several studies show that smaller-scale technologies are more socially and economically rational and efficient (Thomson 1980; Fréon and Weber 1983; Dioury 1985; Durand et al. 1991) and that they may reconcile high returns on capital, low investments, labour-intensiveness and high added value (Fig. 2.4). Finally, they constitute a prerequisite for the new paradigm for community-based resource management (Verdeaux 1980). Many are not declining but advancing, renewing equipment, transforming their boats and gear, and taking advantage of market changes (Durand et al. 1991). Still, the overwhelming opinion among many actors in the fisheries sector, particularly among assessment biologists, economists and policy makers, is that small-scale fisheries in developing countries employ inefficient, wasteful and indiscriminate fishing practices (Chou et al. 1991), ignore gear regulations and legislation (Panayotou 1982; Gulland 1982), are subject to open-access 'Malthusian overfishing' (Pauly 1994; Amar et al. 1996), and therefore need to be managed and controlled one way or the other. Are these notions true, or are they myths and misconceptions? As this chapter is dealing with capture devices, we will discuss here only the rationality of prohibiting non-selective fishing methods which is occurring in most artisanal fisheries.

2.3.4 From gear to management

Capture devices are intrinsically associated with selectivity, and selectivity, or the impact of fishing on an ecosystem, is an essential component of a management programme (Pauly and Christensen, Chapter 10, this volume). Consequently, much effort is devoted to investigations of the efficiency and selectivity of active and passive fishing gears (Fitzpatrick 1989). Recent developments have been motivated and promoted by world and market opinion, leading to devices that allow turtles to escape from shrimp trawls,that reduce entanglement of mammals in drift-nets and purse seines, and that decrease the large volumes of by-catch in the shrimp- and other specialized fisheries (see the purse seine and trawling sections above and Kaiser and Jennings, Chapter 16, this volume).

The importance of selectivity is therefore rooted in most researchers and managers, and any non-selective capture method automatically carries the connotation of being harmful, bad or destructive, or will at least lead to growth-overfishing, seen from the traditional single-species perspective (Shepherd and Pope, Chapter 7, this volume).

Mesh size- and gear restrictions are among the most easily applied and widely used management regulations. Consequently most nations have imposed legislation, which bans certain gears and mesh sizes, with the aim of protecting the resource (Gulland 1982). Although many of these regulations have originated from the problems associated with the large-scale fisheries, they are often uniformly applied on all sectors. However, selectivity seems much more a problem for industrialized fisheries, which on average dump about 45% of their catch, while small-scale artisanal fisheries discard on average only 5% (Bernacsek 1989), despite the fact that they mostly operate in more multispecies environments. Although numerous authors have already pointed to the problems of defining the 'right' mesh size in a multispecies fishery, the notion of regulations on selectivity still persists. In addition, small-scale fisheries often use a variety of gears, both traditional and intermediately modern. Many of these gears, and particularly the traditional ones such as seines, small mesh sizes, drive- or beat fishing, barriers, weirs, are often classified as illegal under the pretext of being non-selective with assumed negative impacts on the fish populations. However, the actual impact of these methods is rarely investigated and the true aim of the regulation may be to protect for political or social reasons the position in a fishery of another less efficient gear (Panayotou 1982). In the few instances where the actual impact of non-selective illegal gear used in small-scale fisheries has been studied, it is in reality an open question how 'detrimental' these fishing methods are. Two such case studies are from the floodplain fisheries in Zambia (Kolding et al. 1996; Chanda 1998), and the artisanal beach seine fishery on the Cape coast in South Africa (Bennett 1993; Clark et al. 1994a,b; Lamberth et al. 1995a,b,c).

In fact, non-selective harvesting patterns are in principle ecosystem conserving. All species are preyed upon at various rates during their lifespan, and for teleosts the highest mortality is usually during the early life history phase (Myers, Chapter 6, Hutchings, Chapter 7, both Volume 1). Thus theoretically, the 'utopian' but optimal exploitation pattern, by which an ecosystem could be maintained in balance, is fishing each trophic level and fish population in proportion to the rate of natural mortality (M_i) it is subjected to (Caddy and Sharp 1986; Kolding 1994). However, as all fishing gears are more or less species- and/or size-selective, such non-selective 'utopian' exploitation patterns can be achieved only by employing a multitude of gears simultaneously. The multigear, multispecies artisanal floodplain fisheries often seem to be producing an overall species, abundance, and size composition that closely matches the ambient ecosystem structure (MRAG 1994; Kolding et al. 1996; Claridge et al. 1997; Chanda 1998; Hoggarth et al. 1999a,b). On the ecosystem level such an exploitation pattern may be considered unselective across the species diversity range, and floodplain fisheries, particularly in Asia, seem to have persisted, with the only change coming from natural fluctuations, despite a very high fishing effort. Judgement on this is limited by the length of the data series we have.

In other words, the multi-gear, which is generally unselective, fishing pattern employed in many small-scale fisheries, combined with the ability of fishermen to change their target species within a single trip (Laloë and Samba 1990), is the closest example of the optimal exploitation pattern that exists. Therefore, the established fishing practices versus legal frameworks may easily become not only an infinite tug of war, as seen in most instances where small-scale fisheries have resisted the implementation of gear-restrictive regulations, but also a completely futile tug of war, as seen from the perspective of ecosystem conservation.

2.3.5 Can we manage small-scale fisheries?

The survival of traditional management systems, or perhaps more commonly, the persistence of small-scale fisheries under unmanaged conditions, is challenged and often overwhelmed by the tendencies of modernization, accumulation and concentration in which increased capital investment and the creation of global markets affect the means of production. Accelerating technological sophistication in capture methods, as well as subsequent increasing conflicts between commercial and small-scale fisheries, may be seen as the capitalistic way of delaying the economic consequences of declining resources (Crean and Symes 1996), as evidenced by the growth of advanced gear technology and distant water fishing fleets (Alverson and Larkin 1994). The universal solution to these conflicts seems to be characterized by the intervention of the state in terms of technocratic regulation systems based on mesh and gear restrictions, TACs and quotas (Beverton 1994). However, when both artisanal and industrial fishermen are exploiting the same resource, a total quota is certain to favour the large-scale fisheries, which have greater catching capacity. Unavoidably, the livelihood of the small-scale fishery will be reduced while no economic surplus would be generated in the fishery as a whole (Panayotou 1982). Unfortunately, science is used (and shaped?) to legitimate the implementation of these regulation systems and thus shield the policy makers from confronting the basic sociological objectives of fisheries management. By focusing on single-species TACs, quotas, and enhanced selective harvesting strategies and gear development, the mainstream research is better suited for those having the equipment and vessel technology to make a quick kill on targeted species, than for the small-scale fishermen working outside the global markets. Incidentally, the dominating scientific paradigms thus protect and favour the interests of the corporate structures and do little to investigate the truth behind the possible myths and misconceptions related to small-scale artisanal fisheries, as evidenced by the relative absence of scientific literature on this sector. On the contrary, the independent, and often technically 'illegal' response, by small-scale fisheries to increased regulations in order to safeguard their traditions and livelihoods, is used to brace and support the views on this group as being backwards, indiscriminate and destructive in their fishing patterns. Nevertheless this sector proves that it is still capable of reacting and innovating at the level of its organization.

2.4 CONCLUSIONS

The gear used in industrial fisheries is characterized by changes brought about by technological innovation. This, coupled with the intense competition between fishers to catch their share of the catch, has led to larger boats, nets and electronic fish-finding equipment. The emphasis in the past has been on improving the catching power and efficiency of vessels and fishing gear. The increasing demands of management are now leading to the use of technology to improve the selectivity of fishing, with devices such as the sorting grid, inserted into the trawl tunnel, helping to reduce bycatch. Further devices, such as satellites, will be increasingly used to monitor fishing effort spatially and temporarily, so making it easier to ensure that fishers are following the regulations,

There is an urgent need to remedy the lack of quantitative information on small-scale fisheries. In terms of capture devices there is a particularly important need to establish the selectivity of the various gears individually and in combination in order to evaluate their impact on the ecosystem. Faced with the complexity and heterogeneity of the operating conditions of small-scale fisheries, the present national and international efforts in small-scale fisheries seem concentrated on management implementations. However, without the necessary fundamental research, these implementations will be based on the reiterated dogma and may face the same failures as the many previous attempts to 'modernize' these fisheries.

ACKNOWLEDGEMENTS

The authors are grateful to Pascal Bach for his valuable help in the preparation of the longline section, and to Bente Karin Hoddevik and Anne Britt Skaar Tysseland for preparation of the figures.

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3 Marketing Fish

J.A. YOUNG AND J.F. MUIR

3.1 INTRODUCTION

With a few exceptions, the fisheries sector has been slow to adopt the concept of marketing. Historically the emphasis has been on fish stocks and production, and this broadly continues, in catching what is there to be caught rather than selectively delivering what the market prefers. Even in aquaculture, a primary focus has been on system capacity and production output. In most cases, distribution systems have grown around this supply-driven base, with the onus on market agents to match consumer needs with the product available, rather than to proactively determine what might be supplied. However, with growing control and regulation over fishing effort, allowable catches and landings of target species, and with common problems of oversupply in aquaculture, it is increasingly important that producers in all fishery sectors maximize the value of their product. Notwithstanding the deep-seated sociocultural traditions, people go fishing not just to catch fish but also to generate income (Hannesson, Chapter 12, this volume). Neither is aquaculture just about the technical achievement of farming aquatic species; enterprises have to deliver benefits too. Marketing is fundamental to the realization of such goals. This chapter explains some of the principal ways in which marketing can contribute to establishing and improving the welfare gains that can be generated from fishery sector production, and considers how this might be approached in the future. It also highlights some of the often ignored links and interdependencies between marketing objectives and other sectoral issues, not least being fisheries resource management and the emerging presence of aquaculture production.

3.2 MARKETING AND MARKETS

Though widespread in use, the term 'marketing' is often misunderstood or misapplied, and it is therefore useful to offer working definitions. We are concerned with a range of aquatic-derived food products, generically described as fish or seafood. The system within which a related set of product purchase decisions is made, by sellers, buyers and/or consumers constitutes the market. The marketing (or supply) chain may involve various intermediaries in exchanges prior to consumption. Whether in developed or developing economies, the concept of marketing is concerned with the processes of identification, creation, communication and delivery of values. Marketing is underpinned by the process of generating information about the products and markets which are of interest, to enable *identification* and understanding of what consumers want and value. Having identified what is valued, the next task is to *create* these values in products to be marketed, to enable and promote their consumption. However, in many cases, existing or potential consumers may be unaware of the attributes created in products, or unwilling to incur time or costs in gathering information about these. To overcome this, and achieve other promotion objectives, the penultimate task is to *communicate* with identified target markets. Having communicated with target buyers, the remaining task is to *deliver* the values to the target markets, via the products created.

The marketing function must be ongoing and cannot be effective if it is enacted only periodically, or on an *ad hoc* basis. It must be proactive because consumers, and the various markets that they constitute, constantly change and evolve. The product attributes that individual buyers, consumers and organizations value today are almost certain to differ from those which were valued only a year ago and will probably be different six months hence. The dynamics of such change are evident not only in the various seafood markets, but also in the markets associated with productive inputs such as vessels, gear, aquaculture systems, and the raw materials used in the capture or culture process.

The increasingly rapid pace of change within markets, for foods or other goods and services, creates additional challenges for the marketing function. Quite apart from the time and effort required to identify what markets have demanded in the past, it can be much more demanding to determine what markets currently want and to forecast their future preferences. The consequent processes of product creation, communication and delivery also take considerable time and effort. Thus, when new products are launched they often only respond to yesterday's needs rather than those of the moment, which will change as other firms take their own competitive actions, and as external factors affect consumer behaviour. To avoid the trap of responding to past changes, markets must constantly be monitored and analysed to anticipate emergent trends in preferences. This chapter emphasizes the importance of the sequential nature of these processes. However, before doing so, it is important to understand the environment in which fish marketing decisions are made.

3.2.1 The fish marketing environment

The key elements of the marketing environment for fish are shown in Fig. 3.1, reflecting the complexity of the challenges involved. Within international food markets capture fisheries are unique, as they constitute the last major sector to rely on a hunted supply base. However, this supply increasingly interacts with aquaculture production. The potentially destructible basis of capture stocks, not least due to excess capital investment, and the rapid expansion of investment in aquaculture, coupled with the high perishability of the product and the vagaries of the consumer, have combined to make the fish marketing environment increasingly dynamic and vulnerable (Fairlie et al. 1995). Unlike the case for most manufactured products and services, the marketing of foods commonly has to contend with a range of exogenous uncertainties influencing the production process (Marshall 1996). However for capture fisheries, and to a lesser extent aquaculture, marketing decisions have to accommodate an even greater degree of external influence, arising from individual and combined interactions of the natural and human environments.

One instance of such interaction might be a change in stock migration patterns, perhaps due to changes in seawater temperature or salinity, which may fundamentally alter availability – and thus viability – of a product intended to satisfy various intermediaries along a supply chain. For example, the Western mackerel stock (*Scomber scombrus*) in the EU Exclusive Economic Zone (EEZ) has varied its migratory patterns over the past 20 years, swimming further offshore and deeper, necessitating changes in the gear used and larger vessel hold capacity (Lockwood 1984, 1988; Whitmarsh and Young 1985). Similarly, changes in taste, driven perhaps by social trends, may stimulate demand for a particular product processed from a stock hitherto underutilized, or one which can only now be exploited due to technical progress in fishing gear, aquaculture techniques or processing technology (Connell and Hardy 1982; Whittle and Wood 1992). Such events are often irregular, unpredictable and thus cannot be planned for. As illustrated in Fig. 3.1, the importance of interdependence is also identified, whereby variation in one element will impact on others within

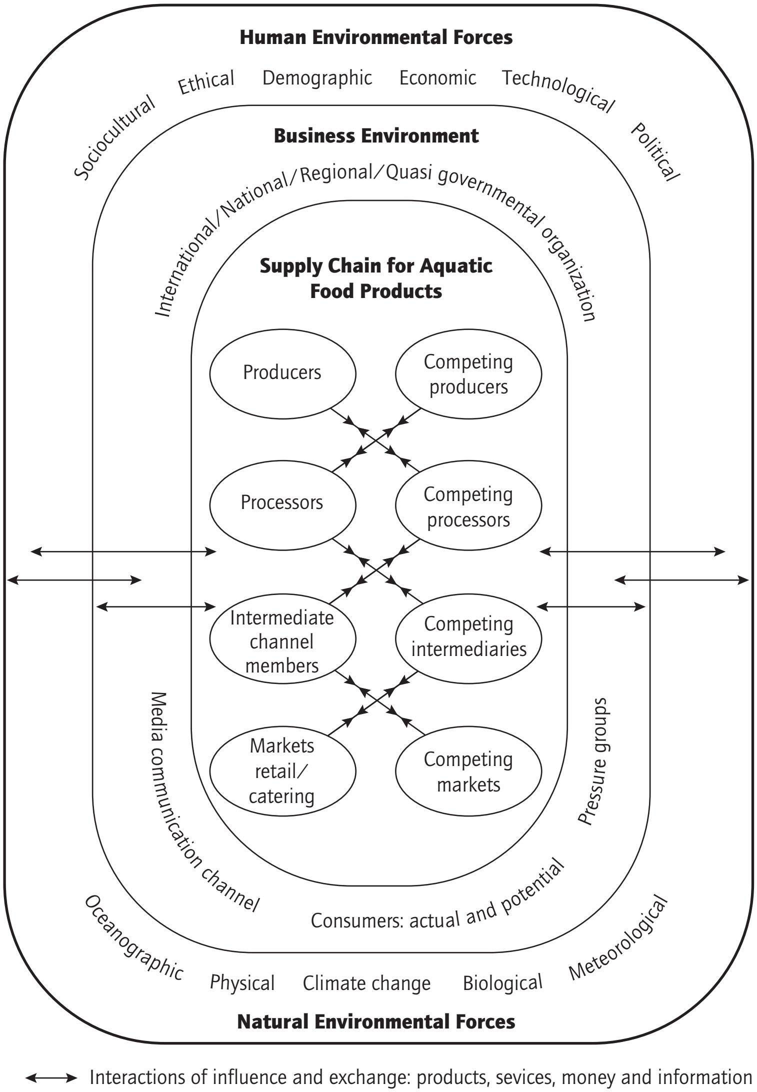

Fig. 3.1 The fish marketing environment.

the chain. (For a broader discussion of such interactions of business and natural environments see McDonagh and Prothero, 1997 and Fuller 1999.)

3.2.2 The international markets for fish

The global biogeography of resources has ensured long-standing if varied patterns of fish consumption throughout history. At various periods international trade has both flourished and withered, having been established on the spatial divide between points of production and consumption (Coull 1972). Aquaculture technologies have also created new opportunities in specific environments and global locations (Paquotte 1998; FAO 2000). Modern transportation, notably by air, has enabled a complex logistics network to be created, with far greater movement of product around the world. Thus for farmed Atlantic salmon (*Salmo salar*), over 50% of global demand is supplied from Norway alone, much of which is marketed fresh or chilled (Liabo 1999). The resultant pattern of trade flows is also defined by the distribution of those willing and able to pay, and those still having fish resources to trade. However, if marketing is to contribute to the benefits to be attained by suppliers and consumers, it is necessary to understand the main international markets and their respective sources of supply.

An ample caveat should first be made, to underline the fact that despite trends of globalization, the formation of trade blocs such as the EU Single Market and other unifying forces, fish markets, as for other foods, still exhibit distinctive national, regional and local patterns of behaviours (Gentles and Skeldon 1994; Gentles and Roddy 1999). Such variations may limit the applicability of wider generalizations. However, though it is impossible to provide here the fullest level of detail, we hope to equip the reader with some understanding of the means by which more detailed data may be found, as is done in Section 3.3.

There are three main markets for fish: the EU, USA and Japan, reflecting the combination of population size, wealth and demand for diverse ranges of foods. Traditional access to supply has also been a factor in their importance. Clearly, many other significant markets are to be found, sometimes more disparate, and with varying and sometimes more specialist product demands. The former Soviet states, and major population centres such as China and South Asia are particularly important in quantity terms, and may be expected to increase their trading presence as their markets become more open and incomes increase. Since the FAO's first estimates of world production 50 years ago, the fishery sector has developed rapidly, to the extent that an increasing number of stocks are overexploited, few underexploited resources remain, and aquaculture is contributing an increasing share of output and a greater share of value (FAO 1997; Hart and Reynolds, Chapter 1, Volume 1). During this period, the production of marine fish, crustaceans and molluscs grew from 18 to 90 million tonnes. From a point at which only North Pacific and North Atlantic fisheries were developed, accounting for 47% and 46% of total harvest respectively, areas initially noted as possible for fisheries expansion, mainly off Central America, Peru and Chile, in the Caribbean, off West Africa and off Australia, New Zealand, the South Pacific Islands and the East Indies, have increasingly been brought into production, and into the ever-growing global trade system. From the major areas of traditional aquaculture supply in South and East Asia, an increasing output of high market value production has also developed. In many other regions, such as Europe, North and South America, and Australia, new industries have grown rapidly, to the extent that major supply sources exist in almost every continent. In 1990 aquaculture accounted for just over 10% by volume of international supplies and some estimates have suggested that the 30% share in the early part of the new millennium may reach 45% by the year 2025 (FAO 1997; Muir and Young 1998).

The push towards a greater dependency on international trade is evident in many markets, and has been stimulated by overall growth in the consumption of fishery products. In 1996, 195 countries reported exports, and 180 recorded imports of fishery products; though numbers had slightly increased due to subdivision of formerly unified states, this confirms a substantial global interdependence. Global supply for direct human consumption in 1997 was estimated at 92.5 million tonnes, some 15.9 million tonnes more than in 1994, exceeding the estimated rate of population growth, with apparent per capita availability of food fish rising to almost 16 kg. Of the 1997 production, some 24% – 29.5 million tonnes – were used for reduction to fishmeal and oil, a ratio similar to that recorded in initial records. The value of international fish exports was estimated to have risen from US$17 to US$52.5 billion from 1985 to 1996. This was initially associated with greater trade in low-value commodities such as fishmeal, reducing value per volume, but more recently has tended towards increased value due to higher prices. Developing countries recorded a trade surplus of US$16.6 billion in 1997. Fishery products represent more than 75% of total merchandise exports for Iceland, the Faeroe Islands, Greenland, Maldives and Seychelles, and between 10% and 75% of exports for a further 20 countries, including Chile, Ecuador, Kiribati, Madagascar, Mauritania, Morocco, Mozambique, Namibia, Peru and Senegal. By value, more than half of fishery export comes from developing countries, mainly imported into developed countries, and is increasingly influenced by aquaculture. However, though Thailand was the leading world exporter between 1993 and 1996 (US$3.4 billion), Norway took the lead in 1997. Farmed shrimp and salmon, respectively, have been key components. With 1997 imports valued at US$15.5 billion in 1997, Japan was the leading importer, while the United States accounts for ~10% of world fish imports. Together with the European Union (including the value of the intra-EU trade) these three areas imported 75% by value of internationally traded fishery products (FAO 1999).

The EU represents a particularly interesting case of trade development given its relatively recent creation and its diverse composition, combined with the supply-side factors and policy measures that have affected its source of product (Wise 1984; Cunningham et al. 1985; Holden 1994). Traditionally, principal supply sources within the EU have been from capture fisheries in the North Sea, the North Atlantic and the Mediterranean, all of which have experienced declining yields over the past 20 years. In the UK, for example, landings of cod (*Gadus morhua*), the most popular fish species, were by the 1990s less than 15% of those in the early 1970s (MAFF 1999). Within the pelagic sector, vagaries of supply have been no less dramatic, hindering attempts to encourage consumers towards these alternatives, despite their acknowledged price and health attributes. The problems of balancing sustainable fishing effort with the social and economic costs of fleet reduction over a multinational shared resource have defeated many policy measures. Indeed the situation could be intractable, if only because biological time-scales for returning stocks to higher sustainable levels exceed the time-scales for political power. Longer-term changes in traditional external relationships, e.g. in 'third-party' fishing agreements in Northwest and Southwest Africa, and in access to transboundary stocks such as North and West Atlantic groundfish, are also reducing EU landings. Although EU aquaculture has recorded notable gains in output, overall supply shortfalls continue, and the EU appears likely to become increasingly dependent on external sources of supplies on the international market.

The scale and composition of the growth in demand is varied, and notable differences exist both between countries and within their borders. For example in Germany, annual fish consumption in the northern regions is estimated at up to 30 kg per capita, compared with only 10 kg in the interior (Young et al. 1993). In France and Scandinavian countries consumption averages around $32\,\mathrm{kg\,yr^{-1}}$, but this is much less than, for example, the $58\,\mathrm{kg\,yr^{-1}}$ found in Portugal (FAO 1999). While steadily rising demand can be observed in many economies, an exception would seem to be in the former Soviet states, where infrastructural change in supplies and relative buying power has resulted in diminished consumption (Westlund 1995).

The overall market for aquatic food will also tend to expand through population growth (UNDP 1997), and unless per capita income levels become severely constrained, might well widen the diversity of foods demanded. Variations in preferences for foods can be well entrenched, even within individual countries and regions, and have their origins in the sociocultural, psychological and economic context, though these in turn will change and will be open to influence. Just as some sections of a future larger population will continue their current aversion to fish, others are likely to maintain and expand the role of fish within their diet. The dynamics of the market highlight the need for ongoing information about the patterns of fish consumption and identification of what is wanted by contemporary consumers.

3.3 DETERMINATION OF VALUES

3.3.1 Sourcing information

Improvements in information technology have brought about massive expansion in the ability to identify the characteristics of different markets for fish products. This have been paralleled by the need for such information to meet the demands of competition. Databases are available with varying degrees of access from an ever-widening range of providers. Notwithstanding the risks of information overload and the challenges of defining and discriminating data quality, capturing data has undoubtedly taken root as an essential and affordable tool to assist marketing decisions (Bickerton et al. 1998; Tapp 1998; Reedy et al. 2000). Wider discussion of the processes and techniques of marketing research is not possible here but can be easily accessed (e.g. Chisnall 1997; Kent 1999; West 1999; Kumar 2000; Malhotra and Birks 2000). Although not fisheries-specific, these texts provide a methodological template for the information sources and data from websites mentioned here. To answer the characteristic questions of market research a sequence is generally followed, beginning with exploratory research and secondary data sources. Since many problems require more specific answers than are available in published sources, a range of primary data collection techniques is then commonly employed. Typically these might include some combination of different types of questionnaire (structured and unstructured), in-depth interviews, focus groups, observation and experimentation, depending on the quantitative and qualitative data required. Much of this information is often already held by individuals through daily involvement and contacts within the industry. However, to be effective, a systematic and ongoing approach is required to collect and interpret the relevant data for marketing decision making.

At the macro scale many information sources are available, which have been improved considerably over recent years through their availability online. Traditionally, the lag between data collection and publication, driven by the slowest country to gather and then submit returns, has rendered much data of value more for retrospective analysis than for proactive marketing. However as data have become increasingly available and more up-to-date the potential value of market databases has increased. At the international scale a fairly sophisticated level of perspective can be gleaned from the UN Food and Agriculture Organization (FAO) (*www.fao.org/fi/*) and related regional sites of Infofish (*www.jaring.my/infofish/*), Globefish (*www.fao.org/fi/globe/globfish/fishery/*) and Eastfish (*www.eastfish.org/*). Specialist agencies such as the Organization for Economic Co-operation and Development (OECD) (*www.oecd.org/agr/fish/statdata.htm*) are also useful sources.

The European Union is officially covered through the aggregation of national statistics at Eurostat (*www.europa.eu.int/comm/eurostat/*) Marsource (*www.marsource.maris.int/*) and sectoral agencies within individual countries provide their often more detailed perspectives at sites such as the UK's DEFRA (*www.defra.gov.uk*) or Spain's MAPyA (*www.mapya.es*). A number of semi-governmental organizations are also to be found within most countries, providing a further layer of more detailed information. The Sea Fish Industry Authority (SFIA, UK) (*www.seafish.co.uk/*), Institut français de recherche pour l'exploitation de la mer (IFREMER, France) (*www.ifremer.fr/*) and Fund for the Regulation and Organization of Fish and Aquaculture Products (FROM, Spain) (*www.from.mapya.es/*) are typical of such organizations. Parallel structures are found within the USA; the United States Department of Agriculture (USDA, *www.usda.gov*) and National Marine Fisheries Service (NMFS, *www.nmfs.noaa.gov*) provide the official fisheries perspective, which is then further subdivided into regional pan-state authorities. In the other major market, Japan, national data are available from (*www.yahoo.co.jp/government/institutes/*) and finer detail from (*www.maff.go.jp/eindex.html*) (Nakamoto 2000). Intergovernmental fisheries bodies such as North Atlantic Fisheries Organization (NAFO, *www.nafo.ca/*), International Commission for the Conservation of Atlantic Tunas (ICCAT, *www.iccat.es/*) and International Council for the Exploration of the Sea (ICES, *www.ices.dk/*) also provide valuable data.

Additional data are also to be found at an almost indeterminate number of trade association and private-sector sites. In some cases these may be gathered at the aggregate international or national level, such as for the Federation of European Aquaculture Producers (FEAP) (*http://www.feap.org/*), whilst in other cases information is provided to communicate a wider range of services, such as Howard Johnstone US (*www.hmj.com/*), Seafood Business (*www.seafoodbusiness.com*) in (*www.fishmonger.com/*) and in New Wave (*www.worldcatch.com*). A range of more specialized consultancy services exist and in some cases this tailor-made research function, e.g. TNS (*www.tnsofres.com*), or Stirling Aquaculture (*www.stir.ac.uk/stirlingaquaculture/*) may prove more efficient in targeting specific needs. Whichever site are selected numerous links are to be found and through a process of triangulation the more spurious statistics can often be identified or better estimates made. Little mention has been made of the various hard copy and more traditional information sources since these are more widely known but are also becoming less attractive in comparison to the data online.

3.3.2 Systems of exchange

The need for better understanding of what is valued by consumers within target markets is not just confined to the post-harvest stages of the supply chain. It is also important for producers to understand what the market values and how much buyers are prepared to pay, particularly as increasingly restrictive limits are placed on the volume and composition of what can be caught. Skippers can use market information to make decisions about when to stop fishing and land their fish, and, in more mobile operations, also decide where their fish will be landed. Likewise, for aquaculture, market information can feed into short-term production and harvesting strategies (Nagle and Holden 1995).

The starting point in understanding market price signals is that of first-hand sale. The initial exchange in the fish marketing chain is undertaken in a variety of ways throughout the world. At one extreme, with vertical integration between the catching or production sector and the buyer/processor, product may simply transfer internally between corporate divisions. However even within a single commercial entity, distinct profit centres with market-defined transfer prices may be retained (Milgrom 1989).

In other instances, contracts are used to determine the exchange process. These require some degree of specificity about the product so that each party is clear about what is and is not acceptable. Typically, this may suit conditions where there is a greater homogeneity of supply, such as with frozen-at-sea fish where targeted species will be processed onboard according to a predetermined practice and landed to tight product specifications. In other fisheries that are more directed and less opportunistic it may also be possible to satisfy buyer criteria in advance. Aquaculture production, with specific control over quality and timing, may also meet such criteria. Contract sales have the advantage of reducing uncertainty for both producer and buyer. Suppliers are aware of the price they can expect for product of a particular specification, whilst, assuming availability, buyers can be guaranteed of raw material to satisfy their own processing and market commitments.

However, the vagaries of capture supply have tended to encourage the retention and refinement of a traditional system, which is better equipped to deal with more heterogeneous conditions. Auction systems of exchange attempt to equate market demand to the available supply of a range of different species, each of varying size and freshness grades, of a highly perishable product within a short period of time. Fish auction markets represent a complex exchange arena, not least because of their dependence upon the harvesting of a renewable and potentially sustainable resource, which can also easily be destroyed. As noted elsewhere, the bioeconomic characteristics of fisheries have tended towards overexploitation and consequent wide fluctuations in supply (Hannesson, Chapter 12, this volume).

In different countries auctions tend to have their own mix of buyers, in many cases typically drawn from fish processing companies and other channel intermediaries, who will seek to transform the raw material in some way before it is sold on. Supplies to the market may come from a range of sources: landings from boats based at the same port, foreign vessels, and additional supplies brought to larger markets by other routes. Sourcing widely helps to even out natural fluctuations in supplies. The ownership structure of fish auction markets, like the harbours themselves, varies from private, public, cooperative or trustee status, and each undertakes a management function reflecting the interests of the parties involved. It typically involves some scale of charges being applied according to the value of the fish sold, and therein lies the incentive for auctioneers to extract the highest possible price from participating buyers.

Auctions are traditionally based upon an initial display of the available fish so that buyers can inspect the quality and determine their procurement strategy, which will also be influenced by supplies likely to be available at other ports. Sales are commonly held on a once-daily basis and are completed within a couple of hours, time and temperature control being critical constraints. In effect, the supply is fixed because fishermen cannot in practice return to sea and land more fish within that same period even if favourable market conditions emerge, just as buyers can only deal with a given quantity before product quality deteriorates. For these reasons, it is important that information searches are undertaken thoroughly by all parties. If the highest bid prices are to be realized from buyers it is necessary to ensure that the positive attributes of the available product are communicated to them. This market intelligence is, of course, supplemented by a network of contacts with other markets as the sales progress. Notwithstanding the available information flows, the vagaries of the raw material supply chain encourage price uncertainty and thus volatility in the market prices realized (Wilson 1980). Significant price movements within short time periods are commonly found, irrespective of whether a price incremental (with ascending bids) or a 'Dutch' price decremental auction system is used.

In either system, the intention is to identify the buyer willing to bid the most for a given lot or selection of fish, and a sequential selling strategy is commonly employed to effectively skim the market. This is achieved by selling the fish from individual boats in near homogeneous lots. For example, the largest and freshest cod would be offered for sale before moving to the next lower size grade of cod and so on in similar fashion for each of the other species. With price incremental systems, the greater transparency of the bidding process, whereby ascending bids are sequentially invited, should result in the eventual buyer only paying one money division above that of the nearest rival bidder. This is not so with a Dutch auction, because the first to bid automatically secures the product and this may be well above the maximum of the next intending buyer. However, in both systems high bids are encouraged, as competitors have no prior knowledge of the quantity that may be taken at any successful bid level. There is always a risk that the highest bidder may take most or all of the offered supply. Buyers may also cut their margins in order to secure product and may be willing to risk generating extra yield from a given lot to cover a high bid. In price incremental auctions a competitor may simply want to drive up a rival's raw material costs and so generate a comparative advantage. This can be achieved by participating in the bidding process but, using market intelligence, intuition and a bit of luck, withdraw just before the rival reaches their ceiling price. Traditionally, in display auctions, uncertainty is also promulgated by the secretive way in which bids are communicated to auctioneers, although with automated clock systems this element has been reduced. In addition to making bid-price decisions on the basis of information available in the market at the time, buyers must also incorporate more opaque information about future supplies to the market and anticipated demand.

Inspection of fish quality is undertaken in a variety of ways, ranging from the physical removal of a sample of the product, such as is done with coring tuna in Tsukiji market in Japan, through to more formalized grading systems according to specified criteria. In the EU, for example, designated species are graded according to size and freshness criteria, and boxes are labelled accordingly prior to sale. However, this scheme owes more to underpinning a system of producer income support, which operates by establishing a floor price below which fish is withdrawn from sale, rather than providing product information. Traditionally, buyers have relied upon their own assessment of quality.

Hitherto, fish auctions have largely depended upon the presence of buyers in person, or proxy, at sales, However, innovations in information technology have lessened this requirement, and buyers in some markets can bid remotely without actually seeing the product prior to purchase. Such schemes are found onshore in Iceland, for example, where dispersed landings hinder the geographical concentration of buyers. Instead they are linked through an online system and sales at prearranged times are simultaneously conducted from a number of locations. A rather similar concept of remote auctions is also to be found in the northeast Atlantic pelagic fisheries, where vessels will conduct an auction with shore plants before deciding where to land their catch. Historically the drawback to such remote systems of exchange has been the need to know the characteristics, such as freshness, size, texture etc. of the product being sold – certainly if high prices are to be encouraged. Earlier versions of remote bidding in the 1980s commonly suffered through the inconsistency of grading schemes. Product perceived to be of uncertain description naturally tended to discourage buyers from making high bids and so left fishermen dissatisfied with prices. Branding strategies, such as the 'Silver Seal' product of Scheveningen in the Netherlands, which is confined to fish no more than one day old, have been attempted, but more widespread gains are likely as technology enables accurate product information to be sent to, and verified by prospective buyers. In effect this accelerates the traditional process of establishing trust in a particular supplier.

Digital online images are increasingly available, and other remote sensory stimuli such as smell via electronic noses exist. All have a significant role to play in matching supply with demand across the more accessible international marketplace of the future. The technology already exists for boats to supply markets with electronic details of their catch as it is caught, and certainly prior to their making a decision to land. Though contract purchasing has been the norm in the aquaculture sector, this technology also opens out possibilities of offering product information before it is harvested, and opening access to a wider range of buyers. In any event, incorporating additional electronic product cues into the virtual marketplace will be to the potential advantage of both buyer and seller since it should improve the marketing decision-making process along the supply chain. Ultimately, the ability to realize higher prices is critically dependent upon buyers and consumers perceiving product to be of higher value, and in turn this raises questions as to how further values might be created in the raw material of the resource base.

3.4 CREATING VALUES

3.4.1 Handling and storage

The process of creating values in the raw material is an integral part of the marketing decision-making process. This must be based on the specific fishery or aquaculture system, and starts with the method of capture or production; the selected fishing gear or the harvesting system will influence and/or irrevocably alter the attributes of the product landed. Gear types are discussed by Misund et al. (Chapter 2, this volume), but examples may illustrate the complexity of the gear selection decision. Many factors are at play, including: regulations, selectivity, geographical location of the resource at different seasons, financial viability of gear types, technical constraints and changing market preferences.

Perhaps the clearest instance of how value may be created through the mode of capture and subsequent handling is in cases where product is sold alive. Such methods typically require the stock to be taken with minimal stress and physical damage, and, consequently, enclosing devices such as traps, stake nets and some forms of lines may be employed (Misund et al, Chapter 2, this volume). For aquaculture, crowding and brailing devices are commonly employed, with specially designed transfer pumps to holding units. Where the fish is trawled or towed for some time in a net, constrained too tightly, and/or subject to mechanical shock, damage will tend to be sustained to at least some proportion of the product. For pelagic fisheries, purse seining is generally recognized to yield superior quality product to that produced from trawling, as the fish is enclosed rather than dragged. However, trawls can be used in a much wider range of sea states and can take fish at greater depth, and may be more profitable to work, regardless of the potential for lower quality output. Aside from the more obvious effects of physical damage, a range of evidence suggests links between stress encountered during capture and subsequent changes in biochemistry which may affect texture, taste and keeping quality (Lemon and Regier 1997; Ehira and Uchiyama 1986; Kaylor and Learson 1990; Perez-Villareal and Pozo, 1992). This may especially be the case in faster swimming pelagic species, but may also apply in other fisheries, whose established capture methods may have hidden the potential to improve quality.

Good post-harvest or onboard handling practice is fundamental to the quality of the end product, few of whose determinants of perceived quality, if any, can be restored once removed. Keeping to recommended practices, temperatures and time intervals between the stages of gutting, storing and otherwise dealing with the catch will help to create values which can be built upon later in the supply chain. Methods may change according to season and market demands, and at different times the handling options may take on different priorities. For example, when abundant fish are encountered late in a trip the skipper might decide to concentrate on catching more fish and landing them round rather than spending time gutting. Innovations in handling the large volumes of fish found in pelagic fisheries have resulted in fish pumps being adopted to transfer fish from the net into the hold and to land onshore. In other demersal fisheries, and in some aquaculture sectors, fish may be bled at slaughter to produce a whiter flesh colour, or reduce blood spots, and prolong shelf-life. In other cases fish may be stored in different sizes of containers mixed with different types of ice, to optimize cooling conditions and hence preserve shelf-life.

Whatever the origin, a key prerequisite is the exchange of a raw material that will provide a basic building block to which further values can be added. For a number of reasons, the transfer of fish from the boat at the point of exchange has often been identified as a weak link. Similar issues can be observed in aquaculture systems. Assuming fish is cooled down after capture or harvest, there can be a break in the temperature-controlled environment when it is laid out for inspection by buyers. The significance of this break in the chilled or cold chain depends on its duration, and on ambient temperatures; in some cases fish may be brought from contact with ice to a market with air temperatures of 30 °C or more. Values may also be lost through additional handling of product by both prospective buyers and ancillary staff. This is especially so where product is stored in bulk and then graded according to species, size and other quality criteria. Even where the need for such handling is reduced through boxing at sea, or on harvest, physical damage often happens through overfilling of boxes and excessive pressure then being placed upon the fish in the vessel's hold or in storage areas, and possibly when stacked on the market. In one recent study of white fish landed at the EU's largest port, Peterhead, Scotland, it was found that overfilled boxes resulted in an 8% weight loss and, more significantly fish from boxes not overfilled attracted prices up to 15% higher (Harman 2000). The use of larger containers affording more protection for the fish, combined with more accurate weighing, grading and recording of where and when particular lots were captured or harvested, is likely to become more prevalent and should help to reduce the loss of value at these stages. Such measures of product traceability are central to the concept of Hazard Analysis Critical Control Points (HACCP) and are likely to become a prerequisite of more and more marketing channels, including downstream processing.

3.4.2 Processing methods and market influences

Fish processing is essentially concerned with the transformation of a raw material into an almost limitless array of products offering a range of different values. Historically, processing was undertaken to preserve fish to enable its storage and later consumption when alternative protein sources were not available. The evolution of different processing techniques, notably salting, drying, smoking, freezing, canning, chilling and other methods is well documented (Cutting 1955; Burgess et al. 1965; Aitken et al. 1982). More recently, fish-processing technology has been to the fore in the wider arena of food science and technology, not least because fish is one of the most perishable foods and has therefore generated very demanding technical requirements. Fish has been used successfully in a variety of technical innovations in processing and so appears in an extensive range of products (Connell and Hardy 1982; Young et al. 1992). Product diversification is manifest in the increasing number of new products, some using different species, continually entering the market.

New product development has evolved from the simplest levels of whole fresh fish, through progressive increments of gutted, filleted, deboned, steaked, and otherwise modified raw material, and through processes such as smoking, marinating, adding sauces and the inclusion of other non-fish foodstuffs to add value. The differentiated bundles of attributes thereby built into the products may incorporate additional intangibles such as convenience in storage, in preparation, and in consumption features. Packaging in a widening array of options including chilled, vacuum skin, and modified atmosphere packs, frozen packs, cans and pouches also provide the opportunity to further differentiate the end product. The pack format, shape and presentation, and in particular, the opportunity for labelling and branding, all provide an important channel to communicate further with the consumer. This is especially significant within the retail food market where products have to compete with an ever-widening array of fish and non-fish substitute products.

Critical to the success of the contemporary processed fish product has been the incorporation of attributes driven by consumer wants within the wider market for foods. Creating products with values which are perceived to be important by the consumer, rather than simply because processors have the technical ability to include them, is a significant determinant of product success. Effective marketing necessitates understanding the position a value occupies within the mind of the consumer, and why it is located there. Having gathered the information about the competitive position of the product attributes within the market, and a clear understanding of what consumers perceive to be important, decisions can then be made as to how these attributes might be created within the product range.

Consumer perceptions of fish, with some exceptions, have generally become more favourable over recent times. In many countries, a notable trend has been the increased concern with healthy eating, in which fish is perceived very favourably. For many white fish species, a frequently cited point is the low level of fat, while for the typically more oily pelagic species, high levels of omega-3 polyunsaturates may confer important benefits against cardiovascular diseases (Marshall and Currall 1992). Health concerns have been further stimulated through food scares, especially with BSE (bovine spongiform encephalopathy) in the UK, where high-profile media attention has ensured more widespread coverage and greater suspicion of traditional foods (Smith et al. 1999), leading to increased interest in the potential safety and nutritional benefit of foods such as fish. However, despite some gains, it must be noted that this more favourable disposition has not eliminated many of the traditionally negative perceptions harboured by potential or actual fish consumers. Although negative perceptions vary internationally, reflecting the diversity of social and cultural influences which have shaped broader patterns of food consumption, their continuance remains a significant barrier to the wider acceptance of fish, generically or as specific products, amongst different user groups. Consumers' perceptions are also prone to negative influence, and, in the UK, publicity surrounding a single television programme about the alleged toxicity of farmed salmon and its environmental impacts fuelled a widespread media coverage berating the industry (see, for example, Millar 2001; Alba and Dennis 2001). Differences in the values placed on fishery products by different groups, and their susceptibility to influence, has in turn stimulated a range of organizations to attempt to communicate the values of fish more effectively to consumers.

3.5 COMMUNICATING VALUES

The product and all the attributes created within it present a potentially powerful mechanism to communicate signals to buyers and consumers. However, sellers cannot afford to rely upon spontaneous purchase or consumption of products, because these acts themselves first require individuals to be aware, and perceive the value, of the products, often against competing messages from alternative products. Informing individuals about products involves a range of promotional tools and a variety of media, which are discussed more generally elsewhere (Cooper 1997; Shimp 2000; Schultz and Kitchen 2000). Advertising, publicity, sales promotion, personal selling and direct marketing, increasingly via e-commerce, all have specific advantages and disadvantages in different situations, and a combination of these will commonly be employed to achieve communication objectives.

The promotion of fish is undertaken by a range of different organizations around the world, each with more specific remits and organizational structures. For some organizations, promotion, often primarily advertising, is the sole activity, whilst others have a more eclectic industry focus which may, for example, include post-harvest work, gear technology and so on. Organizations are also funded in a variety of ways: some receive public-sector grant support on the basis of the social or economic importance of the industry to a particular locality. More commonly, support may be derived from some form of taxation or levy paid on the product purchased or sold, and funds raised may contribute to the identified promotional objectives. Many such organizations also serve as the principal centralized source of market information and may be accessed by other firms operating within those markets, as discussed in Section 3.2. On the international scale, FAO Globefish and the various regional divisions of Infofish, Eastfish, Infosamak, Infopesca and Infopeche cover the widest remit. Elsewhere, various national and regional organizations also operate, e.g. Fonds d'intervention et d'Organisation des Marches des Produits de la Pêche Maritime (FIOM) in France, SFIA in the UK and Alaska Seafood Marketing Institute (ASMI) in Alaska, USA, each with varying levels of cooperation and sharing of resources.

Communication of product values occurs in a multitude of ways and is by no means confined to advertisements; in many cases potential buyers are not consciously aware of their active reception of signals sent. Each day individuals may be subject to hundreds of signals, many of which will simply pass with little, if any, recognition. Elsewhere, for example in a supermarket, the shopper will encounter brands and other point-of-sale support which will communicate something of the attributes of the product, and may encourage (or discourage) a subsequent decision to try the product. Branding is a pervasive tool, employed to achieve a number of objectives, including product differentiation, price differentiation, increased brand (product) awareness, customer loyalty and repeat purchasing. It can be done at a variety of levels ranging from the generic, covering one or a range of species, possibly from a particular geographical area, or through the product range of a particular retailer or caterer. It may also be applied to just some part of the product range of a fish processor, possibly a premium-quality product, enhancing price and image, or at the other end of the spectrum, a low-price product, encouraging volume sales, and allowing margins to be retained in price-competitive conditions.

Over recent years, and especially within aquaculture, more use has been made of branding to indicate attainment of a given quality standard defined by meeting specified criteria. Examples in the farmed salmon market are numerous, such as the Tartan Quality Mark for Scottish salmon, some of which also enjoys the distinctive award of the French Label Rouge mark, a standard synonymous with high quality in a range of foods (Lloyd 1999). Such brands are important because they immediately serve as a communication tool to the buyer, and potentially the consumer, that the product has attained a certain guaranteed minimum standard. This standard may of course be surpassed by yet higher quality specifications being applied, at which point the brand would then simply seek to reinforce superior status upon the base credentials of the generic mark. Such generic standards may have the problem of being vulnerable to the adequacy of the monitoring and enforcing system or organization – a task not so easily accomplished uniformly throughout the myriad of supply chains. In the market, products are liable to be judged by buyers according to lowest guardian of the standard, and there is thus the potential for one member of the brand cartel to damage the reputation of other producers.

Campaigns specific to species and/or country or location of origin have been the focus of increased communications effort over the past years, and especially as international trade in fish has grown. In Norway, the fifth largest producer of fish in the world, but with a population of under 5 million, a considerable effort is placed upon promoting the positive attributes of Norwegian aquatic food products. Estimations of the effects of promotional spend on different fish market sectors have been undertaken by a number of academics, notably within econometrics (Bjorndal et al. 1992; Asche and Sebulonsen 1998; Kinnucan and Myrland 1998, 2000). However, in the real-world marketing environment wherein these campaigns run, communications are subject to a multitude of contemporaneous influences which range from fluctuating and competing prices, to the weather, and make this a complex and difficult task. Most certainly, it is not a scenario where a given spend can guarantee some certain return in the market.

Promotion strategies are not necessarily confined to increasing trade; attempts have also been made to influence the type of fish eaten by target population groups. For example, in the 1990s a number of organizations responsible for marketing fish in various EU member countries cooperated to communicate the benefits of increasing consumption of small pelagic species. In the 1997 transnational 'European Fish Campaign: Health and Wealth from the Sea' younger consumers were targeted with health messages (high omega-3 polyunsaturates) to promote the consumption of sardines (*Sardina* spp.), herring (*Clupea* spp.), mackerel (*Scomber* spp.) and sprats (*Sprattus* spp.) (*Seafood International* 1997). In addition, stimulation of the domestic EU market would reduce dependence upon export markets and, in comparison to white fish, the pelagics are cheap. The decision to focus upon a particular message is again dependent upon the need to identify and understand what existing perceptions of the product are held, and by which segments of the market, using a range of demographic criteria, so that the communications campaign can be designed accordingly. Elsewhere, communications campaigns have sought to limit consumption of certain fish products. The notable cases of dolphin-friendly canned tuna and the 1990s campaign by some US chefs not to serve swordfish on their menus, are discussed in Section 3.7.2 and highlight the often ignored role of communication in effecting resource management measures. Another instance is the International Whaling Commission (IWC) ban on trading whale products – yet within Japan and Norway these products are still promoted to the consumer in much the same way as other competing foods. Such communications, for and against, different products and capture methods may be seen as an attempt to manage fisheries through demand rather than the traditional supply-side measures. This interaction between marketing and fisheries resource management is increasingly important and is returned to later.

Individual manufacturer brands of fish products should also be recognized as an important part of the communications process, whereby the same fundamental task of getting some particular message across to the target market is attempted. In some instances, these have been undertaken on an international basis, such as Bumble-bee tuna and the infamous Captain Birds Eye, who has the distinction of rebirth, having once been drowned by his creator Unilever. Otherwise, manufacturers' brands are more localized. Within the retail sector an important trend has been the incorporation of retailers' own brands into the product range, a phenomenon that owes much to the growth and dominance of supermarket chains in many countries, as discussed in the next section. Supermarkets have moved from simply being stockists of a manufacturer's brand, to a position whereby the supermarket's name becomes the brand, and the statement about the products to be found therein (McGoldrick 1990; DeChernatony and McDonald 1992; Burt 2000; Walters and Hanrahan, 2000). This change has led supermarkets to become more closely involved in the whole process of developing products, often in close conjunction with manufacturers. Such codeveloped brands are often able to command a premium position within the market and attract a commensurate price and profit level.

Communications about fish within the catering sector are often more concerned with reaching the buyer or user rather than the consumer. Although there are some exceptions where a strong fish brand is present in the away-from-home market, such as Red Lobster restaurants in North America, or Harry Ramsdens fish and chip restaurants in the UK and elsewhere, fish has not approached the levels of awareness encountered in other fast-food and catering sectors such as McDonalds (Ritzer 1993). Whilst end-consumers may not necessarily be the initial target of communications strategies within the catering sector, other channel intermediaries are. Buyers, and users such as chefs, represent a potentially valuable conduit through which positive messages may be sent to diners, and all the more powerfully since communications will be delivered to their stomachs. Chefs and other channel intermediaries may provide the opportunity to encourage adoption of new products and different styles of preparation. This was the focus of an approach by the Norwegian Export Council in promoting the utilization of salmon by chefs in China; a species that hitherto had remained little used in this important ethnic cuisine (Chen 1999). Such routes are potentially invaluable in the case of new species or products, especially where they are unfamiliar, simply because in the catering situation, the consumer is presented with a product solution rather than a new task to be overcome (Maddock and Young 1995).

Of course, in many markets for fish the product is still treated as an undifferentiated commodity, and each transaction is simply based upon the product cues perceived from the product inspection at that time, rather than any others emanating from supporting experience or explicit promotional activity. Communications may confer added values but they can also represent a cost that in some situations is less affordable and not justifiable. Whilst even in the poorest countries, brands, advertising and related promotions activity may be present, communications do not necessarily have to involve large promotional budgets. Although they often do, and especially where wider-reach advertising is employed, increasingly more direct forms of communication are both possible and effective. This has been encouraged through the development of the Internet and the more general trend to e-commerce. Individual manufacturers and other industry organizations now have access to a rapidly expanding audience with whom they can communicate in detail and individually; this was simply not possible even just five years ago. Initially it has been the higher unit value, speciality-orientated products that have tended to be promoted on the net. Such products commonly encounter barriers to market entry because of their more specialized market volumes, higher prices and hence lesser ability to meet the more standard requirements of retail chains or many catering outlets. Notwithstanding the current reappraisals of web-based marketing and sales businesses, the promotion opportunities afforded by the Internet and the evidence of many individual websites operated by some of the very smallest of operations suggests that this channel of communication will also increasingly alter the conventional concept of delivering the product.

3.6 DELIVERING VALUES

3.6.1 Cold and chill chains

The delivery of values within the fish marketing chain is arguably more complex than in any other food product sector. Logistics have to cope with an uncertain supply, which often cannot be confirmed until within a few hours of transportation, to variable locations around the globe in a dedicated temperature-controlled transport environment within the minimum journey time. The comparatively rapid rates at which fish products spoil places a premium upon more rapid transport systems, which cannot always be justified by the unit value of some product categories. This is perhaps taken to extremes in the case of small pelagic products, which combine high endemic rates of perishability with unpredictable loads that can quickly amass very significant volumes and yet still command only limited prices on the market. For example in 2000 the ex-vessel price for herring in the UK was under 10% that of cod, yet both products would incur similar unit transport costs (SFIA 2000). Because of these fundamental characteristics the transportation of fish, especially fresh and chilled product, has increasingly tended to favour road and air distribution rather than rail. However, on intercontinental routes frozen, canned and dried products are also carried by sea.

Marketing channels within the fisheries sector have evolved from the traditional network of port wholesale markets and inland wholesale markets feeding a widening succession of smaller intermediaries and buyers. Like port markets, inland wholesale markets arose because of their ability to provide buyers with a wider and more concentrated range of product from a number of different supply points, so lessening the impact of supply fluctuations. Whilst a number of wholesale markets remain important, e.g. Rungis in Paris, Merca in Madrid, Tsukiji in Tokyo, they typically now handle a lower volume of product, often from a more diverse range of supply sources, and cover a wider range of species. As the market structure of the food industry has become more concentrated, so too has the supply chain changed to meet the needs of the more powerful buyers. This is especially evident in the case of supermarket chains, where their individual group-buying capacity is such that they purchase direct from the fish processor or importers for much of their product range rather than through intermediaries. However, a number of such large organizations still obtain certain more specialist parts of their product range from wholesale markets.

Inland wholesale fish markets also remain important for smaller and often specialist fish retail outlets which need comparatively small volumes, and wish to secure a selection from a number of different suppliers. Many parts of the catering sector may also rely on independent outlets within the wholesale market. As might be appreciated, highly complex supply chains soon evolve within such markets where there are many independent buyers from a number of specialist traders. Complexity is heightened by the typically restricted hours of trading, which result from a perishable product that needs to reach the next stage in the chain with the minimum of delay, often reaching the consumer within the normal working hours of that day. Emergent demands for Hazard Analysis and Critical Control Point (HACCP) systems, and the need for compliance with increasingly stringent health and hygiene regulations have contributed to quite radical revisions of many market structures. However, in a number of instances, traditional supply chains have lagged behind the standards demanded by buyers, resulting in their exclusion from emerging market developments. This has been especially so with supermarkets and so has accelerated more efficient logistics, whether these are managed over a network of regional warehouses or through integrated temperature-controlled infrastructures at the port market.

3.6.2 Fish retailing

Food markets have become far more internationalized over the relatively recent past, and this has resulted in brands being available in many different countries, and a much wider range of competing products being available within most markets.

Changes in individual patterns of consumption, both at home and outside, have fuelled developments within the food retailing and catering sectors. In developed countries especially, supermarkets have gained dominance in the packaged grocery market within a relatively short space of time. For example, in 1973 only half of UK packaged grocery sales was through supermarkets, whereas 20 years later this was typically over 80% (Burt 2000). In the late 1990s the three leading multiple chains in the UK, Germany, the Netherlands and Belgium all held packaged grocery market shares of over 40% (Gentles and Roddy 1999). Fish has followed this trend more slowly, being one of the last fresh food categories to be dominated by supermarkets. Evidence indicates that this is because of lower comparative profitability in this product line, and the product-specific retail skills required (Young et al. 1993). However, the incorporation of fish products, and especially fresh fish displays, may contribute positively to the store's ambiance as a supplier of fresh produce, and supermarkets are increasingly extending their dominance in these sectors. Although there has been a dramatic reduction in the numbers of specialist fish retailers, a significant residual core remains in most markets. Typically, these have been able to exploit niche markets, often based on a competitive advantage of service, product knowledge, product range and quality.

More positively, the presence of fish within the supermarket has increased access to potential consumers, many of whom would not deviate from their shopping pattern specifically to purchase fish. Supermarkets have helped reintegrate fish product options within the less frequent shopping pattern of the food consumer. They have long been leaders in frozen and canned fish sectors, commonly holding 60–80% of the market, because the longer shelf life of these product forms is more suited to less frequent shopping. Before the wider adoption of packaging innovations such as modified atmosphere packs (MAP) and vacuum skin packs (VSP), the shelf life of fresh products was often too short for the shopper's buying cycle. More recently, the involvement of supermarkets with fresh product has increased through incorporation of traditional specialist outlets within their layout. Especially within some of their more recent smaller-scale operations, supermarkets have also been able to benefit from top-up shopping trips, often made by consumers willing to pay a premium for quality convenience products. In Germany, Ireland, the UK and France the supermarket sector now accounts for between 30% and 70% of the fresh fish market (Gentles and Roddy 1999; SFIA 2000).

3.6.3 Fish catering

In broad terms the diverse catering market can be split into two categories: the profit and cost sectors, the former representing hotel, restaurant, café and take-way outlets, and the latter larger-scale typically institutional units such as schools, hospitals and canteens. Consumption of fish within the catering sector is influenced by more general trends in food consumption away from home. Consumer uncertainties about product storage, preparation and odours associated with cooking and/or consumption can be reduced or removed, and consumers can be expected to become more adventurous. The importance of food consumption away from home varies significantly in terms of expenditure and in its role within society and culture (Warde and Martens 2000). Food consumption away from the home accounts for 30% of household food expenditure in France, Germany and the Netherlands, whereas in the UK this amounts to only 20% and this level is only half of that in the USA (Euromonitor 1995; Key Note 1994, 2000). However, within many market sectors a far higher proportion of expenditure will be devoted to eating out, especially at more extreme ends of income brackets where individuals range from being wealthy but time-poor to those without home or cooking provision. Within both the profit and cost sectors there are many individual players, some with a number of outlets. This rather disparate and disaggregated industrial structure is significant, since smaller outlets present lower entry barriers to suppliers and thus provide opportunities to access fish consumers which may otherwise be denied through supermarkets.

Nationally, the relative importance of the catering market for fish varies: typically amounting to just under half the market in the UK but in France, Germany and the Netherlands remaining at around 30% (Key Note 2000; SFIA 2000).

3.7 FUTURE VALUES

Having described the ubiquity of marketing phenomena in food consumption, and considered some of the more established ways in which marketing issues are manifest for fish products, it is useful to outline the ways in which marketing might contribute to the fisheries sector in the future. The tendency to overcapitalization in fisheries and the consequences of excess fishing effort have been discussed elsewhere (Hannesson, Chapter 12, this volume). The aquaculture sector has also grown significantly, and contributes a growing proportion of high-value products, particularly in the fresh and high-quality value-added sectors. It has also contributed increasing inputs to developing country economies and their poorer rural and urban populations, and in some cases has delivered important export earnings. In doing so, it uses a range of resources and may have less desirable impacts (Naylor et al. 2000). Overall, however, the role of marketing in resource management and technical development has tended to be overlooked, both in fundamental issues, and in the various policy instruments devised to address these.

3.7.1 Marketing and resource management

The role, and the potential, of market information systems in influencing fishermen's behaviour was noted earlier in Section 3.2. Because fishermen go to sea to earn a living, decisions about target species, where to land, and price expectation, are inextricably linked to marketing. The tighter regulatory environment in which producers fish requires them to extract the greatest value possible from their allocations. Improvements in ICT (information and communications technology) facilitate access to marketing information systems and now offer far greater scope for more market-based fish-capture decisions. Individual skippers can access market information and use this proactively to target their quarry, in terms of species, size and subsequent onboard handling decisions, with greater certainty than hitherto.

Improvements in information systems may also facilitate the application of resource management measures. Remote detection of the volume and composition of what has been caught is theoretically possible with existing technology (e.g. Strachan et al. 1990) and it is not a great extension of current trends to foresee a regulatory system whereby remote monitoring of catches will become routine. In aquaculture, increasing concern for production and for environmental management may give rise to similar applications in monitoring and verifying processes, and in attesting that specific outputs have arisen from approved systems and management operations. Whilst there may be reservations concerning the imposition of various monitoring processes to remotely identify species, production or capture methods, and to identify and quantify the output, the opportunities to facilitate enforcement, hamper false declarations and support wider consumer confidence have definite advantages.

The effectiveness of resource management measures may be undermined by the understandable attempts of fishermen to extract the maximum value of their quota entitlement. In mixed fisheries it is often impossible to target single species without capturing others, and bycatches can become a significant problem (Kaiser and Jennings, Chapter 16, this volume). The discarding of species, sometimes perfectly edible but simply less valuable in that market, introduces a loss and represents an additional cost to both the fishermen concerned, through time and effort in clearing their gear, and to society at large who might otherwise have used the ditched resource. Ecosystem impacts, though difficult to specify, may also be an issue. Even where catches are well targeted, quota restrictions will tend to encourage the selection of the highest grade sizes (MacSween 1984). High grading can result in more juvenile stock being returned to the sea, often dead or with very little chance of survival; again representing a cost. Regulations which preclude discarding or high grading suffer from the classic problem of enforcement cost. Whilst certain types of equipment may be banned, for example onboard grading machines in pelagic fisheries, or various gear adaptations regulated in size and/or configuration, in many fisheries practical enforcement is at best non-uniform. Interactive onboard monitoring may provide some scope for improvement but areas of interpretation may still cause difficulties. For example, the point at which a skipper is deemed to discard a catch may range from the point at which it enters the net, to its arrival aboard. The impact of stress induced by interaction with the fishing gear may alone be sufficient to cause mortalities. It is arguable whether improved market information systems will reduce such problems – for example by improving the returns available on more costly but better targeted fishing – or exacerbate them – by increasing the temptation to high grade for spot opportunities.

Remote electronic monitoring and recording systems should, however, be able to provide some solution to the practice of misrepresenting fish landings. In the latter part of the 20th century the false declaration of fish landings emerged as a significant problem in a number of fisheries as quotas became tighter (Ahoven 1998; Johnston 2001). Supplying fish through illegal channels, commonly referred to as black fish or grey markets, simply undermined the clarity of market signals elsewhere and represented another instance of the need to incorporate marketing actions within the processes of resource management decision making. Remote recording of catches as they are taken aboard would provide a more accurate mechanism to monitor the uptake of quota from particular stocks, a factor that may be of value in fisheries subject to intensive effort and where the biomass is critically balanced. Logging catches can obviously be fed into market information systems to improve forecasting of supplies as they become available, and, as earlier noted, such information has the capacity for remote auction systems or other transaction mechanisms to be conducted whilst the boat is still at sea.

3.7.2 Green values

In addition to the marketing implications in managing fisheries resources, a related issue is the 'greening' of consumers. The emergence and impact of green values amongst consumers varies in different markets. However, even where considerable disparities exist between nearby countries, as is the case in some EU member states, the tendency is for heightened environmental awareness, manifest in various ways (Wessells 1998; Aarset et al. 2000). Concerns with more sustainable consumption are evident from markets for consumer durables such as washing machines and fridges through to those for fast-moving consumer goods including food and fish products. Whilst consumer concerns for responsible consumption of wild species have been apparent so far in only a comparatively limited number of cases, once the implications of consumption are established, awareness will also become heightened in respect of other species and/or stocks. Similar trends may also be observed in aquaculture (Muir et al. 1999). The precision of the issues involved may be questionable at times, and may represent a mix of concerns for conservation, sustainable management, impacts on bycatch, use of critical resources, social and environmental impacts, contamination risks and food safety (Wessells and Anderson 1995; Wandel and Bugge 1997). A classic example of concerns with conservation, and latterly sustainability, related to dolphin mortalities associated with tuna fisheries. In response, and broadly in line with more formal management regulation, processors have nurtured and widened the market for dolphin-friendly canned tuna through monitoring fishing methods and communicating this attribute on the product label. In another initiative demonstrating concerns with sustainability of fish populations, some chefs in the US removed overexploited species, including swordfish, from their menus in the late 1990s in response to declining stocks (*Seafood Business* 1998). More recent heightening of awareness may be found in the deepwater fisheries to the west of Scotland where the withdrawal of the UK's claim to territorial waters around Rockall in 1998 encouraged international fishing effort. The species targeted are extremely slow growing and highly vulnerable to overexploitation (Gordon and Hunter 1994), raising some concerns amongst consumers about the ethics of buying such products. A number of examples may be found in the aquaculture sector, such as the concerns about social and environmental impacts of farmed tropical shrimp production (Bundel and Maybin 1996; Gujja and Finger-Stich 1996), and the environmental impacts and welfare issues involved in the intensive culture of salmon and other fish species (Mackay 1999; Young et al. 2000; Alba and Dennis 2001; Millar 2001).

Greater awareness of the importance of sustainable fish populations and related environmental concerns might well become more pervasive once the actions of the Marine Stewardship Council (MSC) begin to send regular signals to the markets. This joint initiative started in the mid-1990s, joining the international operators Unilever and the environmental charity World Wide Fund for Nature (WWF) in common action. A central concern is to promote only products harvested from stocks deemed to be managed in a sustainable way. By 2000 only three fisheries – Thames herring, Australian rock lobster (*Jasus novaehollandiae*) and Alaskan salmon (*Oncorhynchus* spp.) – had been approved, although it is intended that more will be added to as other fisheries prove their eligibility (Peacey 2000). Explicit communications with consumers through media and other direct channels, such as packaging and ecolabelling of products, are liable to heighten awareness of underlying issues including the overexploited status of many of the stocks currently prosecuted for fish supplies (OECD 1991; Norberg 1996; Donath et al. 2000; Jaffry et al. 2000). Combined with other activities, such as the FAO Code for Responsible Fisheries (FAO 1995), it seems probable that fish consumers will not be able to avoid being more aware of the impact of their consumption decisions.

The depth of consumer understanding of the impact of consumption remains variable, and even amongst the more committed groups some research suggests that quite considerable gaps in knowledge exist (Aarset et al. 1999). Whilst superficial consideration may suggest that development of aquaculture has the potential to provide an alternative to many existing overexploited stocks, there is a need for a fuller appreciation of the intricacies of interdependencies between trophic levels. The dependence of many high unit value (HUV) carnivorous species upon feeds produced from other, sometimes overfished, low unit value (LUV) stocks will not sit readily within some green consumers' ethical checklist (Tacon 1994; Naylor et al. 2000; see also Pauly and Christensen, Chapter 10, this volume). However, determining that the source feed materials for aquaculture product come in turn from sustainable fisheries and/or agricultural production arguably calls for a level of awareness and commitment that is beyond many current consumers. Nonetheless, consumers increasingly expect that such issues are considered by supermarkets' buyers, and that they can trust such outlets to honour their concerns. Supermarkets, in turn, are increasingly prepared to seek competitive advantages in being able to offer such reassurance.

As in aquaculture, the concern of the contemporary consumer for animal welfare has been fairly muted in respect of captured fisheries products, and certainly when compared to agricultural sectors such as poultry and veal. Thus far the very fact that fish tends to remain out of sight under water until presented, already slaughtered for consumption, may have contributed to its lower profile in the green consumer's sights. However experience from a number of other 'ecowars', e.g. offshore oil exploration, demonstrates the implausibility of any attempt to cover up. Conduct such as the selection of only the most valued parts of captured animals can expect to attract increasingly adverse publicity. Thus the removal of crab claws and the discard of the live animal, or the finning of live sharks at sea with the body dumped to drown, have the capacity to engender widespread retaliation against fisheries generally. Yet shark finning is permitted in all but four countries of the world (*Guardian* 2000). Like all other food production systems, the fisheries sector will need to pay increasing attention to the importance of sustainable and publicly acceptable management practice.

Aquaculture has already experienced close consumer scrutiny on a number of different fronts. The simple proximity of aquaculture developments in the coastal zone and their inevitable conflicts with other users alone have provoked attention. Growing concerns with the environmental impact of aquaculture sites, especially where these are shared with other indigenous groups such as fishermen, coastal farmers, and with divers, tourist and recreational users, will demand more demonstrable controls over the sector's activities (Clark 1992). Similarly, conventional genetic manipulation of stock may be associated in the minds of consumers with transgenic modification of foods elsewhere, and in Europe at least there is widespread antipathy to buying such products. Concerns pertaining to the use of chemical treatments and pharmaceuticals on the fish stock have also drawn adverse comparison with activities in modern intensive agriculture and will not enhance the product position in the consumer's mind (Aarset et al. 2000). The recent interest in using organic principles for aquaculture (Young et al. 2000), the technical issues involved, and the communication of associated qualities to consumers is an interesting, though complex, market response to these and related concerns. This in turn has raised concerns for how captured fish product might also acquire more positive green attributes, and promote these to better effect (Belknap 2000). Notwithstanding such debates, however, food products based upon aquatic resources, cultured or captured, have the potential to send more favourable messages along the food marketing chain than many terrestrial food products. However communicated, these intangible aspects of fish products are likely to figure more prominently in the future.

3.8 CONCLUSIONS

The role of marketing within the fisheries sector has evolved quite dramatically over the relatively recent past. In some parts of the world today the remnants of a production-based, supply-driven orientation are still to be found. But in many more locations, in developed and developing countries, marketing has emerged as a value-driven activity increasingly focused upon raising the unit value of an increasingly scarce global resource, or of an aquaculture output reliant in turn on scarce and increasingly expensive resources. In conjunction with apposite resource management measures and implementation, this emphasis upon deriving more value from the finite resource base could generate positive social and economic gains for those who are involved in the fish industry supply chain, and the adjacent often highly dependent regional economies. However, the possession of the skills, resources and technologies available to develop value from the fishery and aquaculture resources may become increasingly concentrated within larger food industry players. If the interests of the many small-scale operators in the current supply system are to be maintained, their access to marketing capability and their successful application of relevant approaches may be an important development issue.

Constructing values within contemporary fish products has been shown to involve a range of activities that are certainly not just confined to post-harvest processing and selling. Successful marketing of fish products is increasingly driven by an ongoing, proactive and interdependent set of activities that constantly seek to deliver in response to market signals. Many of the values incorporated in the product sold are intangible, such as the psychic income derived from consuming a product that has been captured or produced in an environmentally positive way. In other instances values may be much more similar to those offered with other contemporary foods, such as convenience of storage or ease of preparation. The ability of the marketing function to incorporate and respond to such signals has increased significantly through ICT, and with developing food technology. The capacity of aquaculture to deliver more regular supplies of uniform product, adapted to meet downstream process specification, also offers significant opportunity. Even with existing levels of technology, let alone those on the verge of launch, considerable potential exists for further market development and value creation. Whilst this prognosis may seem optimistic, competing food production sectors have access to exactly the same opportunities. The challenge remains for aquatic food producers to take advantage of change to promote and develop the many positive features of their products, and to use the benefits derived to support the sustainability of their sector.

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4 A History of Fisheries and their Science and Management

TIM D. SMITH

4.1 THE NATURE OF FISHING

St Peter's fishing trip on the Sea of Galilee, recorded by St John, illustrates many aspects of the nature of fishing, as Sahrhage and Lundbeck suggested in their *A History of Fishing* (1992). Peterson's (1993) contemporary translation of the Gospel of St John goes like this:

> Simon Peter announced, 'I'm going fishing.' The rest of them replied, 'We're going with you.' They went out and got in the boat.

Fishing requires capital and labour; someone owns the boat and the nets (perhaps St Peter), and others help with the work on the boats. In this case the total crew apparently numbered seven. Fishing is frequently a family business; two of those helping St Peter that night were themselves sons of a fisherman, Zebedee.

> They caught nothing that night.

Fishing is unpredictable; sometimes catches are large, other times nonexistent, as in this case. Sometimes the fish are large, other times small. Sometimes fishing will be poor for days or years, and is almost always seasonal.

> When the sun came up, Jesus stood on the beach, but they didn't recognize him. Jesus spoke to them, 'Good morning! Did you catch anything for breakfast?' 'No,' they answered.

Fish are marketed in many ways, including informal systems where potential purchasers ask after boats even before they come to the shore, as St Peter might have assumed was happening that morning.

> He said, 'Throw the net off the right side of the boat and see what happens.' They did what he said. All of a sudden there were so many fish in it, they weren't strong enough to pull it in.

Where and when to go fishing has been asked since people began fishing. In this story, the boat owner, St Peter, chose when and where, at least until the trip was nearly over. Then Jesus directed the last net cast. His direction was quite precise, namely off the right side of the boat. Jesus' advice of where and when to fish has been interpreted as divine intervention and alternatively explained as his having made use of an often-reported sudden appearance of fish when the prevailing westerly wind suddenly ceases. The difference in catches when the right and wrong decisions are made can be enormous. For St Peter, Jesus' direction resulted in a net that was too full for the men to load into the boat.

> Then the disciple Jesus loved said to Peter, 'It's the Master!' When Simon Peter realized

> that it was the Master, he threw on some clothes, for he was stripped for work, and dove into the sea.

The motivations of fishermen for what they do, and when they do it, are not simple. Here, St Peter impetuously abandons his boat and crew, as well as the unexpected catch, showing that rational economics of fishing are not always what motivates a fisherman.

> The other disciples came in by boat for they weren't far from land, a hundred yards or so, pulling along the net full of fish.

Landing the catch is central to fishing and must be completed in a timely manner. Facilities for landing range from beaches, as in this story, to ports geared to efficient processing and marketing of the fish (Young and Muir, Chapter 3, this volume). This trip took place near the port town of Ginnosar, on the southwest shore of the lake, near an area of warm salty springs that flow into the Sea of Galilee, now known as Lake Kinneret.

> When they got out of the boat, they saw a fire laid, with fish and bread cooking on it. Jesus said, 'Bring some of the fish you've just caught.'

Fish are marketed and used in many ways. While St Peter's were immediately cooked for breakfast, they were more commonly salted or preserved in garum, a fermented sauce made of Spanish mackerel or tuna guts.

> Simon Peter joined them and pulled the net to shore – 153 big fish! And even with all those fish, the net didn't rip.

Fishery statistics are widely reported, and usually include the size and numbers of fish, as here. Often the location and the amount of fishing are recorded, in this case one net for one night. Fishery statistics are used for various economic purposes, for example for determining taxes and tithes (Holm 1996) and by fishing companies for determining fishing strategies (Evans and Grainger, Chapter 5, this volume). They can also be used to understand the nature of the fishing operations. For example, from St John's story, we can obtain some insight into the fishing gear used. The maximum size of the several cichlid species known as St Peter's fish is 3.5 kg. Thus, the catch of 153 could have weighed as much as half a metric ton, apparently near the upper limit of the fishing gear. Further, a boat from that period recently recovered from Lake Kinneret near Ginnosar measured 8.2 m long and 2.4 m at its widest, consistent with the likely crew size of seven and with the crew having difficulty lifting that weight of fish into the boat.

St John tells this story from the perspective of a few fishermen in a single boat on one night's fishing trip, but even in so limited a framework many aspects of fishing emerge: fishing gear, processing and markets, variability in catches, direction of fishing, and fisheries statistics. If the story had been taken from a slightly wider perspective, say that of the residents of Ginnosar, other aspects of fisheries would emerge. For example, St Peter's large catch, especially if continued, might have been resented by other fishermen as decreasing the fish available to them, or as flooding the market and possibly depressing prices. Similarly, if St Peter's fishing method was divine direction, others might have seen it as unfair competition and argued to restrict its use. However, if Jesus' method was merely keen environmental observation, adoption of it might have begun an escalation of fishing intensity.

Here I briefly sketch the historical development of fishing as a basis for the more complete descriptions in other chapters of many of the aspects of fishing revealed in St Peter's fishing trip. I focus on the specific issues raised in this story, as well as broader issues such as the economics of fishing, fishery management, and environmental and fishing effects on the supply of fish. I rely on, without citing repeatedly, two books: Sahrhage and Lundbeck's *A History of Fishing* (1992) and my own *Scaling Fisheries* (1994). I have cited what I see as their most important original sources, as well as additional sources not cited in those two books.

4.2 ORIGINS OF FISHING

Indications of fishing have been found in archeological sites as early as the Late Palaeolithic period, some 50 000 years ago, revealing a long history of the use of fish by humans. More recently, fish and fishing have been depicted in rock carvings in southern Africa and southern Europe dating from 25 000 years ago. Based on this, Sahrhage and Lundbeck noted that fishing is one of the oldest professions, along with hunting. Unlike hunting, however, fishing continued to be an important occupation even to modern times, and fishing methods have been repeatedly improved over the millennia.

The development of fishing on all continents and in most cultures can be more clearly traced since the early Mesolithic period, 10 000 BC, and can be seen in archaeological artefacts such as kitchen middens, paintings and fishing gear. For example, in the port city of Ginnosar on Lake Kinneret, where St Peter lived, excavations have revealed consistent occupation and evidence of fishing since the Bronze Age. By 4000 BC in some areas the archaeological record is complete enough to reveal the evolution of fishing gear. For example, the evolution from simple to compound fish hooks has been demonstrated for the cultures on Lake Baikal in this period.

In Asia the importance of fishing can be traced back for thousands of years, especially in the Yellow River in China and in the Inland Sea off Japan. Fishing in China was primarily in fresh water, and tended towards the development of fish farming rather than catching technology. However, illustrations of Chinese fishing methods showed them frequently to be unique: for example multiple lines of hooks in complex arrays and trained cormorants with neck rings. Chinese methods were subsequently used in Japan, initially in the Sea of Japan. In the Americas fishing appears to have been imported with the colonizing peoples, with rock paintings of fish and fishing as early as 10 000 BC in Patagonia. In the northern regions sealing and whaling developed, along with more traditional fishing, at least as early as 2000 BC.

4.2.1 Evolution of fishing methods

An enormous range of fishing methods was in use by the time St Peter went fishing on Lake Kinneret. In addition to various forms of fish hooks, perhaps the first and most obvious form of fishing gear – a myriad of nets, baskets, traps, spears, poisons and harpoons – had been developed. Most types of gear have been developed repeatedly, with the specific form tailored to the peculiarities of species and habitat. While the diversity of fishing gear is interesting in itself (e.g. Misund et al., Chapter 2, this volume), more astounding is the continual innovation in form and efficiency. For example, even the basic fish hook evolved from early times into compound hooks, and into barbed hooks. Hooks were used singly and later in groups or gangs, with and without bait, always being adapted and improved.

Similarly, the simplest beach seines and cast nets in use by St Peter evolved into complex purse seines and trawls. A key element in the evolution of fishing gear was the vessels used. While a form of pair trawling (see Misund et al., Chapter 2, this volume) is illustrated on the walls of an Egyptian tomb from 2000 BC, the development of sail-powered vessels allowed this simple gear to proliferate into many and increasingly complex forms (Anon 1921). This historical tendency to expansion was described succinctly in this century by the oceanographer Henry Bigelow (1931):

> [f]or as [human] population multiplies in the countries bordering on those seas, fisheries will correspondingly advance in efficiency of method, and an intensity of effort, extending at the same time farther and farther afield to regions where the supply has hardly been tapped as yet.

When Bigelow wrote he was looking back on a turning point in the development of fishing – the rapid mechanization of fisheries initiated by the adoption of steam power in the late 19th century. As the number of trawling and long lining fishing vessels on the east coast of England decreased by 13% in the 10 years after 1889, the composition shifted from 9% to 42% steam-powered vessels.

Several changes in fishing gear followed rapidly. Most of the new steam-powered vessels were rigged for trawling rather than for long lining. At the same time, the greater and more consistent pulling power of the steam-powered vessels allowed the use of the new larger otter trawls to replace the smaller beam trawls. The new otter trawls were held open by water pressure on large flat 'doors' as the vessel moved forward, rather than by a fixed head-beam (Misund et al., Chapter 2, this volume). These doors were designed after devices used in Irish and Scottish salmon (*Salmo salar*) trolling gear, and were tied to the cables between the ship and the net. Introduced in Scotland in 1892, this markedly more efficient trawl spread rapidly as fishermen continued to compete against one another for higher and higher catches.

As Bigelow pointed out, not only did fishing vessels and gear improve over time, but fishing tended to expand into regions 'farther and farther afield'. Even before the east coast English fleet expanded in size and power in the late 19th century, the areas fished had also been expanding (Fig. 4.1). The spatial expansions in the later periods were allowed by the increased capability of the larger steam-powered vessels, but even before that technology, expansion was evident. Such expansion has been seen in many fisheries, frequently driven by declining catch rates as the fish populations in the nearer areas are reduced. Choice of where to fish then frequently becomes a trade-off between travel costs to and from suitable ports and markets and catch rates in different areas. This trade-off has often pushed vessels ever further into the sea, as seen in the English fleet in the 19th century.

In the 20th century there were many additional advances in fishing vessels and gear. In addition to a gradual shift from steam to diesel engines, some vessels began to process the catch on board. In the 1950s hydraulic winches and the 'power blocks' began to be used, greatly increasing the ability of fishermen to deploy the gear and to lift the filled nets back aboard. Similarly, after the Second World War echo location equipment became increasingly available, allowing fishermen to target their prey before setting their gear, rather than searching with the gear. The results of this evolution of fishing vessels and gear are described by Misund et al. (Chapter 2, this volume).

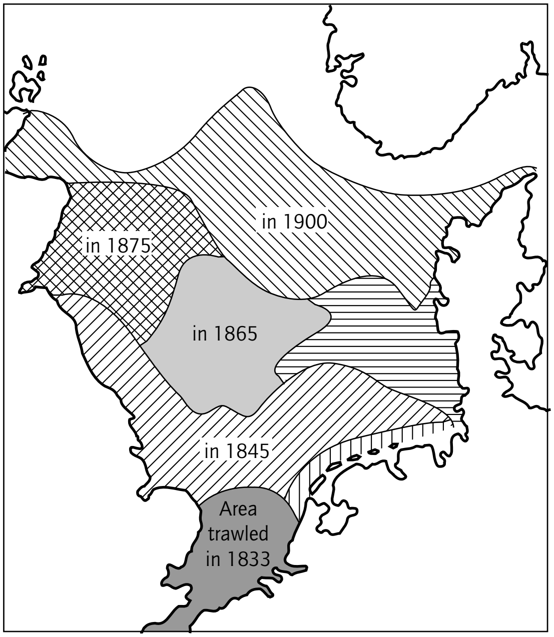

Fig. 4.1 Alward's map of the North Sea showing (cross-hatch patterns) the years in the 19th century when English trawlers first began fishing in increasingly more northerly areas. (Source: from Wimpenny 1953.)

4.2.2 Evolution of ports and marketing

St Peter could have expected to sell his catch by landing on the beach, and this is still often the case in many artisanal fisheries. However, villages and towns often developed in favourable locations for landing and marketing fish. For example, the development of favourable transportation systems can create or ensure the viability of ports, as occurred in 1860 in the English town of Grimsby when the rail lines to London were established. Further, the expansion of fishing grounds sometimes creates new ports.

The existence of transportation systems and markets also has spurred the development not just of particular ports, but of entire regional fisheries. For example, the North Pacific halibut (*Hippoglossus stenolepis*) fishery began to expand in Vancouver and Seattle after the 1880s, with the completion of transcontinental railways in North America, but only as the North Atlantic halibut (*Hippoglossus hippoglossus*) fishery began to collapse (Goode and Collins 1887).

While the existence of a natural harbour is usually a prerequisite, that alone is not always enough. Sometimes fisheries are encouraged as a part of social policy. For example, in the late 18th century a benevolent British Fisheries Society in London raised funds and established the Scottish port of Ullapool in northwest Scotland in a successful attempt to provide employment opportunities in that region (Dunlop 1978).

The processing, preservation and marketing of fish have evolved along with fishing gear and vessels. While fish was undoubtedly first consumed fresh, much ingenuity has been applied to developing methods of processing. Salting fish to dry and preserve it has been done since time immemorial, contributing, for example, to the establishment of rather unpleasant salt mines throughout the Roman Empire. Historically many other methods have also been used, such as fermentation and packing fish in oil. The specific methods of preserving imparted their own sometimes peculiar flavour. For example, the garum used when St Peter was fishing was produced in factories in Italy, Spain, North Africa and Turkey, and was shipped in amphorae through the Mediterranean region. The amphorae were labelled with the manufacturer's name, as well as the date and the quality. Some forms of garum were particularly highly valued, and the method continued to be used until the 15th century in some areas.

Canning was developed early in the 19th century in response to a prize offered by the French Revolutionary Directory for a new method to preserve food. Experiments with fish in the United States and Britain resulted in the first canned commercial fish product around 1822. The technique was combined with the technique of packing fish in oil and was used for French sardines (*Sardina pilchardus*), beginning in 1825. Freezing was applied to fish in the USA in the 1930s by Clarence Birdseye, and along with marketing New England haddock (*Melanogrammus aeglefinus*) as fillets rather than in the round, contributed to the expansion of the market for this formerly disregarded species.

4.3 OVERFISHING

One effect of the rapid increase in fishing power towards the end of the 19th century was increasing arguments about the possibility of too much fishing, or, using John Cleghorn's 1854 term, *overfishing*. Although a suitable definition of this word proved elusive, its possibility was nonetheless hotly debated for decades after Cleghorn, who, to the dismay of his neighbours, argued that herring near his village was overfished. Often the debate was inspired by conflicts between fishermen using different ports or gear. A more efficient net invented in 1872 by an enterprising sardine fisherman in Douarnez, France, for example, was blamed by other fishermen for being too efficient, an efficiency thought to cause subsequent declines in catches due to overfishing. The arguments were sufficiently vociferous that the new design was abandoned.

As fishing efficiency increased towards the end of the 19th century, the overfishing argument moved into the scientific community. It was debated, for example, in 1883 during the Great International Exhibition in London. The disputants were two of the leading zoologists of the time, Thomas Huxley and Ray Lankester. Huxley had long argued for reducing the seemingly arbitrary regulations on fisheries in England, complaining that there was no scientific basis for them and that they unnecessarily hurt fishermen. In the debate, he argued that the great fecundity of fishes implied that 'probably all the great sea fisheries are inexhaustible' (Huxley 1884). Lankester was also impressed with the fecundity of fishes, but saw the production of young fish as important in itself: 'the thousands of *apparently* superfluous young produced by fishes are not really superfluous, but have a perfectly definite place in the complex interactions of the living beings within their area' (Lankester 1884).

Although the Huxley–Lankester debate settled nothing, it did give impetus to the already developing scientific investigations of fisheries. By the middle of the 19th century concerns about fluctuations in fish catches had stimulated the application of science to fisheries. Russian and Norwegian studies of the fisheries and the basic life history of fishes began in the 1850s. Investigations within the US Fish Commission began in the 1870s and initially took a broad ecological perspective, outlined by the Commissioner, Spencer Baird (1872). The initial scientific problem was an almost complete lack of data. The research programme initiated in 1885 by the reorganized Fisheries Board of Scotland, for example, was designed to remedy this, and included both the collection of fishery statistics and (interestingly at the insistence of Huxley) an experimental trawl survey in areas open and closed to fishing to determine the effects of fishing.

4.3.1 Measuring Fishing

St Peter's fishing trip can be described in many ways: for instance, St John recorded the amount of time spent fishing, the number of crew members, and the size and number of fish caught. Other measures that have proven useful in fisheries include the size of the nets used and the number of times the net was cast and retrieved.

Such measures have been used to set taxes, for example on the basis of the number of oars owned by a fisherman, or to determine the tithes due the local parish (Holm 1996). They have also been used as a basis for settling international disputes for determining investment strategies, and for propaganda to promote investment and colonization (Innis 1940). While statistics have been recorded by governments and companies for specific purposes since time immemorial, the Huxley–Lankester debate focused attention on the need for better fishery statistics to underlie development of public policy.

In the 1880s the English Board of Trade began recording additional fishery statistics (Johnstone 1905). Although this was one of the few 'effective organizations' in the English government at that time, scientists examining these new data were not impressed. Only total catches of several species were recorded, and those in a myriad of ill-defined market size classes. Although many improvements in the collection of fishery statistics were subsequently made, adequate statistics for scientific purposes have proven difficult and expensive to collect, and too frequently have been unrepresentative of the continually changing fisheries. Difficulties in interpreting data collected in the ports led to placing technicians aboard fishing vessels to record more detailed data, an even more expensive approach (see Evans and Grainger, Chapter 5, this volume, for more detail of data collection).

4.3.2 'Impoverishment of the seas'

The Huxley–Lankester debate was resolved only after the data from the Scottish fishing experiment were analysed, and reanalysed, over the waning years of the 19th century by three scientists, Thomas Fulton, William Mclntosh and Walter Garstang. Fulton's initial analysis was immediately attacked by Mclntosh, who argued that the experimental data were worthless to begin with because of how they were collected (Mclntosh 1899). Further, despite his initial support, he later argued that the experiment had been unnecessary because it was apparent on inspection of the fecundity of fish that Huxley had been correct. This point of view, however, too often became entangled with vested interests, who were against the regulation of fishing and relied on extensive appeal to authority rather than to scientific demonstration: McIntosh apparently convinced few scientists.

In the middle of the argument between Fulton and McIntosh, Garstang was hired to continue a fisheries research programme at Grimbsy. He undertook to reanalyse the Scottish data because he felt that Fulton's analysis had been too superficial, especially in terms of stratifying by season. He also began an analysis of the Board of Trade's fishery statistics, which had now been collected for a decade.

In 1900 Garstang reported his conclusions from these two lines of analysis in a paper titled 'The Impoverishment of the Sea'. The Scottish experiment, he argued, directly contradicted Huxley. Not only could fishing reduce the abundance of fishes, but the experimental data also suggested, in support of Lankester's 'complex interactions', that fishing one species could indirectly result in the increase of another. Garstang also showed that not only could fishing affect fish, but in the period 1885 to 1895 fishing actually did decrease fish abundance. Using fishery statistics collected in the port of Grimbsy, he also showed that the catch of fish per vessel (standardized for the changes in the fleet with the advent of steam power discussed above) had declined by 33%, while the fishing intensity had increased by 150%, further demonstrating the effect of fishing on the fish populations.

4.3.3 *The Great Fishing Experiment*

Garstang's resolution of the Huxley–Lankester debate did not resolve the question inherent in the fact that 'overfishing' was still undefined. Pursuit of a suitable definition became the task of the first intergovernmental marine scientific body, the International Council for the Exploration of the Sea (ICES) (see Rozwadowski 2002). Arising out of the spirit of internationalism of the 1890s, ICES was established in 1902 on two legs, hydrography and biology. Hydrography was the major motivation for the initial discussions that led to the formation of ICES. The basis for the ICES Hydrography Programme had been well worked out by 1898, drawing on joint work among Scandinavian scientists throughout the 1890s. In contrast, the Biology Programme was initially less central, being added on during the negotiations with carefully crafted language to ensure that the work to be done by ICES would help 'promote and improve the fisheries through international agreements'. While the importance of using oceanography to support the biological programme's goals was often noted in the discussions leading to ICES, the marriage between the two legs proved to be weak at best (Chapman 1962).

The ICES Biological Programme was subsequently elaborated to include studying fish growth and maturity, migration pattens, abundance and reproduction, but with only limited reference to the Hydrography Programme. The biologists began by trying to define overfishing, noting that this could mean either that fish were not allowed to grow to an efficient size, or that too many were caught to allow adequate reproduction (Petersen 1903). Further, they debated if overfishing should be defined entirely on biological grounds, or if economics should enter in (Kyle 1905). In the end they adopted a simple definition for overfishing as 'too severe fishing,' and particularly the situation that 'more fish or better qualities of fish were taken away than the natural production could replace'.

To provide scientific information to support international fisheries agreements, ICES fishery scientists began an ambitious research programme. They adapted and extended many of the field and statistical methods that had been developed in the 1890s, including marking and recapturing fish, determining ages and reproductive condition, identifying different populations or stocks of fish (Sinclair and Solemdal 1988), and conducting research-vessel trawl surveys to determine abundance and plankton sampling surveys to determine egg production. They compiled catch statistics, measured fish at sea and on the docks, and, of course, wrote reports.

Over the first pivotal decade, ICES scientists eventually focused on a single issue, the status of the North Sea plaice (*Pleuronectes platessa*). By 1913 they were convinced that overfishing was in some sense occurring, concluding: 'the fear of an already existing or impending overfishing seems, therefore, perfectly legitimate and justifiable. . . . [T]o deny this danger is to close the eyes intentionally' (Heincke 1913). The scientists had trouble, however, in agreeing how their proposed reductions might be made, deciding in the end that, as an experiment, a minimum size limit might be set at 25 or 26 cm, perhaps phased in over a period of years.

The 1913 recommendation was met with little enthusiasm among ICES countries, even with the possibility of a gradual imposition of size limits. This lack of enthusiasm was not important, however, because the guns of August 1914 signalled the beginning of an altogether more drastic experiment, the reduction of fishing activity during the Great War. This experiment, the Great Fishing Experiment, was far more telling than that proposed by ICES.

Even as the war ended, scientists began assembling fishery statistics. Anticipating difficulty interpreting the postwar market category statistics, scientists collected some additional data by putting technicians aboard some British fishing vessels to record the length of the fish caught. The analysis of the before and after data followed the approach used by Garstang 20 years earlier, comparing the weight of fish landed in each market category and the number of days fished. The results were even more dramatic than Garstang's, showing that the weight of catch per day fished increased by 500% for the largest market category. Further, the cause of the increase was also clear, with fish having become so much larger that the smallest fish landed after the war were larger than the modal size of fish landed before the war (Fig. 4.2) (Borley et al. 1923). The result of the Great Fisheries Experiment was clear: fish populations can recover when fishing is reduced.

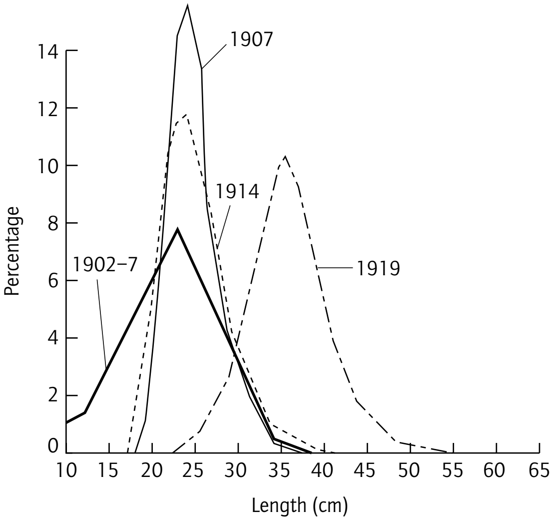

Fig. 4.2 Borley's graph of the percentage of plaice in each length category caught in the fishery on Dogger Bank in the period 1902–7, and in 1907, 1914 and 1919. The greater lengths of plaice caught in 1919 demonstrated that the higher postwar catch rates were due to the growth of fish during the war years, when fishing intensity was low. (Source: redrawn from Borley et al. 1923.)

4.3.4 Operational fisheries oceanography

While ICES scientists over the first decade of the 20th century focused on overfishing of North Sea plaice, other scientists focused on an issue that arose in St Peter's fishing trip: predicting when and where to fish. In Lake Kinneret, the sudden appearance of fish associated with the cessation of the prevailing winds is a good example. Limnological studies have since shown that when the prevailing westerly wind blowing across the north–south orientated lake suddenly stops, a seche is created that results in a predictable upward movement of the thermocline on the west side of the lake where St Peter was fishing. This could explain the miraculous catch. Characteristic of oceanographic explanations, however, this attractive explanation does not work very well because the westerly wind tends to abate in the afternoon, not in the morning when he was fishing.

In Japan, hydrography was pursued to help locate where fish congregate and might more easily be caught. This interest arose after the 1901 ICES preparatory meeting in Oslo, where Japan was represented by an observer. By 1909 Tasaku Kitawara had expanded Japan's nascent fisheries research programme to include systematic oceanographic observations. By 1918 he had identified a pattern in fish distribution called Kitawara's Law, namely that fish tend to accumulate around oceanic fronts (Uda 1962, 1972). Kitawara's Law has stood the test of time, and represents one focus of fisheries hydrography, recently referred to as 'operational fisheries oceanography' by Kendall and Duker in their history of this field (1998).

4.4 A BASIS FOR MANAGEMENT: GRAHAM'S LAW OF FISHING

In 1900 Garstang had shown that increased fishing could reduce fish abundance and in 1920 ICES scientists demonstrated that the reverse could also occur – decreased fishing could allow fish abundance to increase. This completed the loop, and many scientists involved in the 1920s had confidence that the obvious implications of this demonstration would quickly be embraced by ICES countries. However, as St Peter's fishing trip showed, the motivations of fishermen are complex and not always rational. Although greater catches and higher catch rates had been demonstrated to be possible, there was no agreement after the first World War to limiting fishing in order to take advantage of the greater efficiency. Instead, there was a rush to expand the national fleets rapidly, capitalizing on the huge immediate profits to be made.

What caused this intentional closing of the eyes, a behaviour that ICES scientists had identified earlier when they attempted to give advice in 1913? One explanation is the pattern that Michael Graham would later describe as the Great Law of Fishing (Graham 1943). In his work in the 1920s and 1930s, Graham saw a recurring pattern, one that seemed to play out in fishery after fishery. The underlying observation was what had been so clearly demonstrated by Garstang in 1900 and again after the Great Fishing Experiment: catches do not continue to increase in proportion to the amount of fishing. Rather, eventually further increases in fishing result in smaller increases in catches, and profits begin to decrease. To maintain their income, fishermen invest in bigger and better nets and boats, increasing their fishing power and at least temporarily allowing an edge against other fishermen.

Increased long enough, fishing intensity reaches a level beyond which catches no longer increase, and even decline. No matter what individual fishermen do then, they can no longer maintain their income, and economic difficulties set in (see Hannesson, Chapter 12, this volume). Fishermen with large mortgages on their vessels cannot fish less, for then they would not be able to make their payments to the bank. Banks become edgy because the value of the vessels is tied to the abundance of the fish. Incomes of both vessel owners and crew decline. Calls for government intervention soon develop.

In the North Sea, the rapid postwar rebuilding of the fishing fleets in the face of the scientists' evidence demonstrated that the very thing that ICES scientists had agreed not to address, the economics of fishing, resulted in complex motivations that had not been adequately accounted for in the management of this fishery.

4.4.1 *Early Management Institutions*

Although few, if any, marine fisheries were actively managed in the 19th century, fishermen nonetheless had to contend with a sometimes complex suite of rules and regulations. In England, many of these were swept away in the 1880s, being judged not to be supported by science (Huxley 1884). Fisheries expanded rapidly in the early 1900s in the North Sea, and it was the result of that expansion that Graham had to draw on in formulating his Great Law of Fishing. He was also aware, however, that his law also applied to other fisheries. For example, it applied in whale fisheries, where the successive exhaustion of sperm whaling grounds (*Physeter macrocephalus*) in the North Atlantic was clear to Herman Melville. Melville in *Moby Dick* attributed declining catch rates to the whales moving to new grounds to avoid the whalers. As Johan Hjort later showed, however, the exhaustion of the North Atlantic whaling grounds following the invention of the explosive harpoon in the 1870s was caused by removals that were too great, not by movement (Hjort 1933). The Antarctic Ocean fishery for blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales began in earnest in 1925, following the development of the stern-ramped factory ships capable of processing harpooned whales at sea, which freed the whalers from their increasingly restrictive shore-based factories. Management of this international fishery was attempted through the League of Nations, and the International Council for the Exploration of the Sea was drawn in to conduct the needed scientific inquiry. However, management was too weak and this fishery would also follow Graham's Law (Small 1971; Schevill 1974).

The effects of Graham's Law also began to be seen by the 1920s in the rapidly developing New England haddock fishery. Haddock had always been a minor component of the New England fishery, which had focused on Atlantic mackerel (*Scomber scombrus*) and cod (*Gadus morhua*). Frozen haddock fillets, however, had expanded the market and the otter trawl landings increased by 150% over five years. At the same time, at-sea observations on fishing vessels revealed that large numbers of small fish were being discarded because they were too small for the market. Estimates of the discard rates were as high as 30% of the landed catch. William Herrington, then working for the US Bureau of Commercial Fisheries, showed that after 1927 the catch rates began to decline, as Graham's Law predicted. The declines prompted concern, the concern prompted research, and the research prompted more concern. But, as in the North Sea, the concerns never became sufficient to prompt actual management of the fishery. Instead, management measures were discussed and evaluated. Further, experimental trawling was conducted to measure the effect of possibly increasing the size of mesh in the nets, in the hopes that the discarding could be reduced. However, although the fishermen informally agreed 'to avoid, whenever possible, grounds where small fish predominate', they also regularly resurrected Huxley's long-disproved argument that fisheries were infinite.

Graham's Law of Fishing was not inevitable, however, and it was forestalled in at least one fishery, the US and Canadian North Pacific halibut fishery. The fishery expanded so rapidly after the turn of the 19th century, with completion of the rail access to the east coast, that negotiations for international regulations began between Canada and the US before the First World War. A treaty was eventually signed in 1924, establishing the North Pacific Halibut Commission to manage the fishery, and allowing for the hiring of scientific staff. The Commissioners immediately hired William F. Thompson away from the California Fish and Game Commission to oversee the research. Drawing on the (by now standard) fishery research methods of mark and recapture, age determination, oceanographic and egg surveys to establish spawning area, fishery landings statistics, and analysis of fishermen's deck logs, Thompson soon demonstrated that the first part of Graham's Law had already occurred.

The evidence was in the fishery statistics after the three marked periods of increase in fishing effort beginning in 1895, 1910 and 1918. Following each of these effort increases, the catches also increased. After the last two, however, the catch rates declined. Armed with this information, Thompson was repeatedly able to influence his Commissioners to expand the length of the initially agreed seasonal closures, thus successfully avoiding the second part of Graham's Law.

The management institutional structures developed in the first half of the 20th century varied greatly. In the North Sea, ICES provided management advice, usually along the lines of size limits, and international agreements were forged, and reforged. In the US the individual state governments, not the national Bureau of Fisheries, had authority to regulate fisheries. In New England, the necessary international discussions with the several involved countries were limited to a formal dialogue among the scientists. Similarly, the important California sardine (*Sardinops caerulea*) fishery was regulated directly by the California Legislature, with the California Fish and Game Commission having only limited authority on how the catch might be used.

4.4.2 Methods of management

Many methods of controlling fishing were being tried in the early 20th century. Even as early as 1871, the US Fish Commissioner had proposed weekend closures for the scup (*Stenotomus* *chrysops*) fishery in Massachusetts and Rhode Island (Baird 1872). In the failure of state governments to agree to restrictive management approaches, the Commission began advocating the politically popular but unproven method of releasing newly hatched cod fish larvae to supplement natural production (Baird 1887; Dannevig 1910; Taylor 1999). Size limits had often been suggested, ranging from the informal 'biological limit' advocated in the North Sea in the 1890s with a minimum size equal to the size of sexual maturity, to the ever-fluctuating minimum marketable size. Attempts to obtain compliance with size limits often forced discarding of too small fish, but encouraged the use of larger mesh sizes, which allowed smaller fish to escape unharmed.

Area and season closures were also tried, with varying success. The North Pacific Halibut Commission was successful by continually increasing the seasonal closures to the point of having a season diminished to weeks and then days. Salmon fisheries have often been regulated by closing and opening river fishing in a manner designed to allow a certain number of fish to escape to the streams to spawn. By 1938 ICES scientists had developed a management approach for Antarctic whaling based on limitations of fishing effort, although in the end only minimum size limits were agreed to.

Limits on total catches were also proposed, for example by the California Fish and Game Commission for the sardine fishery. But political pressure on the California legislators from those profiting from that fishery was sufficient year after year to prevent any limits being set.

Of these pre-Second World War attempts at management, only a few were successful (Engholm 1961). The bilateral North Pacific Halibut Commission was one, with its own group of scientists. The multilateral Alaska Fur Seal Commission (*Callorhinus ursinus)* was another, although it relied on the various national scientists rather than establishing a dedicated scientific group. But the complexities of the fishing patterns and economics of North Sea nations prevented effective management, as did the lack of federal control in the USA. The ideal form for management controls was a constant topic of discussion and focus of research throughout the first half of the 20th century. In 1927 the head of the US Bureau of Fisheries defined the agency's research objective not as implementing management, but as research to 'devise means and develop methods of effecting real fishery conservation'. The values of the various forms were formally debated by Herrington (1943) and Nesbitt (1943) in the early 1940s, setting the stage for post-Second World War developments.

The success of the North Pacific Halibut Commission was closely watched by fishery biologists in Europe, and served as a model for management after the Second World War. After the war, a series of bilateral and especially multilateral fishery agreements were negotiated. For example, the International Whaling Commission established control, albeit weak control, over especially the Antarctic Ocean whaling. The International Commission for the Northwest Atlantic Fisheries was established to manage trawl fishing off Greenland, Canada and the United States. The Inter-American Tropical Tuna Commission and the International Commission for the Conservation of Atlantic Tunas were established to manage tuna fishing in the eastern tropical Pacific and in the Atlantic, respectively.

4.5 SCIENTIFIC BASES FOR MANAGEMENT

As Director of Fisheries in Norway in the early 1900s, Johan Hjort had undertaken to develop a life insurance plan for fishermen. Based on that experience, in 1907 he made what he later termed a 'bold suggestion' to his ICES colleagues, a suggestion that was not well received but became a turning point for fisheries science (Hjort 1914). His proposal was that they apply the science of Vital Statistics to fish.

Hjort identified three types of information that are routinely studied in Vital Statistics or demography: birth rate, age distribution and migration. Scientists had already developed methods of measuring the first, the fecundity of fish, the sheer enormity of which had fascinated both Huxley and Lankester. They had also developed methods of determining fish migrations by marking the fish and then seeing where they are subsequently caught. Hjort himself had even had some success in determining the age distribution of a population based on the modes in the length distribution.

ICES scientists were sceptical, however, because the latter two components of Hjort's proposal were not well known. Although egg production could be measured, it was apparent that most of those eggs did not survive. Determining how many did seemed an insurmountable problem. Second, although the age distribution could be determined at least roughly from length distributions for fish with seasonal spawning, as Hjort had shown, the determination of the age of an individual fish also seemed an insurmountable problem.

Undaunted, Hjort persisted and he and his colleagues eventually showed that the key to both problems, determining survival and determining age, was in the rings on scales or on otoliths (see Jobling, Chapter 5, Volume 1). By counting the rings they knew the ages, and by looking at the ages of herring over several years, they showed that the fish of some ages or year classes were much more frequently seen than others. This suggested that in some years the numbers or survival of eggs must have been much higher than in others. For example, by 1908 the abundance of four-year-old spring-spawning herring, those spawned in 1904, was greater than any other age. Further, the 1904 year class continued to predominate, with the peak advancing in age year after year (Fig. 4.3). From demographic data like these, fisheries scientists rapidly confirmed Hjort's suggestion that the variability in catches, which prompted the application of science to begin with, was due to extreme variability in survival of young fish (see Myers, Chapter 6, Volume 1).

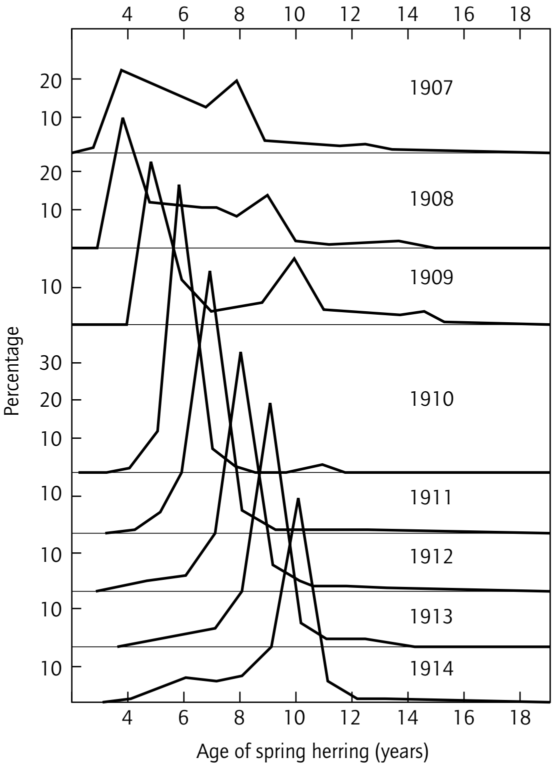

Fig. 4.3 Hjort's graph of the percentages of spring herring aged 2 to 18 years in catches made from 1907 to 1914. The regular advance of the peak percentages from year to year and the relatively low percentages of other age classes demonstrated the persistence of the extraordinarily abundant herring that hatched in 1904. (Source: from Hjort and Lea 1914.)

4.5.1 *Recruitment fisheries oceanography*

Many patterns in year class strength have been identified by fisheries scientists since Hjort's convincing demonstration of year class fluctuations. The ICES Hydrography Programme started to have some relevance to overfishing, which had become the driving focus of ICES. The causes of these fluctuations were hypothesized to operate during the first early days and weeks after the young fish hatched. To test this hypothesis, biologists have compared measurements of currents, temperature and other oceanographic variables extracted from the oceanographer's records, with year class strength measurements derived from fishery statistics or from research surveys (see Myers, Chapter 6, Volume 1).

The application of oceanography to the problem of the variability of year classes was pursued in the

1920s in Northern Europe and North America. In some cases this involved the fishery biologists doing a little oceanography on the side, while in other cases major research programmes were developed. In the 1920s Henry Bigelow, working from Harvard University, pursued the oceanography of the Gulf of Maine for the US Bureau of Fisheries. Oscar Sette followed Bigelow with a Depression-interrupted study of the survival of Atlantic mackerel off New York, and continued this focus in a longer-term study of the California sardine fishery beginning in the 1930s. The problem of explaining the causes of the variability of year class strength continued to fascinate biologists and oceanographers throughout the 1930s and 1940s, but the answers were few and the applications to the practical questions of the ICES Biological Programme were limited. This continued to be the situation at least up to recent times, as discussed by Myers (Chapter 6, Volume 1).

4.5.2 *Modelling age structure*

A more fruitful approach to determining the status of fisheries was to observe the consistent progression of strong year classes as members aged. This was especially clear in the case of the 1904 year class of herring, which continued to support the fisheries for several years after Hjort published his results in 1914. As this year class aged, two things happened. The first and obvious thing was that members of the year class were dying. Some died naturally in the course of things, while others were caught and marketed. The second thing was that the fish grew both in length and in weight. Implications of these two processes for fishing were apparently worked out twice. The first was by Fëdor Baranov in his 1918 paper, 'On the question of the biological basis of fisheries'. Baranov observed that increasing fishing would increase the total mortality rate, and thereby decrease the proportion of a year class surviving to older ages. He also accounted for the growth of individuals, assuming for convenience that fish increased steadily in length, and elegantly showed how to compute the trade-off in potential catches due to the decreasing numbers and increasing individual sizes with age. His approach allowed the determination of the effect of protecting younger fish on the total potential catch over the lifespan of a year class of fish. Unfortunately, published on the eve of the Russian Revolution and only in Russian, Baranov's analysis was apparently not understood until about 1938. His basic equation was built around equation (13.5) in Sparre and Hart (Chapter 13, this volume).

The second time the joint effects of growth and mortality were worked out was by William Thompson by the mid-1930s (Thompson and Bell 1934). In addition to showing that the catch rates had declined after effort had increased (as described above), Thompson demonstrated the interaction between growth and mortality numerically. He showed that the catch rates had to decline because of the increased mortality. Baranov's and Thompson and Bell's analyses provided the starting point for the development of more sophisticated models of the trade-off between the age of the fish caught and the ultimate yield. These developments are reviewed by Shepherd and Pope (Chapter 8, this volume). The first development was by a wartime colleague of Graham, H.R. Hume, who in response to questioning by Graham had completed a simple mathematical analysis of the trade-off between catch from a year class and fishing intensity. At Graham's insistence, in 1947 Hulme and two students Graham had just recruited, Raymond Beverton and Sidney Holt, published a seminal paper (Hulme, Beverton and Holt 1947) on the trade-off between catch and fishing rate (Fig. 4.4). Although growth was represented in an overly simplistic manner, the graph showed succinctly that yield from a year class must ultimately decline as the fishing rate is increased, explaining at least part of Graham's Law of Fishing. Increasing the fishing rate results first in increasing yield in weight, but increasing at a rate that is less than proportional of the fishing rate. This is seen in Fig. 4.4 by the yield curve beginning to bend over as fishing effort increases. Then, as fishing rates increase further, the yield begins to decrease, as seen by the decline of the right-hand side of the yield curve. The most that can be caught, of course, is at the fishing rate corresponding to the peak of this curve.

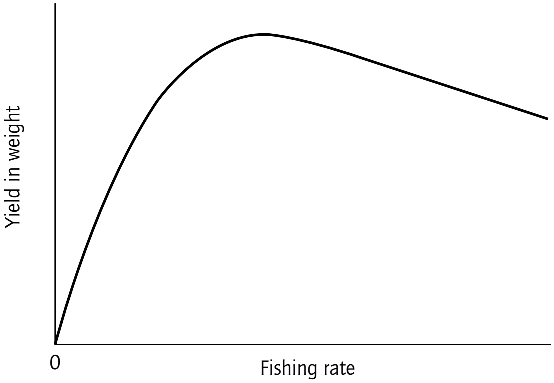

Fig. 4.4 Hulme's graph showing the predicted increase and subsequent decrease in the fishery yield in weight (vertical axis) as the fishing rate (horizontal axis) increases, as implied by a simple mathematical model. This model demonstrated that fishing harder could result in lower catches. (Source: from Hulme et al. 1947.)

4.5.3 Population dynamics

Even though sales in the Trieste fish market decreased over the years of the First World War, Umberto D'Ancona, an enthusiastic young Italian marine biologist, continued collecting his fishery statistics. He noticed that as the total sales declined the mix of species changed, with the proportion of predatory fish increasing steadily. As sales began to increase after the war, he also saw that the proportion of predatory fish declined. These changes were reminiscent of Lankester's 'complex interactions'. Baranov also suggested taking another perspective on interpreting the effects of war on fisheries by explicitly (and unusually at that time) including the fishing industry (Baranov 1926). Both D'Ancona's and Baranov's approaches were far more complex than the approach ICES scientists like Graham had taken in interpreting the effects of war on North Sea fisheries.

In the early 1920s D'Ancona explained his observations to his future father-in-law, Vito Volterra. Volterra was then Professor of Mathematical Physics in Rome, and D'Ancona's data rekindled his interest, dating back to 1901, in the possibilities of applying mathematics to biology. Others had pursued those possibilities while Volterra had worked on the physics of elasticity. One was Sir Ronald Ross, who received the Nobel Prize in 1902 for his studies of malaria. He later developed a mathematical model of mosquitos, malaria and humans. Using his modelling approach, which he termed the a priori method, he showed that malaria could only survive when the mosquito population was above a certain density, but that it could increase very rapidly with only small increases in mosquito density above that level. Similarly, entomologist William R. Thompson (unrelated to the William F. Thompson of halibut fame) developed mathematical models for studying the effects of control methods on corn borers.

A physical chemist, Alfred Lotka, applied mathematics to biology in a much more general way. He described his approach to mathematical modelling in his 1925 book *Elements of Physical Biology*. That book included as a special case exactly the problem that D'Ancona had posed to Volterra, one that Volterra solved and published in 1926. Lotka was quick to point out in response to Volterra's paper that not only had he already solved that problem in his book, but in fact had shown that the behaviour of the model becomes more complicated with the addition of a second competing prey species harvested by the fishermen (for the equation, see Pauly and Christensen, Chapter 10, this volume, equation 10.1).

The mathematical modelling of Ross, W.R. Thompson, Lotka and Volterra had demonstrated that population problems were complex, as Lankester had pointed out in 1883. Indeed, their sophisticated models have become fundamental to ecological studies (Kingsland 1985). However, it was the much simpler approach of a demographer, Raymond Pearl, that was picked up by fishery biologists. Pearl's wartime experience as Chief of the Statistical Division of Hoover's Food Administration Program had impressed on him the constraints on human populations. In 1920 he published a successful prediction of the next US census using a mathematical model of growth that he had rediscovered, the now famous logistic equation.

Pearl's modelling was picked up by Johan Hjort during the First World War, while he studied in self-imposed exile in England. He had resigned as Director of Fisheries in Norway in protest that secret fisheries negotiations he had assisted with were not made public, as had been promised. Following his repatriation to accept a professorship at the University of Oslo after the war, Hjort began to focus on the problems of the developing whaling industry (Hjort 1933). Noting the variability in the recruitment of young fish that he had demonstrated in 1914, Hjort was attracted to whales because 'the fate of the stock is bound up with the fate of a limited progeny'. Thus, he expected recruitment to the population to be less variable than for fish, and more amenable to study (Hjort et al. 1933):

> For studies of population these conditions have the advantage of affording larger opportunities of watching the new generation from birth onward, and thus obtaining definite figures of the numerical strength of the different stages or year classes.

By 1933 Hjort and his students demonstrated how to use models like Pearl's logistic equation to describe the effects of harvesting on a whale population. They focused on the nearly direct dependence of recruitment on population size and the limitation to recruitment by food resources at high population sizes. Pearl had seen this as an inherent limitation, and postulated the existence of a maximum population size, the carrying capacity of the habitat. One essential point in Hjort's analysis was that any sustained harvest of a population resulted in the population decreasing in size, as Garstang had demonstrated in 1900. A second implication of the logistic model of fishing was that as the population size decreased due to fishing, the sustainable catch would at first increase. However, as the fishing intensity continued to increase and the population continued to decrease, there would be a point beyond which the sustainable catch would begin to decline, again just as Graham's Law of Fishing suggested. One important concept that arose from Hjort's model was that there was in fact a maximum catch that could be sustained, a level eventually termed the maximum sustainable yield or MSY (see Schnute and Richards, Chapter 6, this volume, for modern developments).

Graham immediately picked up on Hjort's approach, applying it to the data from the Great Fishing Experiment (Graham 1935). By fitting Pearl's logistic equation to the data from and subsequent to the First World War, Graham showed that postwar fishing had reduced the population below the level giving largest catches, just as his Law of Fishing predicted would happen. But based on W. F. Thompson's success in managing the Pacific halibut fishery, he went on to argue that catches could be increased if fishing effort was reduced. While Graham's prediction from Hjort's model contributed to the 1937 London Fisheries Agreement, the prediction was destined to be tested again by war, rather than by fishery management.

4.6 POST-SECOND WORLD WAR

The approaches taken by Baranov, W.F. Thompson, Hjort, Graham, and Hulme were extended immediately following the Second World War. Hulme's young coauthors, Beverton and Holt, developed his approach by including a more realistic model for individual fish growth, proposed by Ludwig von Bertalanffy, and also structured the analysis in terms of changing age of the youngest fish caught as well as the fishing intensity (Fig. 4.5). This kind of analysis provides one of the mainstays of the modern yield-per-recruit forecasting (Shepherd and Pope, Chapter 8, this volume). In this form the possibility of more than doubling the catch over time simply by increasing mesh sizes to protect younger fish can be seen graphically. Although the regulation of fishing intensity in the North Sea was not likely, control of mesh size was allowed under the terms of the Overfishing Convention that arose out of the 1946 International Overfishing Conference. This analysis, especially as codified and extended in Beverton and Holt's 1957 monograph 'On the dynamics of exploited fish populations', became the basis for most management attempts in the North Sea after the war.

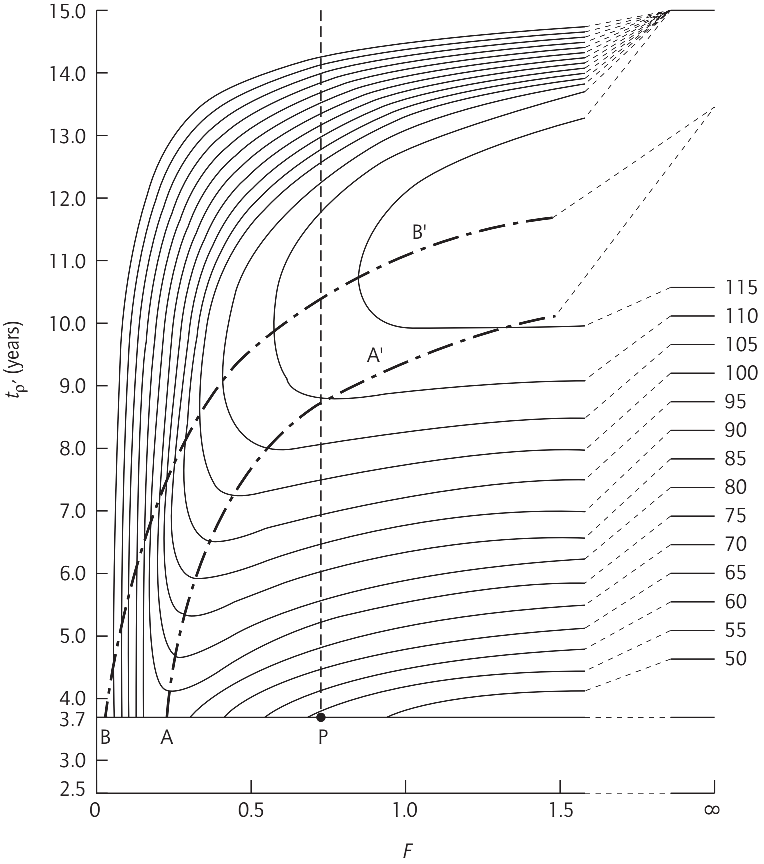

Fig. 4.5 Beverton and Holt's graph showing the change in predicted North Sea plaice catches (1000s of tonnes, solid lines show equal catches as labelled along lower right end of lines) for combinations of fishing intensity (instantaneous fishing mortality rate, F) and minimum age of the fish harvested (t_ρ, years). Predicted catches were highest for minimum ages of harvest around 11 years and for fishing mortality greater that 1.0, decreasing for lower or higher minimum ages and for lower fishing mortality. Before the Second World War the minimum age was 3.7 years and the fishing mortality around 0.7 (solid circle labelled P). The catch was 55 000 tonnes, roughly half of the 110 000 tonnes predicted for that fishing mortality rate if fish were to be allowed to live at least nine years. (Source: Beverton 1952.)

Similarly Hjort's use of the logistic model was picked up by Milner Schaefer in his 1954 paper 'Some aspects of the dynamics of populations important to the management of the commercial marine fisheries'. He developed a method for fitting the model using fisheries statistics, and applied it to data from several fisheries, notably to the then recently defunct California sardine fishery. He showed that by the end of that fishery in the late 1940s the population had been reduced to a fraction of its original size, and that the sustainable catch was far less than the catches in the years before the fishery collapsed. The 'Schaefer Curve' would eventually be applied to Antarctic whaling, which Hjort had focused on when he first developed the approach. Further refinements to this technique have led to modern-day surplus production models (Schnute and Richards, Chapter 6, this volume). In 1960 four scientists were invited by the then failing International Whaling Commission to apply modern fishery population dynamics methods to the Antarctic blue whale fishery. These scientists, Douglas Chapman, Kenneth Allen, Sydney Holt and John Gulland, used the Schaefer Curve to show that the Antarctic blue whale had been decimated from an initial 210 000 whales because its sustainable catch had been consistently exceeded for decades (Fig. 4.6) (Chapman 1964; Small 1971).

The population models elaborated just after the Second World War did not allow for some important behaviour of fish populations and fisheries.

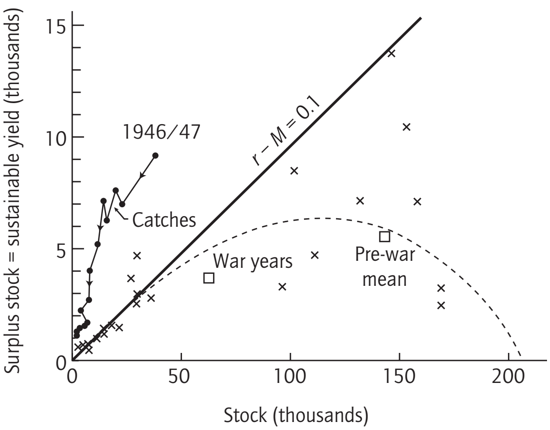

Fig. 4.6 Chapman's graph of the predicted sustainable yield of Antarctic blue whales (vertical axis) at different stock sizes (horizontal axis), showing predicted yields at different stock sizes (×) and actual catches in successive years (•) beginning in the 1946/47 Antarctic season. The theoretical maximum sustainable yield (peak of dashed line) was roughly 6000 whales, and could be obtained only when the population size was 110 000 animals. By the Second World War, the (unsustainable) yields were larger than that maximum and the stock size had been reduced to less than half of the required level, showing that blue whales had already been heavily overfished. (Source: from Chapman 1964.)

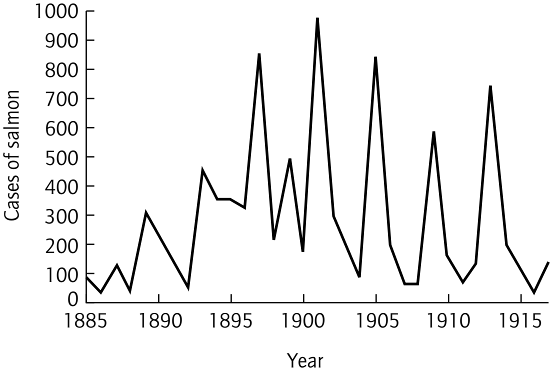

Fig. 4.7 Graph of the numbers of cases of Fraser River sockeye salmon canned from 1885 to 1917, reflecting the extremely high catches every fourth year (e.g. 1901, 1905, etc.) until 1913. The catch four years later (in 1917, rightmost data point) was substantially below the average fourth-year catches, and was blamed on rock-falls from railroad construction blocking the Fraser River at Hell's Gate in 1913. (Source: from Smith 1994, reprinted with permission from Cambridge University Press.)

For example, no matter how one tried, simple equations such as the logistic just could not mimic the cyclic behaviour of D'Anconna's data or the four-year oscillations of the sockeye salmon (*Oncorhynchus nerka*) fishery in the Fraser River in British Columbia. Volterra's and Lotka's approaches, while influential in terrestrial ecology (Kingsland 1985), were not picked up despite Volterra's assurance that his approach would provide 'an easy way of calculating the maximum output of fisheries' (Volterra 1926). Modern developments dealing with interactions between species can be found in Shepherd and Pope (Chapter 7, this volume) and Pauly and Christensen (Chapter 10, this volume). Similarly, the models adopted by fishery biologists did not account for the economics of fishing, and especially the clearly demonstrated behaviour of fisheries to reduce fish populations to low levels even though higher catches would be possible with less fishing effort (see Hannesson, Chapter 12, this volume). In the same manner, the importance of Lankester's 1884 concerns about 'complex interactions', although demonstrated by Garstang and repeatedly by others, continued to be ignored. Finally, Kitawara's and Uta's fisheries oceanography continued to play a large role in the ever-expanding distant water fleets, but made virtually no contribution to science directed at the control of fisheries.

4.6.1 Oscillations

Predictable four-year oscillations in the Fraser River sockeye catches (Fig. 4.7) were early suggested to be due to differences in productivity of four separate populations of fish using the river, each returning to spawn after four years at sea. In 1914, when the upstream migrating salmon reached the notorious Hells Gate passage, they encountered a huge blockade of rocks from the construction of the second Canadian transcontinental railway. Despite heroic efforts to clear the blockade, there were fears that this, the largest of the four populations, would be wiped out. These fears were confirmed when the pattern of the catches abruptly changed four years later. The 1917 catch was much lower than expected, only a fraction of 1914, confirming the biologists' explanation for the oscillations.

After the war William Ricker took up this question, drawing on a study of sockeye salmon in Cultus Lake, British Columbia, that he had begun his career with. That study had been prompted as part of a Canadian review of the effectiveness of its salmon hatchery programme. The focus was on the growth and survival of young salmon over the year they are in the lake, before they migrate down the Fraser River. Analyses of those data convinced Ricker that part of the cause of the four-year pattern, which was intriguingly similar to cycles in catches of fur animals that Elton (1927) had shown from the Hudson Bay Company, was lower individual fish growth rates. He termed this phenomenon 'cyclic dominance' (Ricker 1954), and argued that it occurred because slower growing fish were smaller and hence more vulnerable to predation for a longer time. Similarly, there was the possibility that there would be more predators in the lake if the previous year's salmon hatch had been larger.

Ricker published his analysis in 1950 under the title 'Cyclic dominance among Fraser [River] sockeye'. The same year Lamont Cole, a terrestrial biologist, published a controversial paper titled 'Population cycles and random oscillations'. He raised questions about the reality of some apparent cycles in abundance, claiming that some of the cyclic data could not be distinguished statistically from random numbers. The response to Ricker's and Cole's papers was the identification of several mathematical models that, unlike the simple logistic, could generate the observed oscillations. Some of these involved within-year dynamics such as delayed growth or cannibalism, as Ricker had suggested, while others involved time lags in biological processes.

Ricker expanded his analysis and considered other fishery data as well in his 1954 paper 'Stock and recruitment'. One interesting case was the Georges Bank haddock. Analysing fishery data accumulated since 1912, William Herrington had noticed that the winter abundance of three-year-old haddock tended to be low when the winter catches of adult haddock three years earlier were either high or low. When the adult catches were intermediate, the corresponding three-year-old abundance was markedly higher. Herrington had also noticed that when the abundance of adult haddock was high, adult fish tended to expand their range into that usually occupied only by young fish. He suggested that this spatial expansion may increase competition with the young, to their detriment.

Ricker in 1954 reanalysed Herrington's data, plotting the abundance of the young against the corresponding abundance of their parents (Fig. 4.8). This approach was widely adopted, and biologists began to comb through fishery statistics looking for evidence of changes in population vital rates with population density that might explain the variability in recruitment that Hjort had identified in 1914 and the regular oscillations seen in some fisheries (see Myers, Chapter 6, Volume 1).

4.6.2 Bioeconomics

Modern theories of fisheries bioeconomics, which are reviewed by Hannesson (Chapter 12, this volume) can be traced back to 1905, when H. M. Kyle had argued that the economics of fishing was the essence of the problem of overfishing. The controlling factors were capital invested and income earned, and, along with population productivity, growth rate and mortality, defined the problem. Kyle did not consider capital and earnings to be proper scientific issues, however, because they are not 'subject to natural law'. Further, he argued, even if they were scientific issues, as people like Alfred Marshall in his book *Principles of Economics* were beginning to argue (Marshall 1890), the calculation of 'the precise point where overfishing begins' would be a waste of time because the answer would change if the price of fish changed by even a 'fraction of a penny'.

Kyle's argument prevailed, and biologists and fishery managers steered clear of the economics

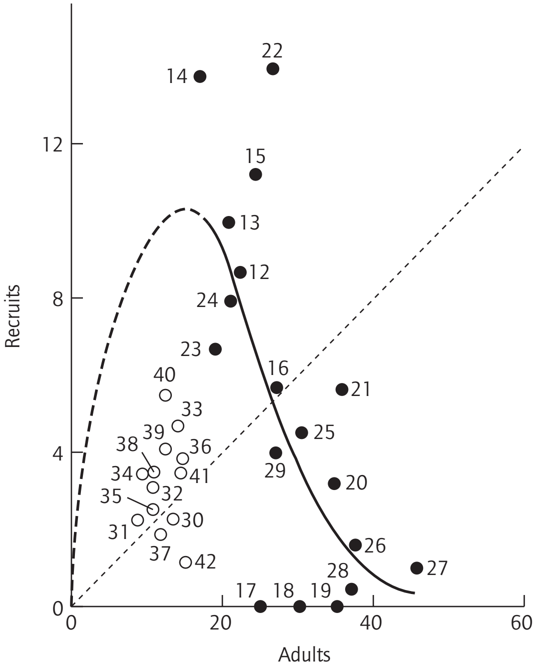

Fig. 4.8 Ricker's graph of the relationship between winter abundance of spawning haddock (adults, thousands of lbs caught per day fished) and winter abundance of the fish resulting from that spawning three years later (thousands of lbs caught per day fished). The diagonal line indicates the case when the abundance of three-year-old fish would be equal to that of their parents in the year the young fish were spawned. The domed curve depicts Ricker's theoretical density-dependence model of how spawning success decreases with increasing size of the spawning stock. Ricker showed that his model fits well to the earlier data (solid circles) when spawning stock was more abundant (solid line), but not to the later data (open circles) when it was less abundant (dashed line). (Source: Ricker 1954.)

of fishing in most countries. William Ricker acknowledged the wisdom of that decision in a 1946 review of the North Pacific halibut fishery, even as he acknowledged the increasing numbers of boats attracted to an ever-shortening open season.

H. Scott Gordon took up the question again in a 1953 paper, agreeing with Kyle that overfishing was primarily an economic problem and suggesting that the problem had been too narrowly focused for the last half century. More generally, however, Gordon argued that only by including fishermen as part of the ecosystem, including both their economics and their behaviour, could the problem of overfishing be addressed. He noted that (Gordon 1953)

> practically all control measures have . . . been designed by biologists, with the sole attention paid to the production side of the problem and not to the cost side. The result has been a wide-open door for the frustration of the purposes of such measures.

The adoption of Gordon's perspective has come only slowly and partially in fisheries, and more recent developments are mentioned in Hart and Reynolds (Chapter 1, this volume).

4.6.3 Complex interactions: predators, prey and the ecosystem

The importance of Lankester's 'complex interactions' was first demonstrated by Garstang analysing the Scottish experiment that resolved the Huxley–Lankester debate. Similarly, while the ICES interpretation of the Great Fishing Experiment was in terms of a single species – plaice – the interpretation by D'Ancona and Volterra in terms of predators and prey was ignored. The simple logistic model, which considered the relationships with other species only in an aggregate and static manner by assuming unvarying carrying capacity and maximum sustained yield, was inadequate for these issues. The effect of predator species on catches, identified as a problem at least as early as the 1880s in France, was also not addressed. The potential for overfishing one of two species harvested by the same fishery, which was first identified by Lotka in 1925, was not addressed even though it was obviously occurring in Antarctic whaling (Tonnessen and Johnsen 1982). The extreme depletion of blue whales demonstrated by Chapman and colleagues was dependent on that fishery also harvesting the more abundant (albeit smaller) fin and sei (*Balaenoptera borealis*) whales. Without the profits from those still abundant species, the whaling fleet could not have afforded to continue to hunt the blue whale remnant to near extinction.

Moving from a multispecies perspective to the even more complex ecosystem perspective, the detailed process of modelling of ecosystem dynamics undertaken under the International Biological Program was not quickly taken up by fisheries scientists. Holt, by then a leading fisheries scientist working for the United Nations Food and Agricultural Organization (FAO), reportedly discouraged fisheries involvement in that approach during a formative meeting with the International Union of Biological Sciences in 1962. Holt argued that 'fishery biology was very largely internationalized and did not really need much more international organization – and at any rate, if it did, this should fall to the province of FAO' and not to the International Union of Biological Sciences (Waddington 1975).

There was, however, developing ecological interest in some fisheries after the war. In 1949, for example, a multispecies trawl survey of Georges Bank was initiated. Although continued only until 1952, a similar survey was resumed in 1963 and continues today as the backbone of the US Government fisheries laboratory in Woods Hole (Smith 2002), where Baird first initiated his broad-scope research programme in 1871. The development of ecosystem perspectives and methods in fisheries is described by Pauly and Christensen (Chapter 10, this volume) and multispecies methods in stock assessment are described by Shepherd and Pope (Chapters 7 and 8, this volume).

The effect of environmental changes on fishes, although discussed since before the beginning of ICES, was not a main thrust of fisheries research prior to the Second World War. Work in Japan had demonstrated the usefulness of fisheries oceanography for answering the same operational questions that St Paul had dealt with on Lake Kinneret so long ago. Further, Martin Burkenroad (1948) had stridently raised the question of the effects of environmental variability in the late 1940s, especially criticizing the basis for management of haddock and halibut during a 1948 symposium. Despite work since Hjort's demonstration of variable year-class strength in 1914, attempts to describe the effects of the environment on fishery recruitment have largely failed (see Myers, Chapter 6, Volume 1). Symposia were held in 1951 and again in 1959 to address '[t]he question of the dependence on milieu-factors of the life in the sea'. Over the next decade controversy raged over the content and value of such a discipline (Chapman 1962; Kendall and Duker 1998). Some argued that such studies were essential if the cause of variability is to be understood, while others argued that they were a waste of time.

Despite the controversy, fisheries oceanography developed as a discipline, eventually acquiring its own journal by that title. However, the causes of year-class variability are still not completely known (Myers, Chapter 6, Volume 1), and the effects of this variability have been included in fishery population models to only a limited degree. The utility of the fishery population models elaborated in the early 1950s without an understanding of environmental effects was challenged by Uda in 1962, when he noted that '[a]fter the World War II, the estimation of fisheries yield or the absolute population size on vital statistics, using the powerful tool of population dynamics have made some progress. However, [some scientists were] . . . convinced soon that the reproduction potentials or recruitments are too much changing in response to the change of natural environments'.

4.7 CONCLUSIONS

The application of science to fisheries problems, beginning in the 1850s, has been fruitful. The underlying mechanisms for fluctuations in fishery catches have been elucidated, at least to one level. The several dimensions inherent in the term overfishing have been understood, ranging from recruitment and growth overfishing, to economic overfishing. The basic principles from demography have been incorporated into the increasingly sophisticated population models, and management measures that would alleviate some aspects of overfishing have been developed. But the lesson from the history of fisheries science is that many problems that were identified in the 1800s and early 1900s remain unsolved. Some of these problems have increasingly been addressed as the scope of fisheries biology has expanded, and as other previously excluded disciplines, such as oceanography and economics, have been integrated into the study of fisheries. However, many of the issues that have not been systematically addressed by fisheries scientists are becoming increasingly important. The bycatch of other species, such as sea birds and marine mammals, has only begun to be addressed (see Kaiser and Jennings, Chapter 16, this volume). Similarly, while many biologists speak of carrying capacity and maximum sustained yield of their species, few are attempting to address the joint effects of even all of the fish species, much less non-fish species, on the ecosystem (but see Pauly and Christensen, Chapter 10, this volume). Similarly, fisheries have frequently been observed to serially deplete target species over time. The example of the Atlantic halibut in the Gulf of Maine mentioned above can be multiplied with many other species (Pauly et al. 1998). The cumulative effect of long-term fisheries can reshape ecosystems without that being recognized because the baseline that biologists too often compare to is the ecosystem as they first encountered it (Pauly 1995; Holm 1996; Jackson 1997; Holm et al. 2002). These areas will have to be addressed by the 21st century fisheries scientists.

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5 Gathering Data for Resource Monitoring and Fisheries Management

DAVID EVANS AND RICHARD GRAINGER

5.1 FISHERIES INFORMATION FRAMEWORK

5.1.1 Information for a fisheries knowledge system

Since 1950 global fisheries have come under ever-increasing exploitation pressures caused by rising demand, technological innovation and efficiency, and the increasing globalization of markets. World production has increased from about 20 million tonnes then to more than 100 million tonnes today (FAO 1996a; see Hart and Reyholds, Chapter 1, Volume 1). It has been argued that this level is approaching the maximum that can be obtained from nature. The reach of fishing fleets into almost all the distant and deep oceans, the utilization of more species, more intensively, and calamitous collapses of important fisheries have provided important evidence that this may be true. Sustainability and a clear understanding of the pitfalls of overexploitation have become the driving forces of international fisheries research and fishery management. Knowledge about all the components of fishery systems has become an imperative alongside institutional mechanisms to put that information into practice. The primary instrument for improved fisheries management is the United Nations Convention on the Law of the Sea (UNCLOS 1982), through which the global fisheries community has begun to bring a more rational and sustainable approach to the exploitation of wild marine fisheries. There have been no equivalent international instruments applied to inland fisheries, mainly because they are enclosed within countries or shared between two or more neighbouring states, but in these cases there are now numerous bilateral or multilateral agreements regulating these fisheries, such as for the North American Great Lakes and Lake Victoria. In addition, the international community has adopted a voluntary instrument, the Code of Conduct for Responsible Fisheries (Code) (FAO 1995), to bridge the gap between international political acceptance of the needs for sustainability and the actual conduct of fisheries. In both UNCLOS and the Code their articles exhort states, organizations and individuals to collect data, develop knowledge and apply appropriate measures.

In this chapter we look at the nature and extent of the information required to populate a 'knowledge system' from which the three interlinked fishery management domains of Policy, Planning and Implementation can draw (see Fig. 5.1)

5.1.2 Fishery information domains

There are many ways in which the information domains within the fisheries sector might be categorized. For our purposes we have chosen to group very wide ranges of information within four main domains. These are addressed in more detail in subsequent sections and many are dealt with extensively throughout these volumes in relation to specific issues:

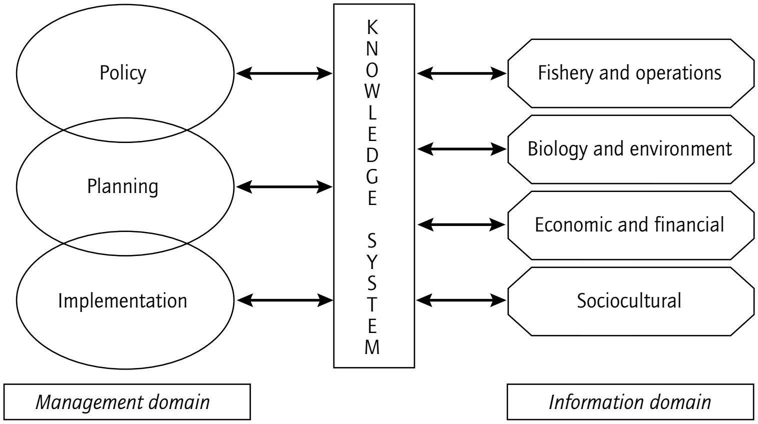

Fig. 5.1 Schematic representation of a fisheries knowledge system.

- Fishery operations: this includes all aspects of the primary capture and processing of aquatic resources. Who caught what amounts of fish, when and how? What operational management information is required?
- Biology and environment: this includes all characteristics of the biology, dynamics and interactions of exploited living aquatic resources and their associated species within the biological and physical framework of the ecosystem.
- Economic and financial: this includes all aspects of the conduct of the fisheries sector, including human resource, financial, economic, production and trade issues.
- Sociocultural: this includes all features that are needed to evaluate fisheries policy and management (including institutional mechanisms) in relation to the distribution of resources, income and food, equity and demographics, and participant dependence and social status.

5.1.3 Information and fisheries management

All these information domains are required for fisheries management in its widest sense within the political and economic systems of states and their regions. The range of issues and the data required for analysis and decision making within these four domains is enormous. Partly this is due to ecosystem diversity but mostly it is due to social, economic and geographic diversity. There are common features of fish stock dynamics and assessments that generally apply universally, even across the thousands of species and stocks targeted by fisheries. But the conduct of fisheries, even on single stocks, generates an array of interacting influences that is both hard to define and difficult to measure, and may well be unique to any one fishery. For example, purse seiners from one country may target a transboundary coastal pilchard stock in areas beyond the reach of small-scale fishers in another country who fish by beach seine.

Increasingly fishery managers acknowledge the need to include politico-socio-cultural, economic and environmental issues within the frameworks that they must consider when addressing sustainable utilization and management decision making. It is no longer the case that fishery management focuses mainly on the issues of how much fish may be taken or how much fishing effort may be applied. Of course, these primary issues define, however imprecisely, the removals from stocks that will maintain sustainability, or progress towards it, and thus support the biological basis of the fishery economic system on which participants depend. Issues of fishing rights, access and tenure also come within the management equation, as does the whole subject of minimization of environmental deterioration from the effects of fishing or pollution.

5.1.4 Information for fisheries policy, the precautionary approach and reference points

There are three main areas of fisheries policy that circumscribe the ways in which fishery managers conduct their activities: contributions of fisheries to food security, contributions of fisheries to the economy, and the effects of fishing on the environment. In all cases, the Code recommends a precautionary approach: precaution to ensure that fish removals for food and other uses are consistent with sustainability; precaution that the use of renewable aquatic resources as an economic activity is maintained to prevent economic and social dislocation and to approach optimum utilization; and precaution to prevent environmental degradation, including biodiversity.

Precaution requires the application of prudent foresight, which takes into account both best available scientific evidence and the uncertainties of fisheries systems when knowledge is incomplete. Fisheries policy is not specifically dealt with in this book, but it is clear that precaution as an accepted policy precondition is becoming more firmly established. The Technical Consultation on the Precautionary Approach to Capture Fisheries and Species Introductions (FAO 1996b) elaborated four key areas in which the precautionary approach needs to be applied: fisheries management, fisheries research, fisheries technology and species introductions. For each one of these, each containing numerous underlying issues, the nature of appropriate precaution needs to be established in the form of operational targets and constraints. Much recent work has been conducted on what this means in terms of fisheries management, less so for the other areas. For example, the basis for the measurement, and hence the data requirements, of fishing capacity and fishing technology efficiency is still in its early development.

For fish stock management there has been significant progress to specify how operational targets and constraints should be measured, particularly through the definition of biological reference points, including target and limit or threshold reference points (Caddy and Mahon 1995; Gabriel and Mace 1998). Many of the following chapters in this book address the analyses and models required to estimate these reference points, in particular the chapter by Sparre and Hart (Chapter 13, this volume).

5.1.5 Fisheries information cycle

Given that national and subnational fisheries policies are derived from a consideration of all the biological, social and economic circumstances that are particular to a country, it follows that the sets of data required to inform a national policy will also be unique. To enable policy to be turned into fisheries management advice that works (i.e. satisfies the goals of policy, responds to environmental and stock variations and changes in economic development), there always needs to be an information cycle that continuously supplies the knowledge system (see Fig. 5.2). At the outset, policy and its objectives need to be interpreted in terms of performance indicators such as biological reference points, against which the results of fisheries management are measured. For example, fishery managers might ask, what is the current level of fishing mortality, a performance indicator, against the fishing mortality that satisfies sustainability which is a current precautionary reference point, either at the limit to biological productivity or at a target during stock rebuilding?

Sometimes fishery performance indicators may be constructed from single variables, such as total catch, but in most cases they will be a combination of variables for which arrays of information need to be collected, for example fishing mortality. In some cases multivariable indicators may be simple combinations of variables; in others, such as for fish populations, the variables may be related in complex mathematical models (see Chapters 6–13, this volume). Whatever the case, planning for the collection of the data necessary for these variables will involve determining their feasibility, priority, frequency, quality and quantity, and whether standards for these can be adopted or derived. Once a performance indicator and its variables are defined according to these determinants, the implementation phase begins through the de-

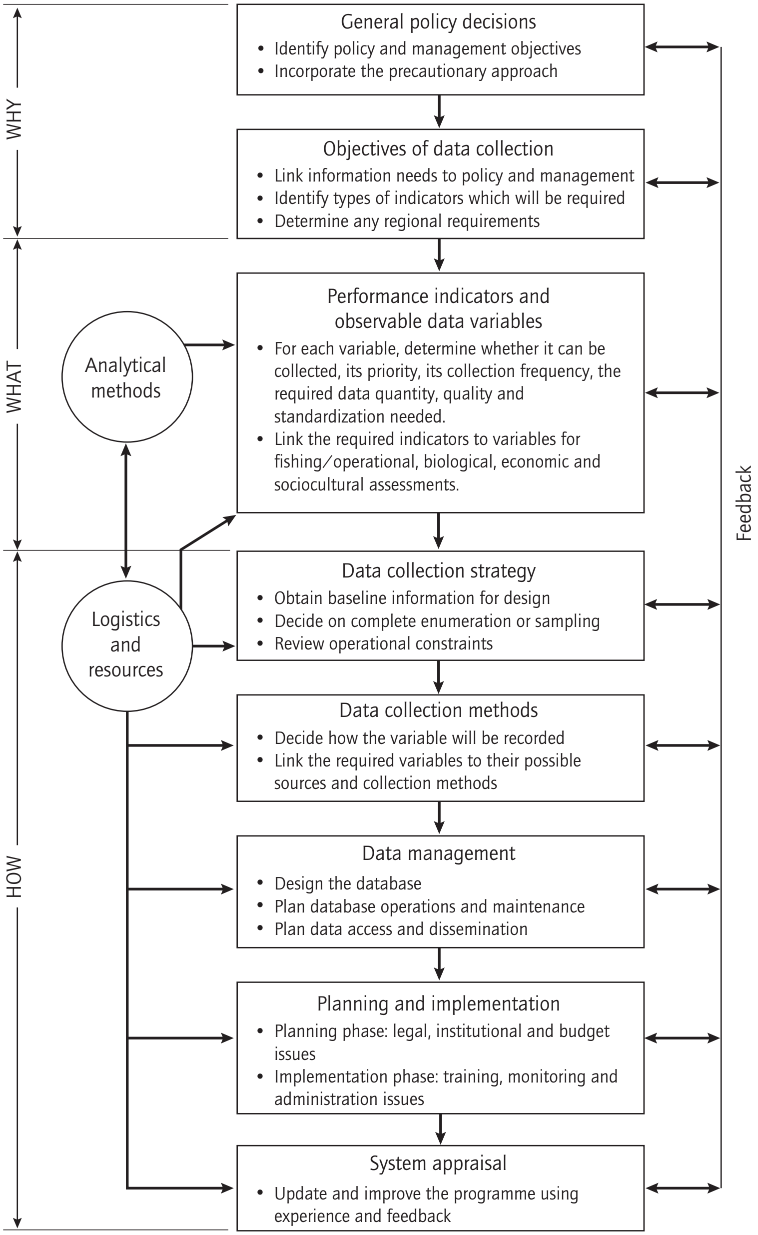

Fig. 5.2 The fisheries information cycle. (Source: from FAO 1999.)

velopment of a strategy, the definition of data collection methods and the means to maintain it, and the establishment of the legal, institutional and budgetary environments in which it will operate. Finally, a system of monitoring is required to determine whether all this effort actually both satisfies proper calculation of the performance indicator and ensures that the performance indicator is appropriate to the evaluation of the effectiveness of the management measures. In some cases this may be relatively simple but for multivariable indicators simulation modelling can assist this feedback process by revealing both the sources of uncertainty and inadequacy in the whole procedure, and the risk or probability that these sources of uncertainty and inadequacy are important or significant.

At each level in the fisheries information cycle there will be many decisions, actions and the application of resources to continuously improve the knowledge base. A few examples are given in Fig. 5.2. The advantages of this are clear. Even within the framework of the precautionary approach, '*States shall be more cautious when information is uncertain, unreliable or inadequate. The absence of scientific information shall not be used as a reason for postponing or failing to take conservation and management measures*' (United Nations 1995). Thus, investment in appropriate information will always reduce the degree of precaution required, and hence will enable a closer approach to the target or limit. Assuming that analytical methods are accurate and interpretation correct then more information means more fish may be caught or fewer controls placed on fishing activity.

Put briefly, investment in data collection and analysis will increase or sustain welfare and earn revenues from fisheries, because it reduces the risk of overexploitation and leads to the establishment and management of sustainable exploitation patterns (FAO 1999). The precautionary approach can be seen as a major incentive for the collection of reliable and appropriate fisheries and environmental information.

5.1.6 Information standards and classifications

Part of the planning process for information collection, once the management objectives and indicators have been decided, requires definition of the data standards and coding to adopt for different classes of variables. The use of standards assists in a wide range of issues from data form design to database comparability and non-redundancy. Where possible the use of standardized and internationally recognized units of measurement, particularly for dimensions and mass, and nomenclature should be adopted. The global network that forms the Coordinating Working Party on Fishery Statistics (FAO is the Secretariat) develops much of this work. The following international classification systems form the basis for many useful standards:

- *Species*: International Standard Statistical Classification for Aquatic Animals and Plants or the FAO 3-alpha species codes developed for commercial fish.
- *Fishing vessels*: International Standard Statistical Classification for Fishery Vessels (FAO 1985).
- *Fishing gear*: International Standard Statistical Classification for Fishing Gear (FAO 1982).
- *Products*: Harmonized Commodity Description and Coding System (World Customs Organization, 1994).
- *Oceanography*: Committee for International Oceanographic Data Exchange.

Many other global organizations have developed standards that may be important to the variables concerned, including the World Meteorological Organization (climate and weather measurement), World Health Organization (nutritional and health values), International Monetary Fund (economic and financial measures), and the International Labour Organisation (human resource classifications).

5.1.7 Information precision and accuracy

Fisheries data and their analysis contribute significantly to the costs of national and regional fisheries management, often equivalent to more than 20% of gross value of the catch, in some cases higher (Larkin 1997). The precision of the data is thus important because, in general, the greater the precision required, the more it will cost to ensure its accuracy. For each data type and each situation it is necessary to define the precision required both for the satisfaction of the variable's requirements and for instructions for data collection. Clearly measures of fish mass will be different for different fisheries; perhaps to the nearest tonne for industrial small pelagic fisheries, or to the nearest kilogram for recreational angling. Similarly, the precision of dimensions needs to be established; to the nearest millimetre, say, for shrimp carapace length or the nearest metre for water depth measurement.

5.1.8 Data sampling and stratification

Consideration of the coverage, location, quantity and quality of data sampling also form part of the information cycle, generally as one of the final stages prior to the actual collection of data. At the beginning, or during revision of an information programme, it is common to undertake fishery frame surveys or censuses in which complete enumeration (100% coverage) of the basic structure of the fishery sector is compiled, including production, infrastructure, employment and community dependence, and may also include environmental baselines. From these surveys, decisions can be made whether to maintain complete enumeration or conduct sample surveys in such a way that the estimate from the data samples is as close as possible to the true value for the data population. The difference between these two is the bias of the estimate, and it is extremely important to calculate and account for this bias by statistical methods. Reducing bias can be undertaken by increasing sample size but also in other ways, partly by random sampling to avoid sampling error and partly at the design stage of the programme. Sampling, of course, takes much less effort and therefore costs less. Some data will always require complete enumeration, such as the information needed to control quota allocations or fishing licence limits.

The main problem of data from sample surveys, quite apart from sample error and accuracy, is that the data population from which they are taken may not be evenly distributed across the location (strata) of the data, whether this is in geographic space, time or other dimension. Subdividing a data population into groups or strata and then randomly sampling those can reduce the data variability to that which represents real differences between the strata, which are then amenable to comparative analysis. The major strata in fisheries are usually one or a combination of space, time, landings, vessels, gears, enterprises, trade, people, the environment and the specific requirements of at-sea fishery-independent research. Subdividing the data population into minor strata, and then randomly sampling those, will enable further reduction of data variability. For example, a major stratum for fish trade might comprise markets/auctions, intermediaries/wholesalers/retailers, or exporters/importers as minor strata.

The key operational constraint of cost is also what drives stratification. The amount of effort, defined as the number of samples, hence cost, falls as bias is eliminated by stratification. At the outset, decisions on the quantity of data by stratum may often be made based on the results of censuses, but simulation can also be undertaken, particularly when revising sampling design based on experience. In general, of course, the larger the sample then the higher the accuracy. However, increased accuracy is not proportional to sample size, hence to the cost or effort applied. Depending on the purposes of the data, there may well be a cost/accuracy combination that satisfies both operational and statistical constraints. Even during sampling operations, such as very expensive trawl or bioacoustic surveys, it is usually wise to continuously estimate bias and to curtail sampling (hence costs) once a minimum satisfactory bias is reached.

Poor data quality, even assuming sample predictability from stratification, can limit any sample's value. Quality is also related to cost since it links directly to operational possibilities and constraints. Compliant participants, realistic data collection schedules, good training and equipment, all take time and cost money. Indeed, the likely quality of data obtainable from the application of available resources for an envisaged data collection scheme will need to be taken into account as far back as the derivation of the performance indicator under consideration. If the quality of data from a devised system cannot match the required accuracy of the indicator then no amount of redesign of the sampling system will substitute, and its estimation should be dropped or another choice of indicator be made.

5.1.9 System appraisal

Fisheries information cycles require continuous and circular reappraisal. Setting up a data collection system and then operating it without continuous feedback and possible revision may waste resources either on unreliable estimates or on oversampled variables. One of the key implementation guidelines suggested for the adoption of the precautionary approach succinctly reflects this issue: '*develop methods for optimising the monitoring system*'. Appropriate choice of indicators, matching requirements to resources, good census and sampling design, and the continuing evaluation and revision of these are needed to optimize a monitoring system.

5.1.10 Information for new directions in fishery research and management

Detecting trends and patterns of variation over time to provide a better understanding of the causal relationships among and between physical, economic and sociocultural factors is key to our approaches to fisheries sustainability, and this is crucially dependent on the collection of reliable data over long periods of time (National Research Council 1999). These understandings will lead to higher levels of appreciation about the linkages between human population growth, utilization of natural resources, environmental degradation and climate change. The Large Marine Ecosystem (LME) approach recognizes five interacting components, comprising ecosystem productivity at all levels, fishery resources and their response to exploitation, ecosystem and habitat health, socioeconomic conditions and governance.

The ecosystem approach to fisheries management recognizes that the chaotic behaviour of marine ecosystems may never allow accurate ecosystem, hence fishery, forecasts more than a few years in advance (Acheson 1995). This is probably doubly true for freshwater ecosystems, given the added uncertainty of changes in inland hydrologic cycles and balances. Nevertheless, short-term predictions can enable early responses to, and modifications of, human interventions (Shepherd and Pope, Chapter 7, this volume). This approach requires commitment to long-term observations of the state and dynamics of ecosystem components; in particular to regime shifts and alternative stable states (Shepherd and Pope, Chapter 8, this volume). Only through the collection of reliable data, from both observations and experimentation, can new and realistic ecosystem models be developed, which can then contribute to longer-term strategic fishery management plans. Investments in better information will not only generate better stock assessments but will also improve understanding and management of aquatic ecosystems.

In addition, new data sources, particularly from satellites, in situ remote sensing and the wider reach of surveys, are improving knowledge of oceanic conditions such as sea-surface characteristics, currents, topography and bottom type. These will all assist in the estimation of the biological, chemical and physical factors that influence aquatic ecosystems and fisheries. New techniques are also rapidly developing for the genetic characterizations of fish populations, which will enable a better understanding of population structure and diversity, population mixing and migration (see Ward, Chapter 9, Volume 1).

Notwithstanding these advances, it is an unfortunate fact that the best scientific evidence may not be made available in the best form to policy makers and even then it will not necessarily be properly used. For example, prior to the formulation of the precautionary approach, the uncertainty recognized in fishery assessments has often enabled fishers to effectively resist management measures, or allowed fishery managers to resist calls for increased allocation. Human systems monitoring is clearly part of an overall approach, indeed part of the ecosystem approach, to fishery management. Institutional mechanisms are needed (1) to specify the information required, including non-formal or traditional knowledge, and then adequately communicate this to policy makers, managers and the public, and (2) to analyse the responses of communities, both individuals and institutions, to economic, environmental and fisheries factors.

In the current debate about community management or comanagement, it is recognized that the key features of the social framework revolve around mutual commitment, understanding of the problems and methods of addressing them and cooperative/collective action, and that this implies open and transparent information communication. The sociocultural information domain has been neglected, but is key to our understanding of the human dimension of ecosystem stability and sustainability.

5.2 FISHERIES INFORMATION DATA

5.2.1 Policy, performance indicators and data variables

Fishery performance indicators are needed to assess the effectiveness of fisheries policies. If the policy indicates, for example, the requirement to increase employment, this can be interpreted in a number of ways through indicators that describe the incremental growth in numbers employed or the relative growth of the employed in relation to general population growth, whether community, regional or national. Employment numbers themselves will often be an aggregation of a number of variables, including at-sea, onshore, support and ancillary industry workers. In other cases, policy may require a reduction in the number of foreign fishing vessels or foreign crew against domestic crew, which has been the case in many countries, post-UNCLOS, both developed and developing. In practice, employment policy in fisheries will often be a combination of these requirements and may need the aggregation of data variables from all the relevant minor strata. Therefore, policy needs to be clear and detailed in order for fishery managers to determine what indicators are required, how to estimate them and what information to collect.

There are three general categories of indicators that inform fishery policy: (1) general patterns and trends such as catch, employment, contributions to GDP (gross domestic product), (2) changes in the infrastructure and institutions that affect fishery management outcomes, and (3) indicators, which are usually expressed as indices, against some pre-established reference point, in particular in relation to fishing, such as Maximum Sustainable Yield (MSY) or Maximum Economic Yield (MEY) (see Chapters 6 and 12, this volume).

The four information domains described above are a convenient classification of the general groups of data required for integrated fishery analysis and decision making. Each domain can be broken down into a number of classes and within each class there may be numerous data types available for inclusion within the information cycle, some permanently included and some temporary or transient. What follows is a general description of the main data types for the four domains, including the classes of indicators generally recognized for the domain. (For detailed description of fishery performance indicators and data variables, see FAO 1999.)

5.2.2 Fishery and operations information domain

This domain includes all the features of the primary capture and processing of aquatic resources: what amounts of fish were caught, when and how and what operational management information is required?

1 Catch and discards, production and stock enhancement

These are the key indicators in relation to fish stock removals and are thus essential for any understanding of the nature of a fishery. In some cases, the only data variables available may be from processed product, which then need to be converted back to whole fish for the estimation of stock removals. To do this, information must be gathered on conversion factors. This class of indicators includes the additions to stocks from enhancement programmes such as restocking or species introductions.

2 Fishing vessels and fishing gear
The physical means of fishery production is also clearly an essential element of basic fishery information and covers the nature of fishing vessels and fishing gears. Depending on the fishery, a wide range of data variables may be required, from vessel length to thickness of net twine (Prado 1991).

3 Fishing effort and sightings
These indicators relate the deployment and activities of the means of production to the catch itself. Fishing effort is the information recorded or derived on the deployment of vessels and gear. The data variables will be different for different operations. A good understanding of the operational characteristics of a fishery is always required before considering the choice of variable, for example accurate position at the beginning and end of a trawl tow will be important for calculating swept area but these may not be necessary for purse seine or pole and line fisheries. Sightings are generally available from patrol vessels, aircraft or other compliant fishing vessels and will also contribute to an understanding of fishing effort through information on place, length of time and type of fishing operations, including whether or not this activity occurred in contravention of effort regulations.

4 Offences and prosecutions, and the dissemination of compliance information
Compliance indicators are also important for the management of fisheries and can be used as key indicators of the response of fishers and others to the fishery management control measures being applied. Information on the knowledge of control rules by fishery participants may also be used to determine the nature of offences, which can be premeditated or unwitting, and feedback to develop improved compliance measures or to change prosecution practices.

5.2.3 Biology and environment information domain

There are three key classes of indicator related to the biology of stocks: stock size, stock structure and community structure. Together these place the stock within the ecosystem, alongside the physical and chemical nature of the environment. All may require an enormous range of data variables, and many will require both gathering data from the fishery and experimental or survey information.

1 Stock size
One of the key indicators long used as a proxy for stock size is catch per unit of effort (CPUE), which is derived from data gathered from the fishery. This is one of many cases where indicators are derived for several reasons, and hence should be considered as the highest priority. Aspects of stock dynamics that affect understanding of stock size are also included, such as knowledge of stock identification and recruitment. For some species, particularly the schooling pelagics such as sardines (Clupeidae) and herring (*Clupea* spp.), fishery-independent experimental surveys may be the only accurate way of determining stock size information.

2 Stock structure
The dynamics and nature of stocks in relation to exploitation is dependent on understanding stock structure across the life history of the species for all cohorts from larvae to reproducing adults. Gathering data on the age, size, sex, maturity and behaviour of individual fish has been the major focus for this class of indicators. Such data offer the means to understand the composition and performance of individual cohorts in relation to the whole stock, from which management rules can be derived that prescribe, for example, the age, size or sex of recruits, or seasonal/spatial limitations such as closed spawning seasons or grounds.

3 Community structure
Within the ecosystem, indicators of the position, importance and interactions of all species, from plankton to top predators, will assist in defining the general community structure. This will be particularly important when fishery policy aims to maintain biodiversity, when fishing operates on multispecies complexes or when conservation requirements demand it such as in relation to marine mammals and birds.

4 Environment

Very large numbers of data variables will contribute to the two key groups of physical environmental indicators: oceanography/limnology and meteorology. As with all other indicators, their priority will be dependent on fishery and geographic requirements. In some areas, for example, dissolved gases and temperatures may remain fairly static, for example over coral reefs, while in other areas these may fluctuate widely, as in upwelling areas. Weather, in particular sea-surface winds and solar incidence, may have important effects on species' life histories. Changes in currents or ambient temperatures may affect reproduction and survival of larvae, or the rate of primary production upon which fisheries depend (Myers, Chapter 6, Volume 1). The gross changes, for example, caused by the El Niño Southern Oscillation, when the enormous equatorial currents of the Pacific are reversed, cause major perturbations in the distribution, survival and growth of many marine stocks, from tuna to dolphins.

5.2.4 Economic and financial information domain

Four groups of information, most of which are common to any production sector, may be used for economic and financial indicators, including (1) the consequences of production such as price, value and employment; (2) financial support which would include investment, subsidy and management; (3) profitability; and (4) the distribution of food, rent and trade. This domain is probably one of the most difficult areas for data gathering in integrated fishery analysis because it requires divulgence of private enterprise financial data that are usually commercial and confidential.

1 Price, value and employment

The price of fish is one of the key variables, together with catch and effort, that is used in numerous fishery performance indicators, from the development of bioeconomic models and reference points (Maximum Economic Yield), to contributions to GDP or access fees (Hannesson, Chapter 12, this volume). Employment figures, using a variety of variables, enable the development of key sectoral growth indicators, such as per capita fisheries product.

2 Investment, subsidy and management

All forms of financial inputs are essential for the analysis of sector development, particularly in assessing market and competition economics. They will include direct and indirect investment in the fishery sector which should include training, and the costs of fisheries management, including research and data gathering, analysis and decision making, and surveillance and enforcement.

3 Profitability

Related to the above, key performance indicators associated with the generation of capital/profit are required together with the technical information on plant and machinery and their depreciation that constitute the sector's assets.

4 Distribution of food, rent and trade

Food balances originating from landings, plus imports, less exports, are important social and economic indicators since they will enable estimation of the changes to per capita food supply and hence to the contribution of the fishery sector to nutrition and health. In similar fashion, economic rent is developed from an appropriate combination of production, prices and costs. At the national scale the performance of the sector in support of the economy needs to be measured through estimation of the volume and value of trade and foreign exchange balances.

5.2.5 Sociocultural information domain

This most neglected area of information is probably also one of the most difficult to investigate as it deals with the multiplicity of measurable factors and non-measurable perceptions that make up human society. It includes three general groups of indicators: the characteristics of relationships which include access to and dependence on fisheries and the social status of participants; the demographics of fisher, processor, marketing and support industries, and their activity patterns; and distribution of income and food. Some sociocultural indicators are amenable to the definition of performance indicators but, unfortunately, many are not, so that targets and limits cannot be easily defined. Particular national or local fisheries situations, policies and traditions will affect the way indicators are defined.

1 Nature of access, community dependence and the social status of fishers
The ways in which the authorities, producer organizations and communities control access and conduct their business by the incorporation of information and rules into business practices, and by conflict resolution, constitute important knowledge under which fisheries management operates. The nature and extent of dependence on a fishery is also a fundamental factor that drives or contributes to fishery management policy, including employment, income and consumption, and historical and cultural association. For example, these factors are major influences on the European Union's Common Fisheries Policy and regional support mechanisms. The financial or cultural values that fishers place on fisheries play an additional role in the determination and evaluation of fisheries policy, including the likelihood of compliance with control measures.

2 Participant demographics and activities
The characteristics of fishers and others contribute to the derivation of fisheries policy and management measures, and may be important in defining the structure and stratification of data collection systems. Fishing and processing practices are often seasonal, using a variety of methods. Fishing locations and methods for target species, involving different sections of the fisher community and their decision-making processes, require an understanding of these patterns. For example, the seasonal migration of nomadic peoples to the coast in Oman for subsistence sardine (*Stolephorus* sp.) harvesting, and involving all community members, overlaps with the near-shore rock lobster (*Palinurus* sp.) harvesting season which is conducted by men. These fisheries, while conducted by the same community, involve completely different demographics, and knowledge of these is fundamental to the strategies for the collection of data and the application of control measures.

3 Distribution of income and food
Key economic and social indicators of fisheries development and management concern the ways in which the income and food resulting from resource use are distributed. Data on earnings by individual, household or company – and the demographics of these – provide basic socioeconomic information from which such indicators can be calculated. In similar fashion, the contribution of fishery resources and products to food security and nutrition are also key indicators of progress. An example is the data required to assess per capita fish consumption and hence diet balance.

5.2.6 Summary of information domains

As with all forms of sector analysis, there is always overlap between the data requirements of different information domains. For example, the numbers of fishers contribute to a variety of indicators, including fishing effort and catch per effort, equity and distribution, and employment and profitability. The numbers of fishing vessels contribute in similar ways.

Each issue, from determining fishery policy to the means of obtaining the data, needs a full consideration of how the steps in the fisheries information cycle can be analysed and used in decision making. This consideration can be undertaken by addressing each issue against a hierarchy of terms. Table 5.1 provides an example of just one economic dimension against a hierarchy of issues that may apply to any dimension in fisheries.

5.3 FISHERIES DATA COLLECTION AND MANAGEMENT

Obtaining information from the fisheries production sector can be a costly and onerous task, and has often led to adversarial relationships between the sector and fishery authorities. The problem

Table 5.1 Hierarchy of terms in fisheries information (using economics as the policy dimension).

Step	Example
Policy dimension	Economic
Objective	Economic efficiency
Criteria	Capital productivity
Reference points	Limit – capital productivity at bioeconomic equilibrium = 0 Target – capital productivity set by policy (e.g. MEY)
Indicator	Financial net return in relation to capitalized value ($return/$capital)
Scale	Fishery, fleet
Variables	Income, investment, vessel replacement value, depreciation rate, inflation index
Data types	Total landings value and costs, taxes and subsidies, capitalized value
Data sources	Fishery administrations, banks, industry, companies

relates partly to a general lack of compatibility between individual/company/community values and those of the fisheries authority, which sets the political, legal and administrative frameworks. It also relates partly to the necessity to impose restrictions on fishery rights, hitherto perceived as inherited territorial or stock-user rights. Additionally, there is the question of the aims of data collection. Without feedback on why data is required, users may question its applicability: 'We never see the results of all this effort to collect data.' This lack of feedback can lead to distrust, to commercially confidential data being leaked to competitors, or data being used for purposes other than the purpose for which it was originally intended, for example for legal or financial investigations. Whatever the causes of conflict or discontinuity in the information relationship, it seems clear that transparency and responsibility in the overall process will tend to remove the obstacles.

Comanagement can help synchronize public- and private-sector values through commitments of both groups of the fishery sector to the tasks of fisheries management: (1) assessment, (2) setting of objectives, (3) selecting management measures, (4) allocation among users and over time, and (5) compliance control and enforcement. The more involved fishery users are, and the closer agreement between them and fishery authorities, then the more successful will be the conduct of fisheries management. The development or improvement of fisheries data collection and management schemes thus begins at the strategy level.

5.3.1 Data collection strategies

Whatever the objective or performance indicator required, any strategy will follow a series of natural steps:

- Historical data: evaluation of existing data, its content, availability and accessibility.
- Operating characteristics: evaluation of the fishery, fleet, markets, or institutions through census or frame survey.
- Approach: decide on complete enumeration or sampling; conduct analyses of cost-benefit and cost-effectiveness; assess operational potentials and constraints (institutional, financial and human resource requirements).
- Design: decide on stratification; develop collection methods such as data forms, standards and training.
- Test: conduct test or pilot schemes with stakeholders, such as data collectors, companies, communities or other institutions, or a selection of these, to validate the design and methods.
- Feedback: review results of tests to ensure that data types, quantity, quality and origin are sufficient and necessary for the estimation of the performance indicator.

Effectively, this information strategy implies looping through the entire information cycle as a preliminary trial prior to full implementation.

5.3.2 Stratification

Two levels of stratification are generally used to subdivide data sources; major and minor strata (Table 5.2). Major strata are natural groupings outside the control of the design. Minor strata, which sub-divide the major strata, are selected as part of the design process to reduce data variability within

Table 5.2 Examples of major and minor fishery stratifications.

Major strata	Minor strata
Spatial	Province of country or major city – Districts (islands, villages) – Home port (place of registration) – Base port of fishing – Community of residence – Landing place – Fishing grounds
Time	Fishing season – Basic time period (week, month, year) – Day/night
Enterprises	Companies/cooperatives – Processing plants – Type of support industry
Trade	Markets/auctions – Intermediaries/companies – Exporters/importers
Vessel/gear group	Fishing fleet – Gear – Fishery (defined by fleet/target species/gear) – Vessel type (small scale, semi-industrial, industrial, joint venture, foreign)
Experimental fishery	Geographical areas/depth zones/bottom types/habitats – Time period/day–night – Gear/fishing operation
Landings	Commercial species group (catch/effort, value) – Commercial size/treatment group (catch/effort, value) – Ecological species groups – Landings agent
People or households	Demographic subgroups – Fishing community – Fishing fleet – Economic sector (harvest, post-harvest, market, support industry) – Status (captain, crew, owner)
Environment	Habitats (floodplain, lake, mudflats, mangroves, upwelling areas) – Season – Physical oceanographic/limnological criteria

the stratum, to produce homogenous subsets and minimize statistical bias.

Choice of minor strata can be complex. To subdivide strata into groups with the highest degree of homogeneity means that data collection will often need to sample a large number of strata. However, increased strata sampling requires more resources. In practice, a balance of available resources and statistical stratification requirements always needs to be made.

5.3.3 Operational considerations

The financial, human and institutional resources required to undertake data sampling and complete enumeration can often be considerable. Clearly, the choice of performance indicator and the data variables it needs, and the methods of collecting the data, are constrained by the availability of these resources. Careful estimation of resource needs at all stages can be undertaken and tested during strategy development, but even during full implementation of a data collection programme there needs to be some flexibility. This should be built into the overall data collection programme, so that reduction in resources leads to a planned reduction in the collection of lower priority data, and not to emergency cuts which have unknown consequences. For example, if the number of data recorders is reduced by 25%, is the sampling frequency reduced, or are certain data sets omitted altogether, while maintaining sampling rates on the higher priority variables? Once a scheme is adopted and resourced, it is fairly simple to plan for reductions, or increases, say, if some limits are temporary.

5.3.4 Data sources and collection methods

The wide range of data required for fisheries management is generated at all levels in the fisheries sector; thus sources include harvest, post-harvest, market, support industry, consumer and government agency. Unfortunately the simple vertical transmission of such data to fishery management authorities often ignores the needs of stakeholders in the management of their own roles. Feedback of available information that is of benefit to stakeholders always encourages better participation in the provision of data. The management of data flows, as a key function of a cooperative management framework between the fishery sector and governance, forms a major consideration in the development of comanagement arrangements and institutions.

There are always information flows between the various subsectors. The expected catch from a fishery is used to plan private investment in fishing vessels and plant, or bring them into operation. The prediction of landings is used to plan processing and storage capacity. Quota allocation is used to plan marketing and sales. Consumer preferences are used to plan products (Young and Muir, Chapter 3, this volume). For fisheries comanagement to succeed, a vital part of the role of fishery authorities is to facilitate these exchanges, in addition to their more traditional requirements, for an understanding of the biological and economic status of fisheries.

As part of the planning of a data collection programme it is valuable to identify the matrix of data types required against the likely primary source, plus the secondary sources, which can be used to validate the data. Logbooks from fishing vessels – as primary sources of operations data – can be verified using records of landings and these in turn can be verified through factory output information.

The methods of data collection are extremely varied and depend on the nature of the variables. Five different groups of methods can be employed, even within a single fishery:

- Registration: This is often the most direct means to obtain complete enumeration of the means of production and is usually implemented through some form of licensing arrangement required by law; it can apply to fishing vessels, factories, fishing gear, companies or individuals.
- Questionnaires: These are forms that have to be completed and submitted by individuals. Care must be taken in their design to require only data that are relevant to the respondent. If such questionnaires are routine, any supporting documentation – how to complete the form, etc. – might also include the results of previous questionnaires, thus providing feedback. The levels and types of questionnaire information may range across the full spectrum of general data needs, but it is also a particularly useful method when seeking to gather perceptions and opinions.
- Interviews: Face-to-face interviews are directed and compiled by data recorders, often called fishery enumerators. As with questionnaires, the design of the survey forms and the questions posed needs to take into account the likely availability of the information and the capacity of the interviewee to provide it. This is most often the best method for small-scale and artisanal fisheries where limited literacy or inadequate communication channels are available. This form of data collection through structured 'interview' is also the method most employed for sample surveys, where enumerators sample the required data variables under a specific frequency or location schedule. Less structured approaches to interviews include the use of (1) *focus groups*, which represent a particular issue, and (2) *panel surveys*, in which a random sample of respondents from a group is used as a representation of the whole group.
- Direct observations: Obtaining data through direct observation in ways that do not require input from fishery participants is the most common way of obtaining independently verifiable information. *Observers* (at-sea, or at landing sites) record fishery operations and biological characteristics, whereas *inspectors* are deployed to also collect information that may be immediately used for compliance control, such as quota management, the enforcement of management measures such as closed areas, or for data verification and validation. *Scientific researchers* independently observe the biological, population and environmental characteristics of a fishery. This can often be supplemented by the use of *key informants*, whose specialized knowledge, rank or skill enable direct observations beyond the scope offered by the employees of the fishery authority, for example academics, community leaders and wardens, or cooperating fishers and companies. Lastly, technology may be employed through in situ or remote sensing for data generation, including the use of satellites and data buoys, or the operation of vessel monitoring systems (VMS). The opportunities for VMS are still in their early stages of development, but it is likely that

increasing numbers of fishing vessels will be subject to these devices in the future. With integrated instrumentation it is believed possible to independently verify, along with the Captain and his company, most variables deriving from fishing operations and from the environment, including climate and oceanography, along with precise spatial and temporal data on the conduct of a fishery and its location.

- Reporting: VMS can also offer a means to directly report details of catch and effort and hence substitute for paper reporting. However, most fisheries rely on the regular submission of logbooks, which is often a legal condition of licensing. They often provide highly detailed information – a complete enumeration of activities – that enable a range of stock assessment methods, and can contribute to ecosystem research. At the post-harvest, sale and trade levels, records kept for commercial purposes can also be required. For example, it may not be possible to estimate the mass of small pelagics that are landed in bulk until scale readings from conveyor belts or pumping systems are taken; or, species composition from an artisanal fishery cannot be assessed until grouped at the market for sale. On the financial scale, where required performance indicators include structural and economic assessments, regular reporting through fishery statistical surveys, which may be voluntary or compulsory, may often be required.

Again, the development of an information matrix that identifies the data required with an appropriate method for each fishery is a useful tool in developing a strategy for a data collection programme.

5.3.5 Data management

Fishery data can often be used for several purposes, some of which require the raw form, some aggregates. Therefore, all data should be stored in their primary form. This is partly to ensure data integrity and validity, and partly to offer the opportunity to aggregate or transform data without the loss of information.

Computerization and the use of database management systems for all forms of data are now the established norms for information management. With the growth of high-speed telephone lines, area networks and the Internet, maintenance of data can be undertaken in a distributed manner rather than through the centralized processing of paper or mainframe computer systems. This can ensure that data entry and documentation and primary data processing are undertaken as close as possible to the data source and by those responsible for its collection.

So much of the primary data required for fisheries management is considered as commercially confidential that it is important to ensure that data management systems protect it from corruption and unauthorized access. Indeed, even within 'official' groupings, data that reveal the identities of catch, income or investment may not be necessary for their analysis, and therefore access to that level of detail may be limited. Data control and security features should always form a major consideration for the human–computer interface, whether this is related to the data entry procedure, data access or to the dissemination/publication of analyses.

5.3.6 Planning and implementation

Planning phase

The information cycle described above also provides the basis for planning and implementation of data collection strategies and programmes. During the planning phase it is essential to ensure that fishery policies are supported by appropriate legal mechanisms, including the powers to obtain information. Institutional mechanisms are also needed, most often by establishing linkages through committees and working groups and the procedures and communications necessary for information flow between the private, public and non-government sectors.

Working practices need to be established that enable a data collection programme to proceed. Ideally, these will be designed around the tasks, rather than the structures, performance or methods of the administration. This is not always possible, given the nature of bureaucracies, but an understanding of working practices and their flexibility to respond to change is vital for planning any new or revised programme. This has clear links to the financial and budgetary aspect of planning. Once instituted, a data collection programme should develop the time series from which fishery performance analyses are made. Medium- to long-term budgetary allocation is essential prior to implementation to ensure the required continuity. However, planning and strategy development should also account for enforced budgetary reductions, through prioritization, sample scheme flexibility, and a clear description of their consequences.

Implementation phase

Trial or test programmes prior to implementation not only verify the methodology, they also test the acceptance and level of support from the data suppliers. This support can be maintained during implementation in many ways, including the demonstration of the benefits and the provision of incentives, or by the application of penalties.

Continuous feedback is required to support data collection programmes and to ensure their continued applicability, as emphasized in the information cycle. Thus, training in new or revised methods as programmes proceed, and consultation to ensure data collection practices are the most up-to-date and meet all stakeholder requirements, should be maintained as an integral part of implementation.

5.4 FISHERIES INFORMATION PRESENTATION

Fisheries data most often relate to time series or spatial distributions (two- and three-dimensional). Sometimes both time and space – the four dimensions – are required to make sense of the data. In other cases, data sets may consist of two or more variables, which may or may not be related to one another. To cope with the often-large data sets that are generated it is usually necessary to present data in ways that (1) provide the evidence upon which statistical conclusions are made and (2) provide a means to reveal the information that the data contain, through the use of data tables and data graphics.

5.4.1 Data tables

In the first case, the evidence is the data itself, or aggregates arranged in appropriate strata. Data tables are essential for this proof and typically consist of columns of independent variables (time, space or major strata) with their associated numbers in the rows described by minor strata or their combinations. Thus, a time series of catch, by fishery, by species would typically be represented as in Table 5.3.

Key presentational principles are shown in this table:

- Arrangement: strata type and the independent variable in columns; major strata (in this case fishing method) and aggregate data highlighted; and minor strata (in this case species data) are subsidiary to major strata.
- Format: numbers right-aligned; same font as text with slightly smaller point size; table margins indented from text and centred on page; optimum use of white space; and frames (grid lines) are mini-

Table 5.3 Total catch in metric tonnes by fishery by species, 1996–9 (hypothetical).

Fishery/species	1996	1997	1998	1999
Longline	17 200	19 300	18 300	20 700
skipjack	10 000	11 000	10 000	12 000
albacore	1 200	1 300	800	700
yellowfin	6 000	7 000	7 500	8 000
Demersal trawl	26 000	24 000	23 400	31 200
cod	25 000	22 500	22 500	30 000
hake	1 000	1 500	900	1 200
Pelagic trawl	50 000	40 000	45 000	65 000
mackerel	15 000	12 000	13 500	23 000
herring	35 000	28 000	31 500	42 000
Purse seine	35 000	12 000	32 000	25 000
herring	20 000	7 000	18 000	17 000
sardine	15 000	5 000	14 000	8 000
Total	**128 200**	**95 300**	**118 700**	**141 900**

mal, clear, of minimum weight, and placed to delineate major strata.

5.4.2 Data graphics

Using simple principles of graphic presentation usually leads to a better view of the information content of data. Indeed, graphics are often the only way of revealing information since they can be used to accurately depict large data sets, which are nearly always multivariate. There are numerous ways of visually presenting data: histograms (column, bar), line and scatter plots, proportional plots (pie, area, radar) to three-dimensional surfaces. The most common is the column histogram, which enables standard presentation of the independent variable along the x-axis, for example the passage of time, and a variety of ways of presenting data for single and aggregated strata.

In general, graphic presentations should reveal the information content of data by:

- showing the data by representing the substance rather than the method of presentation;
- avoiding distorting the data – either graphically or by showing the data out of context;
- presenting many small numbers in a small space, and making large data sets coherent;
- encouraging visual comparison of differences and revealing the data at both lower and higher levels of detail; and
- serving a clear purpose and being closely integrated and relevant to the statistical and verbal descriptions of the data.

Figure 5.3 contains some of these principles using the data from the major strata in Table 5.3. This graphic depicts some design principles that support the way information in presented as shown above, including:

- The representation of numbers as physically measured on the surface of the graphic should be directly proportional to the numerical quantities represented. (Note: the common use of three-dimensional bars adds nothing to the information content, and a poor choice of perspective can even lead to visual distortion.)
- Clear labelling should be used to minimize distortion and ambiguity about the data. Legends should be placed in support of the data.
- Variation in the data should be shown, not design variation. The choice of stacked columns here provides visual comparison of the variations in

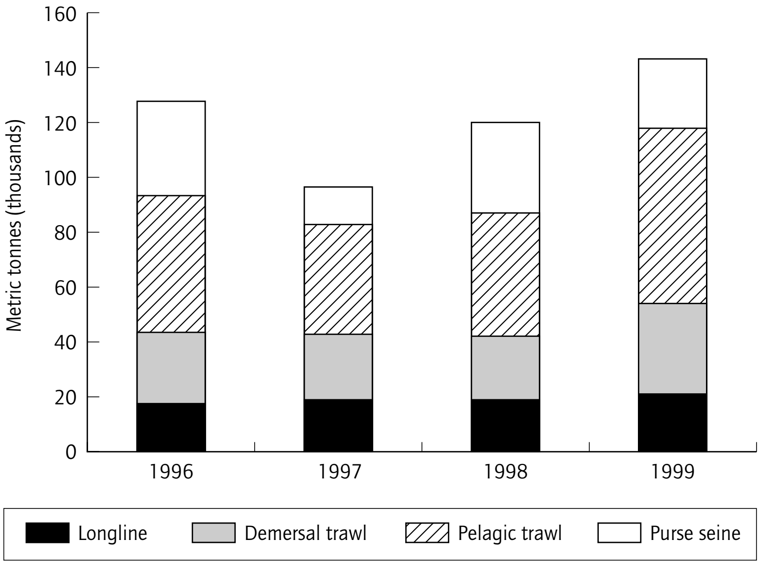

Fig. 5.3 Total catches (metric tonnes – thousands) by fishery, 1996–9 (hypothetical).

both fishery and total annual catches. (Note: multiple graphics within documents should use the same or very similar formats, as they often also form a visually coherent series.)

- Maximize the ink related to the data (areas, points, lines and text), which draw the eye to the data itself. Minimize the ink related to design (grids, axes, fills and other decoration – often called chartjunk). (Note: the common use of cross-hatching creates moiré effects that can visually disturb the information content of the graphic.)

Although not presented here, the often-depicted times series of money (and derived indicators) should usually use deflated and standardized units of monetary measurement rather than nominal units. For a wider appreciation of data graphics, refer to the Graphics Press series by E.R. Tufte (1987, 1990 and 1997).

5.5 CONCLUSIONS

Fisheries management faces a complex web of relationships between the environment, the ecosystem and human interventions; each is part of an overall 'natural' system, which can and should be managed with the goal of long-term sustainability. The sustainability of a fishery, in itself, is important for human welfare reasons, but not at the expense of stock (or biodiversity) deteriorations, which would result in benefit declines. Similarly, stock sustainability, in itself, is important for ecosystem reasons, the consequences of deterioration potentially having environmental effects, known or unknown, now or in the future. Information on the components of this web and the dynamics of their interactions must take a holistic approach; no one area is more relevant than another, even though the weighting and priority of some data may be higher than others.

Gathering data for resource monitoring and fisheries management is an expensive and highly complex task for which there are no single prescriptions. Fish stocks and the fisheries that depend on them are all unique because the conditions that affect them are always uniquely characterized by their physical and chemical environment, their ecosystem and the nature and extent of the human interventions on them. Information uncertainty, unreliability or inadequacy translates into inability to establish the prudent foresight that the precautionary approach demands. Nevertheless, if proper understanding of fish stocks and the appropriate application of fishery management measures are to be achieved, there are principles that can be applied to the collection and presentation of data which will inform the knowledge system upon which decisions for sustainability can be made.

The fisheries information cycle begins with the recognition of the areas in the fishery system over which we can exert some influence. Fisheries management controls human intervention, the fishery, but also links to the prevention of harmful man-made environmental disturbances. It is driven by policy decisions and management objectives. These must be clearly defined both to enable managers to implement them, and also to have methods to assess whether decisions have worked, and what to do about it if they have not. Fishery performance indicators are thus defined by the objectives of policy. Stock sustainability is quite clearly key to the whole system and may require a range of performance indicators in understanding how this is to be achieved. Assuming targets can be established for performance indicators (and some, particularly sociocultural, may be very difficult) the observable data variables can be defined, together with a wide range of data characteristics, from prioritization to standardization. Once data variables are defined (*why* and *what*) it becomes a practical task to collect them in a manner that is amenable to statistical and other analytical procedures (*how*). This is usually accomplished through the establishment of a data collection strategy or through strategies that take into account various operational constraints and likelihoods, which then indicate the methods that need to be applied, including the temporal and spatial limits that satisfy statistical evaluation. Introduction of the data collection system that implements the methods will involve a number of actions including the design of databases to hold the information; legal, institutional and budgetary planning; training in, and monitoring and administration of the system, including mechanisms for system appraisal that may feed back and influence any level of the information cycle.

Integrated fisheries information management systems, through which all information domains are properly represented and their data made available for analysis, are the key to the present and future ability to undertake sustainable fisheries. In the past, attention has been heavily weighted to the biology and population dynamics of fish stocks for good reasons; it was the essential start. However, if fisheries are to be managed at or near the global limits now becoming recognized, it is crucial that all information domains enter into consideration, in particular the human elements that characterize a fishery, both now and under some future sustainable arrangement.

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Part 2

Stock Assessment

6 Surplus Production Models

JON T. SCHNUTE AND LAURA J. RICHARDS

6.1 INTRODUCTION

A sustainable fishery requires a productive fish stock. On an evolutionary scale, most stocks have adapted to a long history of changing circumstances. Theoretically, this implies an ability to respond to sudden new causes of mortality, such as that imposed by a fishery. If the population responds with additional productivity to compensate for fishing mortality, then this increase can be called 'surplus' production.

A finite carrying capacity represents one possible mechanism for surplus production. According to this scenario, the biomass expands to a level that can be sustained by the environment. If the biomass becomes larger, then competition for scarce resources increases overall mortality and causes the biomass to contract. Fishing imposes mortality that reduces the biomass below carrying capacity. At this lower level, reduced competition among surviving animals and greater relative abundance of resources allows the population to respond with surplus production. Theoretically, the biomass can be held indefinitely at a level below carrying capacity, and the fishery can continue to operate on the corresponding surplus production.

Essentially, every assessment model of a sustainable fishery involves the concept of surplus production, although models vary in their detailed descriptions of population dynamics. Early production models used differential equations to describe a single stock restricted by a finite carrying capacity. These represent population growth by a process analogous to the growth of individual animals. Thus, the collective biomass has an asymptotic capacity similar mathematically to the asymptotic size of a single fish. Our analysis in this chapter makes this analogy precise through a differential equation that links historical growth models with the production models of Schaefer (1954, 1957), Pella and Tomlinson (1969) and Fox (1970, 1975). Smith (Chapter 4, this volume) provides an historical perspective on the development of surplus production models.

The modern approach extends these classical models by including more biological detail, such as explicit assumptions about recruitment, mortality and growth (Sparre and Hart, Chapter 13, this volume). The emphasis has shifted from differential to difference equations that relate more obviously to the data available from most fisheries. All models, whether classical or modern, deal with three essential questions:

1 What processes govern the population dynamics of fished stocks?

2 Given these processes, what is a 'safe' harvest level that produces an 'optimal' catch while maintaining a 'healthy' stock?

3 What do the available data reveal about the assumptions in question 1 and the answers to question 2?

Question 2 requires defining certain key criteria encapsulated by vague adjectives: safe, optimal and healthy. One classical approach comes from the carrying capacity scenario described above. A closed fishery produces no catch, and the stock maintains itself at carrying capacity. By contrast, a very intense fishery drives the population to extinction, leading eventually to zero catch. Theoretically, some intermediate level of fishing mortality should give the maximum sustainable yield (MSY) under equilibrium conditions. In the Schaefer model, for example, the equilibrium relationship between yield and biomass has a parabolic form, where maximum yield occurs when the biomass is held at 50% of carrying capacity. Thus, the model suggests this level of abundance as a reference point for a healthy stock size associated with an optimal catch. Both classical and modern models can be used to define a variety of similar reference points, depending on goals set for the fishery and the marine ecosystem.

Mathematically, the three questions cited above correspond to three distinct phases of the analysis. First, a model must be articulated that describes the hypothetical stock dynamics. Second, model properties must be investigated to determine the effects of various fishing strategies. Third, quantities within the model must be compared with actual data to estimate reference points needed to implement the chosen strategy. In modern terminology, quantities internal to the model are called 'states' and the model itself is a 'state space model'. For example, the model might describe the dynamics of stock biomass, which is not observed directly. This hidden state variable does, however, influence various observed quantities, such as the catch or an abundance index. The available data may or may not be adequate to estimate all the hidden states, as well as fishery reference points.

Anyone wishing to pursue the history of production models can expect a fairly intense mathematical journey. A reader need only glance at the historical papers by Pella and Tomlinson (1969), Fox (1970, 1975) or Schnute (1977) to find equations in abundance. Mathematical models serve as metaphors of reality. The strength of mathematics lies in its ability to explore consequences. A few assumptions can produce an elaborate description of fish population dynamics, where mathematical results guide biological interpretation and understanding. On the other hand, mathematics is limited by its complete dependence on the assumptions, which might be wrong. Some of the models presented in this chapter have remarkable elegance, but this does not guarantee that they correctly represent nature. Given the complexity of marine ecosystems, a modeller must treat any stock assessment model with extreme scepticism directed towards assumptions that might fail. No single approach offers a panacea that applies to all situations (Sparre and Hart, Chapter 13, this volume).

We focus our discussion on two surplus production models that encapsulate classical and modern points of view. The first uses a differential equation proposed by Pella and Tomlinson (1969). We compare this framework with difference equations obtained from a more extensive age-structured analysis (Schnute and Richards 1998). These two approaches have features in common, but also significant differences. Each example gives mathematically tractable results that shed intuitive light on the inner workings of fishery models. Our comparison leads to a few results never published previously, although other aspects of the material appear in greater detail elsewhere (e.g. Quinn and Deriso 1999).

Consistent with the history of this subject, our presentation has a high technical content. For perspective, we organize most of the mathematics into tables, and focus primarily on the underlying concepts. We often omit proofs, but emphasize logical relationships between assumptions and conclusions. We regard models as tools for thought, rather than ultimate descriptions of reality. These tools can be used to the greatest advantage by understanding them in detail. Features of simple models can guide the development of more complex models. We ask readers to approach our material with a sense of adventure. Scaling a mountain to gain perspective requires a passage through numerous difficulties and lesser vistas along the route.

Equations in our summary tables follow a simple numbering system; for example, (T6.2.3) refers to equation 3 in Table 6.2. Subscripts usually indicate time or age variables, which may be discrete or continuous, depending on the context. For instance, B_t, w_a, and w_∞ denote biomass at time t,

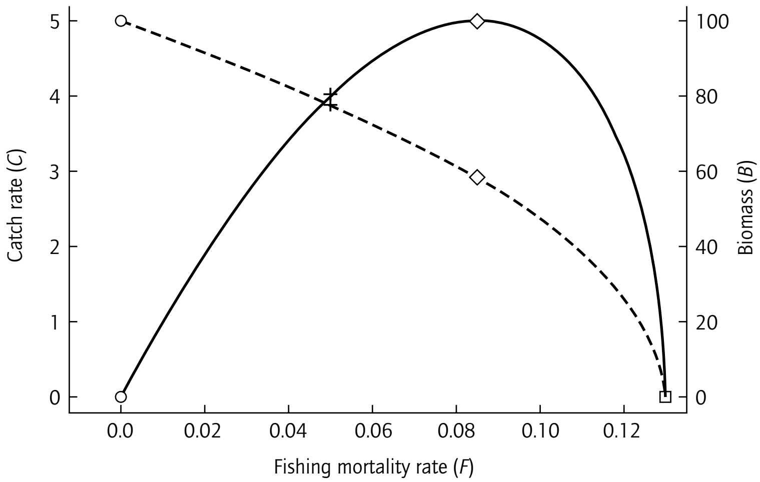

Fig. 6.1 Key concepts in surplus production models, where the equilibrium catch rate *C* (solid line) and biomass *B* (broken line) depend on the fishing mortality rate *F*. Symbols indicate the following conditions: pristine stock (○); fishery at MSY (◇); stock extinction (□); and a precautionary fishery with catch rate lower than MSY (+).

weight at age *a*, and asymptotic weight as $a \to \infty$. An asterisk indicates a value associated with stable MSY conditions. Thus, the maximum sustainable catch rate C^* occurs when the biomass B^* experiences an optimal fishing mortality rate F^*. A prime symbol denotes a value associated with pristine conditions, that is, a stable unfished stock. (Remember that 'prime' means 'pristine'.) Thus, B' is the pristine stock biomass, sometimes designated B_0 in other fishery literature. We retain the temporal meaning of the subscript 0, so that B_0 denotes the initial biomass at time $t = 0$. This may or may not be the pristine biomass; thus, the condition $B_0 = B'$ indicates that the model begins with an unfished biomass. Models describe the evolution of time-dependent states, given a vector Θ of model parameters that typically remain constant in time. Sometimes, however, the distinction between parameters and states weakens, and it becomes simpler to think of every quantity in the model as a state.

We give models two levels of interpretation. First, we emphasize the biological meaning of assumptions and corresponding results. Second, we examine each model from a systems perspective, in which some states act as controls that determine other states. For example, an effort rate E_t might alter the population biomass B_t and produce a catch rate C_t, as indicated by

$$E_t \mapsto B_t, C_t. \tag{6.1}$$

In this scenario, the biomass B_t usually acts as a hidden state that cannot be observed directly. Thus, in practical terms, (6.1) reduces to

$$E_t \mapsto C_t, \tag{6.2}$$

which translates to the more romantic statement 'Boats go out to sea and come back with fish.'

6.2 GRAPHICAL MODEL

Before developing formal mathematics, we use a simple graph to illustrate the key features of a surplus production model. Figure 6.1 portrays the long-term impact of a fishing mortality rate *F* on a stock biomass *B*. In the absence of fishing ($F = 0$), the stock maintains itself at the pristine level $B' = 100$ biomass units (e.g. tonnes), which is the natural carrying capacity. As *F* increases, *B* drops below B', and this reduced biomass leaves room for growth. The fishery harvests the resulting surplus production, generates a catch rate *C*, and maintains the biomass at level *B*. All quantities in Fig. 6.1 represent long-term conditions. Thus, the mortality rate *F* maintains the catch rate *C* by removing exactly the surplus production available from the biomass B. Conceptually, F represents the fraction of B removed per unit time to produce the catch rate $C = FB$, measured as the biomass captured per unit time.[*]

A high mortality rate can potentially drive the population to extinction. In Fig. 6.1, for example, $B = 0$ when $F = 0.13$; thus the stock cannot maintain a removal rate greater than 13% per unit time. Following Schnute and Richards (1998), we denote this critical point as $F^\dagger$. (Remember that 'dagger' means 'death' to the population, i.e. extinction.) Thus, two conditions imply a catch rate $C = 0$: no fishing ($F = 0$) or extinction fishing ($F \geq F^\dagger$). A mortality rate F between these extremes ($0 < F < F^\dagger$) produces a positive catch rate $C > 0$. In particular, the maximum sustainable catch rate $C^\star$ corresponds to an appropriate mortality rate $F^\star$. The following short table summarizes the three stock conditions identified so far, as designated by accents in the text and symbols in Fig. 6.1:

Condition	Accent	Symbol
Pristine	′	○
MSY	⋆	◇
Extinction	†	□

Suppose that time is measured in years (y) and biomass in tonnes (t). Then Fig. 6.1 implies the following reference points: $B' = 100\,\mathrm{t}$, $F^\star = 8.7\%\,\mathrm{y}^{-1}$, $B^\star = 57.8\,\mathrm{t}$, $C^\star = 5\,\mathrm{t}\,\mathrm{y}^{-1}$, and $F^\dagger = 13\%\,\mathrm{y}^{-1}$. In particular,

$$F^\star = \frac{C^\star}{B^\star} = \frac{5\,\mathrm{t}\mathrm{y}^{-1}}{57.8\,\mathrm{t}} = 8.7\%\mathrm{y}^{-1}. \tag{6.3}$$

More generally in Fig. 6.1, the fishing mortality rate F expresses the annual catch rate C as a fraction of the biomass: $F = C/B$. By comparison with equation (6.3), the additional parameter

$$\psi = \frac{C^\star}{B'} = \frac{5\,\mathrm{t}\,\mathrm{y}^{-1}}{100\,\mathrm{t}} = 5\%\,\mathrm{y}^{-1} \tag{6.4}$$

gives an overall measure of stock productivity by relating the maximum sustainable catch rate to the pristine biomass.

Figure 6.1 makes a useful topic of conversation with fishermen embarking on a new fishery. According to this scenario, the biomass can initially be reduced from 100 t to the optimal $B^\star = 57.8\,\mathrm{t}$, producing a windfall catch of 42.2 t. This might happen over two years in a fishery that takes more than 21 t per year. Unfortunately, such a high mortality rate, much greater than $F^\dagger$, would rapidly drive the stock to extinction. After the initial windfall, the catch must be curtailed to a much slower rate near 5 t per year. Fishermen who have become dependent on four times this rate may suffer economic ruin. Furthermore, the figure represents a population that declines more rapidly as the mortality F approaches the critical $F^\dagger$. In the uncertain world of fishery management, it might be dangerous to adopt even the theoretically optimal catch rate $C^\star = 5\,\mathrm{t}\,\mathrm{y}^{-1}$. A more precautionary approach (marked '+' in Fig. 6.1) could be achieved with $B = 78\,\mathrm{t}$ and $F = 5.1\%\,\mathrm{y}^{-1}$, producing an approximate catch rate $C = 4\,\mathrm{t}\,\mathrm{y}^{-1}$. Such a policy would reduce the risk of extinction by maintaining the biomass at a higher, more robust level.

The graphical model in Fig. 6.1 has two components, a dome-shaped catch curve and a descending biomass curve. A mathematical model that represents these components must include at least three parameters: a maximum level for the biomass (B'), a scale parameter for the catch relative to the biomass ($\psi = C^\star/B'$), and a location parameter that determines the position of the dome ($F^\star$). For example, a relatively high $F^\star$ in Fig. 6.1 gives a dome shifted towards the right end of the catch curve. Any equivalent set of three parameters can be used as surrogates for (B', ψ, $F^\star$). For example, our first model includes B' explicitly, but captures ψ and $F^\star$ through two other parameters labelled α

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[*] In some non-equilibrium contexts, this relationship between the instantaneous rates C and F implies an accumulated yield $Y = (1 - e^{-F\tau})B$ during the time interval τ. Models presented later in the paper clarify such alternative formulations. For now, experienced readers can take note of the limit $C = \lim_{\tau \to 0} Y/\tau = FB$.

and γ. Mathematical analysis of the model gives formulas for (ψ, F^*) in terms of (α, γ). Keen readers can sneak a glance ahead to equations (T6.3.2) and (T6.3.7) in Table 6.3. Furthermore, for those who want an even better preview of things to come, equations (6.12) and (T6.1.6) define the curves $C(F)$ and $B(F)$ portrayed in Fig. 6.1. How do the simple ideas in the graphical model suggest such prolific mathematics? Read on.

6.3 CLASSICAL DIFFERENTIAL EQUATIONS (MODEL 1)

The scenario in Fig. 6.1 represents equilibrium conditions achieved after a sustained fishing mortality rate F. Because actual fisheries take place on populations in flux, an appropriate mathematical model must also capture the system dynamics. Theoretically, a stock with a carrying capacity corresponds to a system in which the biomass B_t tends to move towards a particular state B'. Differential equations can easily be formulated to capture this behaviour. For example, suppose that the biomass B_t follows the differential equation $dB_t/dt = f(B_t)$, where

$$\begin{cases} f(B) > 0 \text{ if } B < B' \\ f(B) < 0 \text{ if } B > B' \end{cases}. \tag{6.5}$$

Then B_t increases or decreases, respectively, if B_t lies below or above B'. Either way, B_t moves towards B', which acts as a stable equilibrium point that can be interpreted as the carrying capacity.

Production model 1, defined by equations (T6.1.2)–(T6.1.5) in Table 6.1, includes a parameter B' that plays this role. Given an effort rate E_t, the model sequentially defines five states: the fishing mortality rate F_t, biomass B_t, catch rate C_t, cumulative yield Y_t, and abundance index I_t. In symbols,

$$E_t \mapsto F_t, B_t, C_t, Y_t, I_t. \tag{6.6}$$

Figure 6.2 represents model 1 as a flow diagram, in which model equations define linkages among state variables. From a systems perspective, the reader can confirm that each equation (T6.1.2)–(T6.1.5) in the table plays the corresponding role shown in the figure.

Table 6.1 Production model 1, based on a differential equation proposed by Pella and Tomlinson (1969).

Model

$$\Theta = (B', \alpha, \gamma, q_1, q_2) \tag{T6.1.1}$$

$$F_t = q_1 E_t \tag{T6.1.2}$$

$$\frac{dB_t}{dt} = \frac{\alpha B_t}{\gamma}\left[1 - \left(\frac{B_t}{B'}\right)^{\gamma}\right] - F_t B_t \tag{T6.1.3}$$

$$C_t = \frac{dY_t}{dt} = F_t B_t \tag{T6.1.4}$$

$$I_t = q_2 B_t \tag{T6.1.5}$$

Second formulation

$$B_\infty(F) = \left(\frac{\alpha - \gamma F}{\alpha}\right)^{1/\gamma} B' \tag{T6.1.6}$$

$$\frac{dB_t}{dt} = \frac{(\alpha - \gamma F_t) B_t}{\gamma}\left[1 - \left(\frac{B_t}{B_\infty(F_t)}\right)^{\gamma}\right] \tag{T6.1.7}$$

Solution for time step $[t, t+\tau]$ with constant F_t

$$B_{t+\tau} = B'\left\{\frac{\alpha}{\alpha - \gamma F_t} - \left[\frac{\alpha}{\alpha - \gamma F_t} - \left(\frac{B_t}{B'}\right)^{-\gamma}\right] e^{-(\alpha - \gamma F_t)\tau}\right\}^{-1/\gamma} \tag{T6.1.8}$$

$$B_{t+\tau} = B_\infty(F_t)\left\{1 - \left[1 - \left(\frac{B_t}{B_\infty(F_t)}\right)^{-\gamma}\right] e^{-(\alpha - \gamma F_t)\tau}\right\}^{-1/\gamma} \tag{T6.1.9}$$

Biologically, (T6.1.2) assumes that the rates of effort and fishing mortality are proportional, with proportionality constant q_1. The differential equation (T6.1.3) represents a variation of that proposed by Pella and Tomlinson (1969), where our version uses parameters more appropriate for the biological description here. The right side of (T6.1.3) has the properties (6.5) when $F_t = 0$. Consequently, B' corresponds to the stock's carrying capacity in the absence of fishing. When $F_t > 0$, (T6.1.3) includes a biomass loss proportional to the fishing mortality rate $(-F_t B_t)$. Assumption (T6.1.4) actually contains two equations. The first defines the catch rate C_t as the derivative of cumulative yield Y_t, and the second equates this rate to the loss of biomass due to

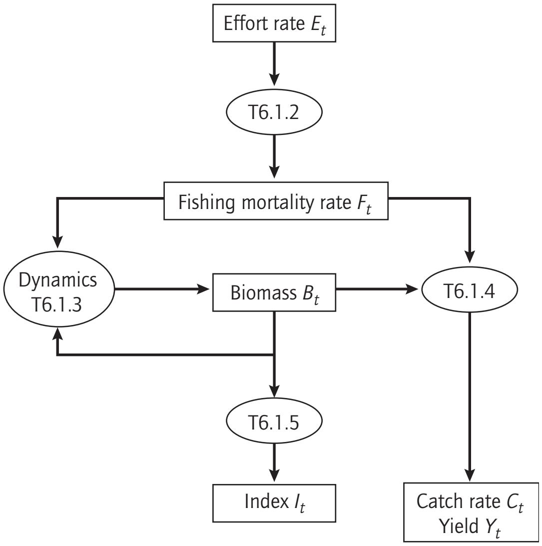

Fig. 6.2 Flow diagram for model 1 in Table 6.1, showing the state variables calculated from each equation (T6.1.2)–(T6.1.5).

fishing in (T6.1.3). Finally, (T6.1.5) assumes that the index I_t is proportional to the biomass, with a second proportionality constant q_2.

The vector Θ in (T6.1.1) includes five parameters: the carrying capacity B', two additional parameters (α, γ) for the differential equation (T6.1.3), and the two proportionality constants (q_1, q_2). We assume that $\alpha > 0$, where this parameter governs the biomass growth rate particularly at small stock sizes ($B \approx 0$). As illustrated below, γ determines the overall shape of the catch curve, where $\gamma > -1$. Almost every equation in this chapter has a valid limit as $\gamma \to 0$, although we generally do not present the explicit analytical form.

Combining (T6.1.2) and (T6.1.4) gives the proportionality

$$U_t = \frac{C_t}{E_t} = q_1 B_t, \tag{6.7}$$

where the catch per unit effort (CPUE) U_t acts as an index of the biomass. Model 1 extends this concept in (T6.1.5) by allowing another index I_t, which might be different from U_t. Such an index might come from a fishery independent survey or even from alternative compilations of catch and effort data. For example, a CPUE index might be obtained from the median catch to effort ratio taken from many individual tows (Richards and Schnute 1992). This index would not, in general, be the same as the ratio of total catch to total effort from all tows combined.

A model based on differential equations necessarily involves instantaneous quantities for the continuous time variable t. The dimensional units of each state variable and parameter provide a useful guide to model interpretation. For example, if effort is measured in boat-days and t is measured in days, then the effort rate E_t would have the units of boat-days per day, or simply boats. Conceptually, E_t denotes the quantity of gear operating at time t. In (T6.1.3), F_t represents the fraction of the biomass B_t removed by the fishery per unit time. Thus, F_t must have the units day^{-1} so that the term $F_t B_t$ agrees dimensionally with the derivative dB_t/dt. From this, it follows that q_1 in (T6.1.2) must have units (boat-day)$^{-1}$. In effect, q_1 gives the fraction of biomass removed per boat-day of fishing.

Similarly, C_t in (T6.1.4) corresponds to the rate of biomass removal measured, for example, in kg per day. Rates cancel in the ratio (6.7), so that U_t has the conventional units of kg per boat-day. We include the cumulative yield Y_t to represent the catch removed over a time period. Thus, from (T6.1.4) the yield during the time interval $[t, t+\tau]$ is

$$Y(t+\tau) - Y(t) = \tau \overline{C}_t = \int_t^{t+\tau} C_t \, dt, \tag{6.8}$$

where the integral can also be used to calculate the mean catch rate $\overline{C}_t$.

Analytical properties of the differential equation (T6.1.3) reveal important features for its biological interpretation. With a fixed fishing mortality F, the asymptotic biomass $B_\infty(F)$ can be computed explicitly as (T6.1.6). As F increases from 0, the formula shows that $B_\infty(F)$ declines steadily from the carrying capacity $B' = B_\infty(0)$. For $\gamma > 0$, the population is driven to extinction when $F = F^\dagger = \alpha/\gamma$; thus, $B_\infty(\alpha/\gamma) = 0$. If $\gamma \le 0$, the population can theoretically sustain arbitrarily high harvest rates, and $B_\infty(F)$ represents a steadily declining function for all $F > 0$.

Biologically, $B_\infty(F)$ represents a carrying capacity that is adjusted downward from B' by the fishing mortality F. The original differential equation (T6.1.3) can be proved equivalent to the second formulation (T6.1.7). Compare (T6.1.3) when $F_t = 0$ with (T6.1.7) when $F_t > 0$ to see that fishing pressure effectively replaces α by $\alpha - \gamma F_t$ and B' by $B_\infty(F_t)$.

Equation (T6.1.3) also has the convenient feature that it can be solved analytically if F_t is held constant. For example, consider a time step $[t, t + \tau]$ during which the fishing mortality is held at its initial value F_t. If the biomass starts at B_t, then the final value $B_{t+\tau}$ is given by (T6.1.8). The slightly more intuitive solution (T6.1.9) comes from the second formulation (T6.1.7). Biologically, (T6.1.9) says that $B_{t+\tau}$ represents a movement from the initial state B_t towards the asymptotic value $B_\infty(F_t)$.

As we mentioned in the introduction, working through these details can be a rather intense mathematical journey. Conceptually, however, model (T6.1.2)–(T6.1.5) has just a few key properties that concern us. First, it describes a fishery in which the effort influences stock abundance, catch, and other state variables, as represented by (6.6) and Fig. 6.2. Second, it captures the concept of an inherent carrying capacity B'. Third, it has convenient analytical properties that enable us to explore its global behaviour, such as a reduced carrying capacity under fishing pressure. Fourth, it represents a fascinating piece of intellectual history. At the time these methods were developed, differential equations played a common role in population analysis. Computers were not as readily available then as now, and analytical results greatly assisted the understanding of model behaviour. In fact, exact solutions always serve as valuable tools for thought.

6.4 SPECIAL CASES (MODEL 1)

Fisheries do not generally produce useful instantaneous data, such as the catch rate C_t. Typically, the data only become meaningful when accumulated across time to give, say, the total annual catch from the yield calculation (6.8) with $\tau = 1$ yr. Thus, application of model 1 depends on a method of integration to a meaningful time-scale for the data. For example, if F_t remains constant during the time interval $[t, t + \tau]$, then (6.8) and (T6.1.4) imply that

$$Y(t+\tau) - Y(t) = \tau\overline{C}_t = F_t\int_t^{t+\tau} B_t dt = \tau F_t \overline{B}_t. \qquad (6.9)$$

Thus, the cumulative yield and mean catch over this interval depend directly on the mean biomass $\overline{B}_t$. Unfortunately, the integral of B_t in (6.9) cannot be computed analytically from (T6.1.8) or (T6.1.9) for general values of γ.

Table 6.2 shows model results for three particular choices of γ, where $\overline{B}_t$ in (6.9) can be computed explicitly if $\gamma = -1$ or 1. We also show limiting values of the analysis as $\gamma \to 0$, although $\overline{B}_t$ cannot be represented analytically in this case. Historically, Schaefer (1957) and Fox (1970) used models corresponding to $\gamma = 1$ and $\gamma = 0$, respectively. We show below that the case $\gamma = -1$ has a strong connection to the von Bertalanffy growth model, although it has anomalous properties as a fishery model. Jobling (Chapter 5, Volume 1) discusses the application of the von Bertalanffy model to the growth of individual fish.

Formulas in Table 6.2 have somewhat more obvious biological interpretations than their counterparts in Table 6.1. For example, (T6.2.1) and (T6.2.4) show clearly that $B_\infty(F) \to 0$ as $F \to \infty$ when $\gamma = -1$ or 0; however, when $\gamma = 1$, (T6.2.6) implies population extinction at the critical fishing mortality level $F^\dagger = \alpha$. The results (T6.2.2), (T6.2.5) and (T6.2.7) illustrate that $B_{t+\tau} \to B_\infty(F_t)$ as the time step $\tau \to \infty$. The formulas (T6.2.3) and (T6.2.8) for mean biomass $\overline{B}_t$ show a tendency towards $B_\infty(F_t)$, with a correction related to the change from B_t to $B_{t+\tau}$.

As mentioned earlier, mean values $\overline{B}_t$ relate more directly to fishery data than instantaneous values B_t. Schnute (1977) investigated this problem when $\gamma = 1$ and arrived at a formula similar to (T6.2.9). Consider a fishery with regular time steps of length τ (e.g. $\tau = 1$ yr). Suppose that the effort rate

Table 6.2 Three special cases of model 1 in Table 6.1, with constant fishing mortality F_t during the time interval $[t, t+\tau]$.

Von Bertalanffy: $\gamma = -1$

$$B_\infty(F) = \left(1 + \frac{F}{\alpha}\right)^{-1} B' \tag{T6.2.1}$$

$$B_{t+\tau} = B_\infty(F_t) + [B_t - B_\infty(F_t)]e^{-(\alpha+F_t)\tau} \tag{T6.2.2}$$

$$\overline{B}_t = B_\infty(F_t)\left[1 - \frac{B_{t+\tau} - B_t}{\alpha\tau B'}\right] \tag{T6.2.3}$$

Gompertz: $\gamma = 0$

$$B_\infty(F) = e^{-F/\alpha}B' \tag{T6.2.4}$$

$$B_{t+\tau} = B_\infty(F_t)\left[\frac{B_t}{B_\infty F_t}\right]^{e^{-\alpha\tau}} \tag{T6.2.5}$$

Logistic: $\gamma = 1$

$$B_\infty(F) = \left(1 - \frac{F}{\alpha}\right)B' \tag{T6.2.6}$$

$$B_{t+\tau} = B_\infty(F_t)\frac{B_t}{B_t + [B_\infty(F_t) - B_t]e^{-(\alpha - F_t)\tau}} \tag{T6.2.7}$$

$$\overline{B}_t = B_\infty(F_t) - \frac{B'}{\alpha\tau}\log\left(\frac{B_{t+\tau}}{B_t}\right) \tag{T6.2.8}$$

$$\frac{\exp\left(\frac{\alpha\tau\overline{B}_{t+\tau}}{B'}\right) - 1}{\exp\left(\frac{\alpha\tau\overline{B}_t}{B'}\right) - 1} = \frac{\alpha - F_t}{\alpha - F_{t+\tau}}\,\frac{e^{(\alpha - F_{t+\tau})\tau} - 1}{e^{(\alpha - F_t)\tau} - 1}\exp\left[\left(\alpha - F_t - \frac{\alpha\overline{B}_t}{B'}\right)\tau\right] \tag{T6.2.9}$$

E_t remains constant during the interval starting at time t. Then (T6.1.2) and (6.7) imply that

$$F_t = q_1 E_t = q_1 \overline{E}_t, \tag{6.10}$$

$$\overline{B}_t = \frac{\overline{C}_t}{q_1\overline{E}_t} = \frac{1}{q_1}\overline{U}_t. \tag{6.11}$$

Substituting (6.10)–(6.11) into (T6.2.9) gives an equation that involves only the fixed time step τ, three parameters (B', α, q_1), and the observed mean data ($\overline{E}_t$, $\overline{U}_t$). Thus, when $\gamma = 1$, model 1 can be converted to a difference equation that relates directly to data collected from the fishery. Keen readers can glance ahead to equation (6.24).

For the mathematical adventurer, we briefly sketch the proof of (T6.2.9). Eliminate $B_{t+\tau}$ from equations (T6.2.7) and (T6.2.8) to obtain a single equation that relates B_t and $\overline{B}_t$. Solve for B_t as a function of $\overline{B}_t$. This implies a similar expression for $B_{t+\tau}$ as a function of $\overline{B}_{t+\tau}$. Substitute these computed values of B_t and $B_{t+\tau}$ into the right side of (T6.2.8). The result, which involves only means $\overline{B}_t$ and $\overline{B}_{t+\tau}$, reduces to (T6.2.9).

6.5 EQUILIBRIUM (MODEL 1)

Theoretically, the equilibrium version of a dynamic model gives projections for long-term yield in relation to a sustained harvest rate. In model 1, a constant effort rate E corresponds to a constant fishing mortality rate $F = q_1 E$. This level of fishing pressure eventually gives a stable biomass $B = B_\infty(F)$ and produces the catch rate

$$C = F\left(1 - \frac{\gamma F}{\alpha}\right)^{1/\gamma} B' = \frac{\alpha B}{\gamma}\left[1 - \left(\frac{B}{B'}\right)^{\gamma}\right]. \tag{6.12}$$

Thus, C can be computed from either equilibrium value F or B. As can be seen from (T6.1.6), the first equality in (6.12) follows from the equilibrium version of (T6.1.4): $C = FB = FB_\infty(F)$. The second equality comes directly from (T6.1.3)–(T6.1.4) at equilibrium.

This equilibrium analysis brings us full circle back to the graphical model in Fig. 6.1. As indicated in the preview, (6.12) defines the dome-shaped catch curve $C(F)$. Similarly, (T6.1.6) gives the descending biomass curve $B(F)$, where we now use the notation $B_\infty(F)$ to denote the asymptotic biomass associated with a sustained fishing mortality F. Table 6.3 lists analytical expressions for various reference points in terms of the model parameters (T6.1.1). These results suggest potential alternative model parameters. For example, (T6.3.7) implies that

$$\alpha = (1+\gamma)^{(1+\gamma)/\gamma}\psi; \tag{6.13}$$

consequently, $\psi = C^\star/B'$ can replace α in (T6.1.1). We have already seen in the discussion of Fig. 6.1 that an equilibrium analysis requires at least three parameters (B', ψ, $F^\star$). Remarkably, equivalent parameters (B', ψ, γ) govern the full population dynamics in the differential equation (T6.1.3) of model 1, where

$$F^\star = (1+\gamma)^{1/\gamma}\psi. \tag{6.14}$$

The proof of (6.14) follows from (T6.3.2) and (6.13).

Figure 6.3 illustrates the roles of ψ and γ in model 1. Curves in Fig. 6.3(a) portray the equilibrium catch $C(F)$ for various values γ, where the

Table 6.3 Various reference points for model 1 in Table 6.1, expressed as functions of model parameters (T6.1.1) with $\gamma > -1$.

$$E^* = \frac{\alpha}{q_1(1+\gamma)} \tag{T6.3.1}$$

$$F^* = \frac{\alpha}{1+\gamma} \tag{T6.3.2}$$

$$F^\dagger = \begin{cases} \dfrac{\alpha}{\gamma} & \text{if} \quad \gamma > 0 \\ \infty & \text{if} \quad \gamma \le 0 \end{cases} \tag{T6.3.3}$$

$$B^* = (1+\gamma)^{-1/\gamma}B' \tag{T6.3.4}$$

$$C^* = \alpha(1+\gamma)^{-(1+\gamma)/\gamma}B' \tag{T6.3.5}$$

$$I^* = q_2(1+\gamma)^{-1/\gamma}B' \tag{T6.3.6}$$

$$\psi = \frac{C^*}{B'} = \alpha(1+\gamma)^{-(1+\gamma)/\gamma} \tag{T6.3.7}$$

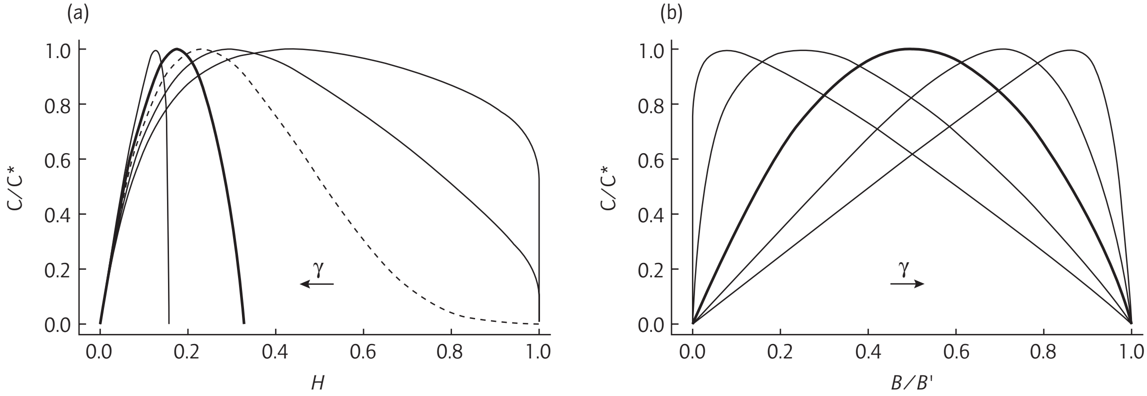

Fig. 6.3 Relative catch rate $C/C^\star$ for the equilibrium version of model 1 as a function of: (panel (a)) harvest rate H in (6.15); (panel (b)) relative biomass B/B'. Panels show catch curves for various values of γ: (a) –0.7, –0.4, 0, 1, 5; (b) –0.9, –0.5, 1, 5, 20. Arrows indicate the direction of increasing γ. Heavy solid and broken curves indicate special cases $\gamma = 1$ and $\gamma = 0$, respectively. Panel (a) assumes that $\tau\psi = \tau C^\star/B' = 0.1$, although panel (b) is independent of ψ.

vertical axis is scaled relative to C^* and the horizontal axis uses the scaling

$$H = 1 - e^{-F\tau}. \qquad (6.15)$$

Conceptually, H represents a harvest removal fraction during the time interval τ in the absence of stock production. Each curve in Fig. 6.3(a) has slope $(\tau\psi)^{-1}$ at the origin. We have assigned this slope the value 10 (e.g. $\psi = 0.1\ \text{yr}^{-1}$ with $\tau = 1$ yr). A lower slope (i.e. higher $\tau\psi$) would shift curve modes further to the right. Figure 6.3(b) similarly represents equilibrium curves $C(B)$ in (6.12) for various γ. Vertical and horizontal axes are scaled relative to C^* and B', respectively.

Biologically, the dimensionless quantity $\tau\psi$ represents the fraction of pristine biomass that can be caught during time τ under MSY conditions. This would be large for stocks with a high potential for harvest, corresponding to a small slope $(\tau\psi)^{-1}$ at the origin in Fig. 6.3(a). Similarly, low values γ correspond to highly productive stocks, for which the maximum sustainable catch rate is taken at a high harvest rate (panel (a)) on a biomass that is small relative to B' (panel (b)). Large values γ indicate weakly productive stocks, where MSY is achieved with a low harvest rate on a biomass near B'. The case $\gamma = 1$ represents an intermediate scenario, in which MSY corresponds to a biomass B^* that is half the pristine biomass B' (panel (b), heavy line).

Figure 6.3(b) suggests two anomalous extremes. From (T6.3.2) and (T6.3.4), the case $\gamma = -1$ theoretically corresponds to a stock with $F^* = \infty$ and $B^* = 0$. Geometrically, as $\gamma \to -1$, curves in Fig. 6.3(b) shift left until the right-hand limb becomes a straight line from the upper left to the lower right. Similarly, as $\gamma \to \infty$, the curves shift right until the left-hand limb becomes a straight line from the lower left to the upper right. In this case, (6.14) and (T6.3.4) imply that $F^* = \psi = C^*/B'$ and $B^* = B'$.

Most of the results derived for model 1 follow from the two key assumptions (T6.1.3)–(T6.1.4), where biomass dynamics respond to an intrinsic carrying capacity B' and an external fishing mortality F. Mathematical logic creates a fascinating biological metaphor. According to this theory, a healthy fishery typically operates on a stock well below the pristine biomass. For example, in the Schaefer case ($\gamma = 1$), a new fishery theoretically could begin by taking half the available biomass ($B' - B^* = B'/2$). After this, however, the stock's harvest potential would restrict the annual catch to $\tau C^* = \tau\psi B'$, usually much less than $B'/2$ when $\tau = 1$ yr. As mentioned in the discussion of Fig. 6.1, fishermen might buy gear and enter the fishery at a time when fish are abundant, with little evidence of a low sustainable harvest potential. Excessive investment seems almost inevitable without strong measures to detect and implement realistic limits during the early phases of fishery development.

The general public, with memories that 'you could once walk across the water on the backs of the fish', may have difficulty with the carrying capacity argument. For example, why would a bank account produce a higher interest rate just because it contains less money? The sceptical modeller does well to examine alternative explanations carefully. Many things can go wrong with model 1. Environmental influences may cause the carrying capacity B' to change randomly or systematically in time. If so, equilibrium analyses could become meaningless. Furthermore, real populations could be subject to depensation, in which the population becomes extinct after dropping below some threshold biomass level (Myers, Chapter 6, Volume 1). The differential equation (T6.1.3) does not allow this possibility, because the growth rate dB/dt increases steadily as $B \to 0$.

6.6 GROWTH MODELS

Fish growth models provide a conceptual link between model 1 and an extended framework that includes more biological detail in the population dynamics. Table 6.4 shows the familiar von Bertalanffy growth model (T6.4.1) for weight w_a at age a (see also Jobling, Chapter 5, Volume 1). The curve extrapolates forward to an asymptotic size w_∞ as $a \to \infty$ and backward to size 0 at theoretical age a_0. This model implies that successive weights at regular age intervals τ, e.g. $\tau = 1$ yr, lie on a straight line (T6.4.2) with intercept λ and slope κ. Mathematically, (T6.4.2) can be considered a first-order difference equation. Given an initial weight w_r at recruitment age r, this equation has the analytical solution (T6.4.3). Thus, model (T6.4.1) with parameters $\Theta = (w_\infty, K, a_0)$ is equivalent to (T6.4.3) with parameters $\Theta = (w_r, \kappa, \lambda)$, where (T6.4.4) shows the parametric relationships.

Table 6.5 extends the growth law in Table 6.4 by adding a transformation parameter γ. Equations (T6.5.1)–(T6.5.3) show three equivalent formulations, where (T6.5.7) illustrates the parametric relationships. In particular, the extended model reduces to the von Bertalanffy model in Table 6.4 when $\gamma = -1$. Furthermore, the extended model satisfies the differential equation (T6.5.4) and the difference equations (T6.5.5)–(T6.5.6). Equations in Table 6.5, except those involving λ, have mathematical limits as $\gamma \to 0$.

Table 6.4 Two formulations of a simple growth model.

Von Bertalanffy: $\Theta = (w_\infty, K, a_0)$

$$w_a = w_\infty[1 - e^{-K(a-a_0)}] \tag{T6.4.1}$$

Brody: $\Theta = (w_r, \kappa, \lambda)$ with given τ

$$w_{a+\tau} = \lambda + \kappa w_a \tag{T6.4.2}$$

$$w_a = \begin{cases} \dfrac{\lambda}{1-\kappa} + \left(w_r - \dfrac{\lambda}{1-\kappa}\right)\kappa^{(a-r)/\tau}, & \kappa \neq 1 \\ w_r + \dfrac{a-r}{\tau}\lambda, & \kappa = 1 \end{cases} \tag{T6.4.3}$$

Parametric relationships

$$w_r = w_\infty[1 - e^{-K(r-a_0)}],\quad \kappa = e^{-K\tau},\quad \lambda = (1 - e^{-K\tau})w_\infty \tag{T6.4.4}$$

Table 6.5 Three formulations of a growth model that generalizes the model in Table 6.4.

Model

$$w_a = w_\infty[1 + \gamma e^{-K(a-a_0)}]^{-1/\gamma};\qquad \Theta = (w_\infty, K, a_0, \gamma) \tag{T6.5.1}$$

$$w_a = w_\infty\left\{1 - \left[1 - \left(\frac{w_r}{w_\infty}\right)^{-\gamma}\right]e^{-K(a-r)}\right\}^{-1/\gamma};\qquad \Theta = (w_r, w_\infty, K, \gamma) \tag{T6.5.2}$$

$$w_a = \left[\frac{\lambda}{1-\kappa} + \left(w_r^{-\gamma} - \frac{\lambda}{1-\kappa}\right)\kappa^{(a-r)/\tau}\right]^{-1/\gamma};\qquad \Theta = (w_r, \kappa, \lambda, \gamma) \tag{T6.5.3}$$

Differential and difference equations

$$\frac{dw_a}{da} = \frac{Kw_a}{\gamma}\left[1 - \left(\frac{w_a}{w_\infty}\right)^{\gamma}\right] \tag{T6.5.4}$$

$$w_{a+\tau}^{-\gamma} = (1-\kappa)w_\infty^{-\gamma} + \kappa w_a^{-\gamma} \tag{T6.5.5}$$

$$w_{a+\tau}^{-\gamma} = \lambda + \kappa w_a^{-\gamma} \tag{T6.5.6}$$

Parametric relationships

$$w_r = w_\infty[1 + \gamma e^{-K(r-a_0)}]^{-1/\gamma},\quad \kappa = e^{-K\tau},\quad \lambda = (1 - e^{-K\tau})w_\infty^{-\gamma} \tag{T6.5.7}$$

This quick tour through growth models, using somewhat unconventional notation, allows us to portray model 1 in a new light. Formally, the biomass dynamic equation (T6.1.7) and the growth differential equation (T6.5.4) are identical, given the notational changes

$$t \to a,\quad B_t \to w_a,\quad B_\infty(F_t) \to w_\infty,\quad \alpha - \gamma F_t \to K.$$

Similarly, the solution (T6.1.9) transforms into the growth model (T6.5.2), given the changes

$$t \to r,\quad \tau \to a - r,\quad t + \tau \to a,\quad B \to w,$$
$$B_\infty(F_t) \to w_\infty,\quad \alpha - \gamma F_t \to K.$$

Thus, as mentioned in the introduction, a precise analogy exists between population growth towards carrying capacity and individual growth to an asymptotic size. Model 1 suddenly appears as an old friend, seen elsewhere in a different disguise. For this reason, we associated particular choices of γ in Table 6.2 with names taken from the literature on growth models. We included the anomalous case $\gamma = -1$ for the connection with von Bertalanffy growth.

The Brody line (T6.4.2) lies behind the Ford–Walford method of estimating w_∞ and κ (Jobling, Chapter 5, Volume 1). It also plays a significant role in formulating our next model. This result takes a similar form (T6.5.6) in the extended growth model, where $-\gamma$ specifies an exponential transformation to linearize the relationship between w_a and $w_{a+\tau}$.

6.7 MODERN DIFFERENCE EQUATIONS (MODEL 2)

Production model 2, defined in Table 6.6 by (T6.6.2)–(T6.6.9), expresses a more complex biomass dynamics than model 1. Mathematically, these eight equations sequentially update eight state variables: recruitment biomass R_t, total biomass B_t, mean weight W_t, fishing mortality F_t, harvest fraction H_t, catch biomass C_t, spawning biomass S_t, and biomass index I_t. From a systems perspective, fishing effort E_t acts as a control:

$$E_t \mapsto F_t, H_t, C_t, S_t, I_t, R_t, B_t, W_t. \tag{6.16}$$

Table 6.6 Production model 2, based on difference equations derived by Schnute and Richards (1998) from a catch-age model.

$$\Theta = (\alpha, \beta, \gamma, \delta, w_r, \kappa, \lambda, q_1, q_2) \tag{T6.6.1}$$

$$R_t = \alpha S_{t-r}(1 - \beta\gamma S_{t-r})^{1/\gamma} \tag{T6.6.2}$$

$$B_t = R_t + \frac{\lambda + \kappa W_{t-1}}{W_{t-1}}(1-\delta)S_{t-1} \tag{T6.6.3}$$

$$W_t = B_t\left[\frac{R_t}{w_r} + (1-\delta)\frac{S_{t-1}}{W_{t-1}}\right]^{-1} \tag{T6.6.4}$$

$$F_t = q_1 E_t \tag{T6.6.5}$$

$$H_t = 1 - e^{-F_t} \tag{T6.6.6}$$

$$C_t = H_t B_t \tag{T6.6.7}$$

$$S_t = B_t - C_t \tag{T6.6.8}$$

$$I_t = q_2\left(B_t - \frac{1}{2}C_t\right) \tag{T6.6.9}$$

The flow diagram for model 2 (Fig. 6.4) shows that sequential calculation starts in (T6.6.5) and proceeds through dynamic equations that sometimes include time lags. Model 2 uses a discrete time step of length $\tau = 1$. Thus, time indices take only integer values, and the notation τ can be dropped. For simplicity, we assume that time is measured in years, although different time-scales may be appropriate for some species. Unlike model 1, states in model 2 always denote annual values. For example, C_t now refers to total catch in year t, rather than catch rate at continuous time t.

Biologically, model 2 assumes a particular functional relationship (T6.6.2) between spawning biomass S_{t-r} and recruitment biomass R_t. A time lag of r years is presumed fixed and known for the species. The model assumes a growth curve (T6.4.3) with parameters (w_r, λ, κ), where w_r denotes the weight of fish recruited at age r. The parameters λ and κ appear in the biomass update equation (T6.6.3), where the biomass B_t at the start of year t includes newly recruited biomass R_t plus biomass surviving from the previous year. The latter component comes from the spawning biomass S_{t-1} adjusted by two factors, a survival coefficient $1 - \delta$ and a growth factor

$$\frac{\lambda + \kappa W_{t-1}}{W_{t-1}}. \tag{6.17}$$

Intuitively, (6.17) comes from a population of fish with mean weight W_{t-1}, where the growth relationship (T6.4.2) produces a mean weight $\lambda + \kappa W_{t-1}$ one year later. Given the biomass B_t computed from (T6.6.3), (T6.6.4) updates the mean weight as the ratio of biomass to number of fish, where the denominator expresses population numbers as ratios of biomass to mean weight.

The remaining equations in model 2 describe the effects of fishing and indexing. As in model 1, (T6.6.5) assumes that fishing mortality is proportional to effort. This produces the harvest removal fraction H_t in (T6.6.6) and catch C_t in (T6.6.7). The spawning stock S_t consists of biomass that remains after the fishery. Finally, (T6.6.9) relates the index I_t to available biomass, assuming that the

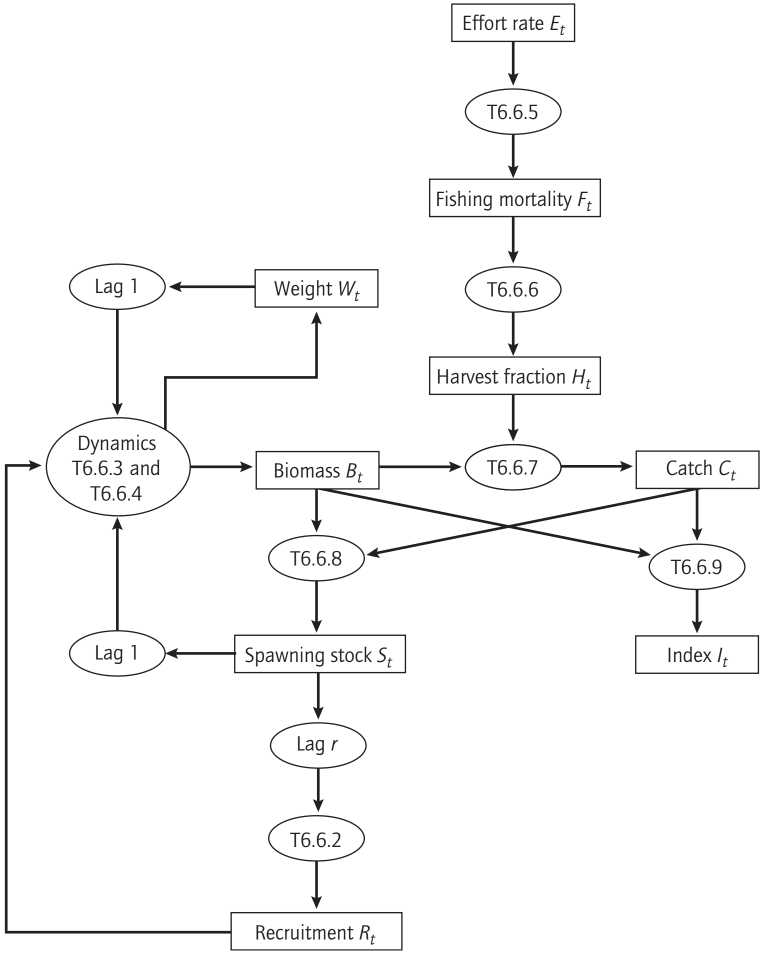

Fig. 6.4 Flow diagram for model 2 in Table 6.6, showing the state variables calculated from each equation (T6.6.2)–(T6.6.9).

index measures conditions halfway through the fishery.

Model 2 assumes a particular annual cycle of events: recruitment, fishing, spawning and natural mortality. Model variations could examine other scenarios, such as concurrent fishing and natural mortality, or natural mortality prior to spawning. The model includes nine parameters (T6.6.1): proportionality constants (q_1, q_2) similar to those in model 1, growth parameters (w_r, λ, κ), recruitment parameters (α, β, γ) for (T6.6.2), and a natural mortality fraction

$$\delta = 1 - e^{-M} \tag{6.18}$$

associated with natural mortality M. Thus, harvest and natural mortality fractions H_t and δ have similar relationships (T6.6.6) and (6.18) to fishing and natural mortality coefficients F_t and M. For small values of mortality, $H_t \approx F_t$ and $\delta \approx M$.

Model 2 incorporates features that reflect a diverse historical literature. Schnute (1985) suggested the recruitment function (T6.6.2), based on earlier work by Deriso (1980). As in model 1, the parameter γ selects from a variety of curve shapes, where a limit exists as $\gamma \to 0$. Special cases $\gamma = -1$, 0 and 1 correspond, respectively, to models proposed by Ricker (1958), Beverton and Holt (1957) and Schaefer (1954). Recruitment curves can increase indefinitely ($\gamma < -1$), ascend toward an asymptote ($\gamma = -1$), or rise to a maximum value and then decline ($\gamma > -1$). Schnute (1985, Figs 2–4) illustrates the possibilities.

We caution the reader not to confuse different roles for γ in models 1 and 2. For example, the case $\gamma = 1$ in model 2 gives a parabolic recruitment curve: $R = \alpha S(1 - \beta S)$. Similarly, the case $\gamma = 1$ in model 1 gives a differential equation with a parabolic growth rate: $dB/dt = \alpha B[1 - (B/B')]$. This, however, implies a hyperbolic relationship (T6.2.7) between B_t and $B_{t+\tau}$, analogous to the hyperbolic recruitment curve $R = \alpha S/(1 + \beta S)$ in model 2 when $\gamma = -1$. From this point of view, it could be argued that Schaefer's combined papers (Schaefer 1954, 1957) really dealt with a hyperbolic relationship, similar to that of Beverton and Holt (1957). At the risk of further confusion, we could add that model 1 with $\gamma = 1$ implies a logistic relationship (T6.2.7) between $B_{t+\tau}$ and τ.

Deriso (1980) and Schnute (1985) proposed difference equations similar to those in model 2. Their results follow mathematically from an age-structured model with three simplifying assumptions. First, natural mortality remains constant across all years and age classes. Second, the fishery has a uniform, knife-edged selectivity on fish at age r and older. Third, maturity also occurs at age r, with fecundity proportional to biomass. Originally, these analyses led to second-order difference equations, with no reference to the mean weight W_t. Schnute and Richards (1998) extended this work to obtain first-order difference equations involving the additional state W_t, which potentially can be measured. Based on the growth model (T6.4.2), their formulation has the simple biological interpretation described above. Mathematically, the linear form of (T6.4.2) allows the growth of individual fish to be accumulated into a similar growth law for the whole population.

6.8 EQUILIBRIUM AND DYNAMIC RESPONSE (MODEL 2)

Model 2 has asymptotic properties similar to those for model 1. With no fishing ($H = 0$), the biomass B_t converges to a carrying capacity B'. As the harvest fraction H increases from 0, the corresponding equilibrium biomass $B(H)$ declines from B'. Analytical results for model 2, however, are not as simple as those for model 1. Table 6.7 shows expressions for equilibrium biomass states associated with H in the control system

$$H \mapsto W, R, B, C, S. \tag{6.19}$$

The three remaining states (E, F, I) in Table 6.6 have simple relationships to those in the shorter list (6.19). Equations (T6.7.1)–(T6.7.7) define a sequential calculation, in which each equilibrium state depends on previous values. Two intermediate values, s and ρ, have useful biological interpretations. The quantity $s(H)$ represents a survival fraction from the combined effects of fishing and natural mortality, and

$$\rho(H) = R(H)/S(H) \tag{6.20}$$

denotes the biomass ratio of recruits to spawners.

Table 6.7 Equilibrium values for states in model 2 at a fixed harvest rate H, where $\rho = R/S$.

$$s(H) = (1 - \delta)(1 - H) \tag{T6.7.1}$$

$$W(H) = \frac{(1 - s)\,w_r + s\lambda}{1 - \kappa s} \tag{T6.7.2}$$

$$\rho(H) = \frac{w_r}{W}\,\frac{1 - s}{1 - H} \tag{T6.7.3}$$

$$R(H) = \frac{\rho}{\beta\gamma}\left[1 - \left(\frac{\rho}{\alpha}\right)^{\gamma}\right] \tag{T6.7.4}$$

$$B(H) = \frac{W}{w_r}\,\frac{R}{1 - s} \tag{T6.7.5}$$

$$C(H) = HB \tag{T6.7.6}$$

$$S(H) = B - C \tag{T6.7.7}$$

Table 6.8 Parameters (α, β) for the model 2 expressed in terms of key reference points.

Given (H^*, C^*)

$$s^* = (1-\delta)(1-H^*) \tag{T6.8.1}$$

$$W^* = \frac{(1-s^*)w_r + s^*\lambda}{1-\kappa s^*} \tag{T6.8.2}$$

$$Q^* = \left(1-\frac{w_r}{W^*}\right)\frac{1-s^*}{1-\kappa s^*} \tag{T6.8.3}$$

$$\alpha = \frac{w_r}{W^*}\frac{1-s^*}{1-H^*}\left[1+\frac{\gamma(1+Q^*)H^*}{1-s^*}\right]^{1/\gamma} \tag{T6.8.4}$$

$$\beta = \frac{(1+Q^*)H^{*2}}{(1-H^*)[1-s^*+\gamma(1+Q^*)H^*]C^*} \tag{T6.8.5}$$

Given (B', ϕ)

$$W' = \frac{\delta w_r + (1-\delta)\lambda}{1-\kappa(1-\delta)} \tag{T6.8.6}$$

$$\alpha = \frac{w_r}{W'}\delta\phi \tag{T6.8.7}$$

$$\beta = \frac{1}{\gamma B'}(1-\phi^{-\gamma}) \tag{T6.8.8}$$

MSY conditions in model 2 cannot be represented analytically in terms of the parameters (T6.6.1), similar to the results in Table 6.3 for model 1. However, a reverse relationship is possible (Schnute and Kronlund 1996; Schnute and Richards 1998). The parameters α and β in (T6.6.1) can be computed analytically from the MSY harvest fraction $H^\star$ and catch $C^\star$. Table 6.8 presents these results in the sequential calculation (T6.8.1)–(T6.8.5). Similarly, in model 1, the simpler relationship (6.13) expresses α in terms of $\psi = C^\star/B'$.

When $H = 0$, Table 6.7 gives a sequential calculation for the carrying capacity $B' = B(0)$, based on the parameters (T6.6.1). The same calculation gives pristine values of other model states, which we denote similarly with a prime accent. In particular,

$$\rho' = \frac{R'}{S'} = \frac{\delta w_r(1-\kappa+\kappa\delta)}{\delta w_r + (1-\delta)\lambda} \tag{6.21}$$

corresponds to recruitment productivity of the pristine biomass $B' = S'$. As $S \to 0$, the recruitment function (T6.6.2) predicts that $\rho = R/S \to \alpha$. In a viable stock, productivity must be larger at small stock sizes than under pristine conditions, that is, $\alpha > \rho'$. By (6.21), this implies that the parameters (T6.6.1) for model 2 must satisfy the condition

$$\alpha > \frac{\delta w_r(1-\kappa+\kappa\delta)}{\delta w_r + (1-\delta)\lambda}. \tag{6.22}$$

Let $\phi = \alpha/\rho' > 1$ be the factor that represents the increase in recruitment productivity from a pristine stock S' to a small stock $S \approx 0$. Then parameters (B', φ) can act as surrogates for (α, β), as shown explicitly in Table 6.8. Walters and Bonfil (1999) used a similar approach in their analysis of Pacific groundfish. The parameter φ often has a clearer biological interpretation than α. Furthermore, estimates of φ might be available from recruitment records for some species.

The parameter φ has no meaning in model 1, where recruitment is not modelled explicitly. However, $\psi = C^\star/B'$ has meaning in both models. To examine the role of ψ in model 2, consider a fixed set of growth parameters (w_r, κ, λ), natural mortality δ, and shape parameter γ. Table 6.8 defines the parameter transition from (B', φ) to (α, β), from which Table 6.7 gives the equilibrium catch curve $C(H)$ in (T6.7.6). This curve defines the maximum value $C^\star$ numerically (although not analytically) and thus gives $\psi = C^\star/B'$. Figure 6.5 illustrates the results of this calculation for a particular case of model 2 with various values of γ. Each curve defines a functional relationship from φ to ψ. The inverse relationship allows φ to be computed from ψ. The scale parameter B' cancels in the calculations leading to Fig. 6.5, so that we have established a numerical equivalence

$$\psi \leftrightarrow \phi \leftrightarrow \alpha \tag{6.23}$$

among dimensionless parameters for model 2, given (δ, γ, w_r, κ, λ). The first equivalence (6.23) comes from a curve similar to those in Fig. 6.5, and the second from (T6.8.7). The figure shows that although any $\phi > 1$ is admissible, ψ has an upper limit if $\gamma < 0$. In certain cases, ψ can theoretically exceed

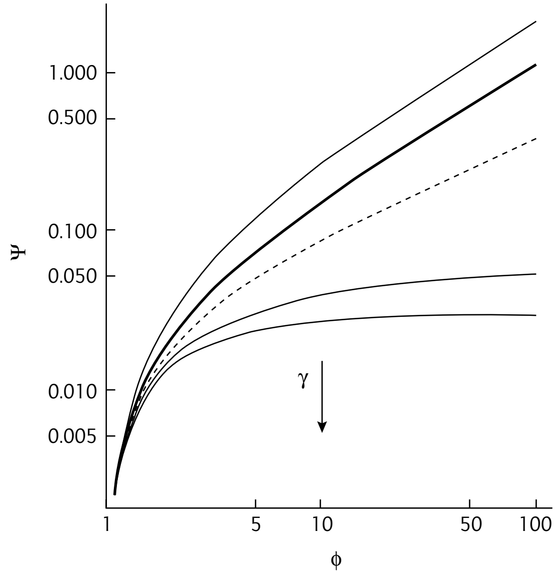

Fig. 6.5 $\psi = C^*/B'$ as a function of $\phi = \alpha S'/R'$ in model 2 with $\delta = 0.1$, $w_r = 0.3$ kg, $w_\infty = 1$ kg, $\kappa = 0.7$. Curves represent various values of γ: $-1.5, -1, 0, 1, 3$. An arrow indicates the direction of increasing γ. Heavy solid and broken curves indicate special cases $\gamma = -1$ and $\gamma = 0$, respectively.

1 ($\psi = C^*/B' > 1$), suggesting an annual catch C^* greater than the pristine biomass B'. Such cases also require a high ϕ associated with extremely large production at small stock sizes.

We have already demonstrated that three parameters (B', ψ, γ) govern population dynamics in model 1. Similarly, given the underlying characteristics of natural mortality (δ) and growth (w_r, κ, λ), (6.23) and (T6.8.7)–(T6.8.8) show that the same three parameters (B', ψ, γ) govern the dynamics of model 2. Figure 6.6 shows catch curves for a case of model 2 with $\psi = 0.05$. These bear a striking resemblance to their counterparts in Fig. 6.3 for model 1. The parameter γ plays a similar role in both models. One notable difference, however, distinguishes Figs 6.3(b) and 6.6(b). In model 1, the ratio $\psi = C^*/B'$ is eliminated by scaling the biomass B and catch C relative to B' and C^*, respectively. Thus, Fig 6.3(b) does not depend on the choice of ψ. (Mathematicians can construct a proof from (6.12)–(6.13).) The more complex model 2 does not share this feature. For example, modal points on the curves in Fig. 6.6(b) shift closer together as ψ decreases from 0.05 to 0.03.

Our model presentations have stressed the role and biological meaning of key parameters. We consider this an important part of model development,

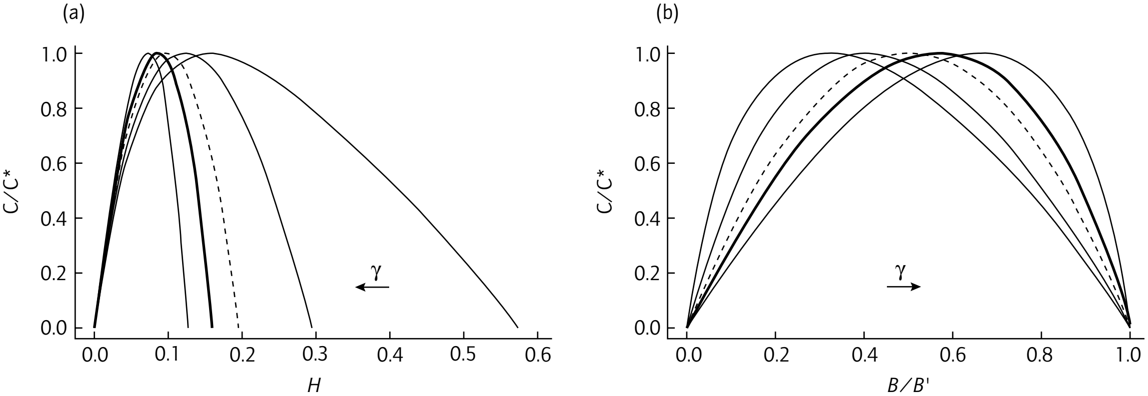

Fig. 6.6 Relative annual catch C/C^* for the equilibrium version of model 2 as a function of (panel (a)) harvest rate H and (panel (b)) relative biomass B/B'. The parameters $\psi = 0.05$, $\delta = 0.2$, $w_r = 0.3$ kg, $w_\infty = 1$ kg, $\kappa = 0.7$ are held fixed in each panel. Curves represent various values of γ: $-1.5, -1, 0, 1, 3$. Arrows indicate the direction of increasing γ. Heavy solid and broken curves indicate special cases $\gamma = 1$ and $\gamma = 0$, respectively.

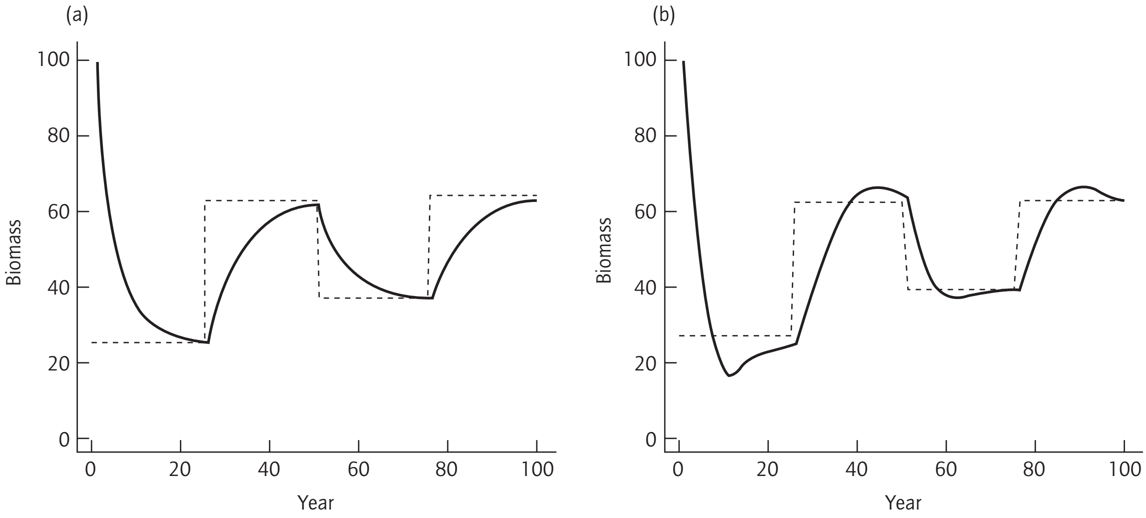

Fig. 6.7 Biomass trajectories for models 1 and 2 (panels (a) and (b), respectively) with $\psi = 0.06$ and $\gamma = 0$, where B' is scaled to 100 biomass units. Model 1 uses a standard time unit $\tau = 1$ yr, and model 2 has the additional parameters $\delta = 0.03$, $r = 10$ yr, $w_r = 0.3$ kg, $w_\infty = 1$ kg, $\kappa = 0.7$. Pristine conditions initialize each trajectory, followed by four 25 yr periods of constant harvest rates: $H = 0.2, 0.07, 0.15, 0.07$. Solid curves represent biomass trajectories, and broken rectangular lines indicate asymptotic biomass levels $B_\infty(H)$ associated with the four harvest rates.

because parameters encapsulate information to be estimated from available data (see also Sparre and Hart, Chapter 13, this volume). Furthermore, three common parameters capture the biological similarity between models 1 and 2, even though they have quite different mathematical derivations. Much of the biological interpretation presented above for model 1 carries over directly to model 2. In particular, both models have a carrying capacity B', harvest potential $\psi = C^*/B'$, and productivity parameter γ related to the MSY harvest fraction H^* and relative biomass B^*/B' (Figs 6.3 and 6.6).

Although the two models have similar equilibrium properties, model 2 produces more complex dynamic trajectories. Figure 6.7 illustrates the dynamic response of model 1 (Fig. 6.7a) and model 2 (Fig. 6.7b) to a sequence of four harvest fractions H, each sustained for a period of 25 yr. The figures show biomass trajectories B_t in relation to the corresponding four equilibrium levels $B(H)$. The parameter $B' = 100$ sets a convenient vertical scale. Both model trajectories are initialized from pristine conditions ($B_t = S_t = B'$ and $H_t = 0$ for $t < 1$). Model 1 follows an orderly progression of decay or growth towards the relevant equilibrium level $B(H)$. Model 2 has a similar trajectory, although biomass levels B_t go beyond the equilibrium value $B(H)$ in each 25 yr period. This tendency to overshoot results from a Ricker recruitment function ($\gamma = 0$) with a long recruitment lag ($r = 10$ yr). Also, the stock has a low natural mortality rate ($\delta = 0.03$) on fish that grow from $w_r = 0.3$ kg to $w_\infty = 1$ kg. Thus, both recruitment and growth contribute significantly to the biomass dynamics in Fig. 6.7(b). Shepherd and Pope (Chapter 8, this volume) also discuss aspects of forecasting.

Figures 6.7(a) and 6.7(b) illustrate a dynamic feature common to many fisheries. The decay towards a low stock level happens more quickly than recovery to a higher level. Particularly with modern fishing gear, humans can often remove fish much faster than nature can replace them. Response times for decay and recovery obviously reflect underlying model parameters, and the ability to estimate these parameters may depend on contrasting fishing conditions, such as those portrayed in Fig. 6.7.

6.9 ESTIMATION: COMPARING MODELS WITH DATA

It helps to understand a model well before using it to estimate parameters from data. We have devoted most of this chapter to a careful examination of models 1 and 2 in the context of surplus production. Nevertheless, the process of working backwards from data to parameters and states remains a very important issue (Hilborn and Mangel 1997). In fact, the definition of error in the estimation phase can actually dominate the structural assumptions in the deterministic model (Schnute 1985, 1987). A complete explanation of this subject is beyond the scope of this chapter, and we confine our discussion to a few illustrative scenarios.

After devising models such as those above, the next question is: what is known and what is unknown? For example, consider Schnute's integrated form (T6.2.9) of model 1 with $\gamma = 1$. Usually, none of the quantities in this equation are known, except the time interval τ, say, $\tau = 1$ yr. As discussed earlier, suppose that annual effort and CPUE data $(\overline{E}_t, \overline{U}_t)$ are observed for a series of years $t = 1, \ldots, n$. Equations (6.10)–(6.11) allow the unknown quantities $(F_t, \overline{B}_t)$ to be replaced with known data, along with the fixed parameter q_1. This suggests the stochastic model

$$\frac{\exp\left(\dfrac{4\psi\overline{U}_{t+1}}{q_1B'}\right)-1}{\exp\left(\dfrac{4\psi\overline{U}_t}{q_1B'}\right)-1} = \frac{4\psi - q_1\overline{E}_t}{4\psi - q_1\overline{E}_{t+1}}\,\frac{e^{(4\psi - q_1\overline{E}_{t+1})}-1}{e^{(4\psi - q_1\overline{E}_t)}-1} \times \exp\left[\left(4\psi - q_1\overline{E}_t - \frac{4\psi\overline{U}_t}{q_1B'}\right)\right]e^{\varepsilon_t}, \quad (6.24)$$

where ε_t is a normal variate with mean 0 and variance σ^2. In deriving (6.24) from (T6.2.9), we have adopted a time-scale in years with $\tau = 1$ and substituted $\alpha = 4\psi$ from (6.13) when $\gamma = 1$. Given the known data, (6.24) determines the residual $\varepsilon_t(B', \psi, q_1)$ as a function of the three unknown parameters for $t = 1, \ldots, n - 1$, and the minimum sum of squares $\Sigma_{t=1}^{n-1}\varepsilon_t^2$ can be used to obtain estimates $(\hat{B}', \hat{\psi}, \hat{q}_1)$. As discussed by Schnute (1977), (6.24) can be written approximately as

$$\log\left(\frac{\overline{U}_{t+1}}{\overline{U}_t}\right) \approx 4\psi - \frac{q_1}{2}\left(\overline{E}_t + \overline{E}_{t+1}\right) - \frac{2\psi}{q_1B'}\left(\overline{U}_t + \overline{U}_{t+1}\right) + \varepsilon_t. \quad (6.25)$$

This implies that parameters could be estimated by linear regression on quantities known from the data.

The formulation (6.24), based on (T6.2.9), assumes that all the error occurs in the process of incrementing $\overline{B}_t$ to $\overline{B}_{t+\tau}$. The effort $\overline{E}_t$ in (6.10) precisely determines the fishing mortality F_t, and the CPUE $\overline{U}_t$ in (6.11) gives an exact index of biomass $\overline{B}_t$. Thus, the model involves process error in the biomass dynamics, but no measurement error in the data.

An alternative approach would consider measurement error in the data but an exact system dynamics. Consider the general formulation of model 1 (γ unrestricted) in the context of small time steps τ. For example, suppose that t is measured in years, but $\tau = 1$ week $= 1/52$ yr. Let the data consist of weekly values (E_t, C_t) with indices t in fractional time, plus an annual fishery independent index $\overline{I}_t$ with indices confined to integers t. The estimation process starts with assumed trial values for the parameters (T6.1.1) and an initial biomass B_1 at the start of the first week. Sequential deterministic calculations from (T6.1.2) and (T6.1.8) produce a complete trajectory of states F_t and B_t for each week t. Introducing measurement error into (T6.1.4) and (T6.1.5) gives

$$C_t = F_tB_te^{\varepsilon_{1t}}, \quad (6.26)$$

$$\overline{I}_t = q_2\overline{B}_te^{\varepsilon_{2t}}, \quad (6.27)$$

where normal residuals ε_{it} have mean 0 and variances σ_i^2 $(i = 1,2)$. Parameters and the initial state B_1

could then be estimated by minimizing the sum of squares

$$\sum_{m=1}^{n/\tau} \varepsilon_{1,m\tau}^2 + \frac{\sigma_1^2}{\sigma_2^2} \sum_{t=1}^{n} \varepsilon_{2t}^2, \tag{6.28}$$

based on data from n years of the fishery. The variance ratio σ_1^2/σ_2^2 could be set arbitrarily to place greater emphasis on the catch or index data.

One significant weakness to the scenarios above lies in the assumption that fishing effort E_t precisely determines the fishing mortality F_t. Typically, effort is poorly known and inconsistently related to fishing mortality. Catch data tend to be better defined, and we prefer models that require catch to be removed directly from the biomass as an overt control, rather than as an observation related to the hypothetical effort control. Although model 1 can be reformulated from this point of view, the difference equations in model 2 make this approach more straightforward.

Consider a scenario in which the data consist only of the annual catch C_t and an abundance index I_t for years $t = 1, \ldots, n$. For simplicity, assume that all states are initialized at pristine levels $(R', S' = B', W')$, as in the calculations for Fig. 6.7(b). Then, given the parameters $(B', \psi, \gamma, \delta, w_r, \kappa, \lambda, q_2)$ and the catch history C_t, Table 6.6 gives equations for a deterministic updating of all states R_t, B_t, W_t, S_t and I_t. Furthermore, $H_t = C_t/B_t$ is also determined from (T6.6.7). Equations (T6.6.5)–(T6.6.6) do not enter this calculation. Similar to (6.27), the parameters for model 2 could be estimated by comparing observations I_t with the model predictions from (T6.6.9). Usually some parameters, such as those related to growth (w_r, κ, λ), would be fixed at values known from biological samples and other external data sources. A variant of this analysis might use observed mean weights W_t, so that comparisons of observed and predicted values of this state would also enter the estimation procedure.

Richards and Schnute (1998) detail the application of maximum likelihood theory for a model similar to model 2, except that they replace (T6.6.4) with an update equation for the mean age A_t. They assume measurement error in the observations I_t and A_t. They also include process error in the recruitment equation, which is somewhat different from (T6.6.2) here, and they add a vector of recruitment values R_t to the list of model parameters. Because their analysis involves both process and measurement error, additional assumptions are required. They choose to fix the ratio of process error to the total (measurement plus process) error.

It is well known for these models that the choice of error structure can significantly influence the outcome (Ludwig and Walters 1981; Schnute 1991; Pella 1993; Polachek et al. 1993). For example, with a given deterministic model and data set, different error structures can produce mutually exclusive confidence intervals for the same parameter or reference point (Schnute 1989). Intuitively, a model filters a signal from noisy data. Deterministic assumptions, such as those in models 1 or 2, specify the desired signal. Error assumptions, similar to (6.24), (6.26) and (6.27), define the noise. With highly variable data, the perceived signal obtained by parameter estimation can depend as much on error assumptions as on the structural model itself (Schnute 1987).

6.10 MODEL EXTENSIONS

Some of the limitations of models 1 and 2 can be addressed formally through model extensions. The most common approach is to add new states or allow parameters to become time-varying states. For example, a variable carrying capacity B' might be represented as a state B'_t. The model then requires an additional assumption to describe the time trajectory of B'_t, such as the random walk

$$B'_{t+1} = B'_t e^{\eta_t} \tag{6.29}$$

where normal residuals η_t have mean 0 and variance σ_3^2. Alternatively, (6.29) could relate B'_t to an external environmental variable or an abundance index for a competitor species. The addition of state variables does, however, increase model complexity and parameter uncertainty.

For illustration, consider model 2 with n years of data (C_t, I_t). If the growth parameters are assumed known and the model is initialized with pristine conditions, then the $2n$ observed data values would be used to estimate the five parameters $(B', \psi, \gamma, \delta, q_2)$. To allow time variation in the carrying capacity B', the model requires an additional n unobserved states B'_t that replace the original parameter B'. In this case, the $2n$ data values must be used to estimate $n + 4$ unknowns. The sum of squares function (6.28) would contain an extra term $(\sigma_1^2/\sigma_3^2)\,\Sigma_{t=1}^{n-1}\,\eta_t^2$ associated with (6.29). As $\sigma_3 \to 0$, this term imposes a high penalty that causes residuals η_t to become small and estimates $\hat{B}'_t$ to converge to the estimate $\hat{B}'$ obtained under the assumption of constant carrying capacity.

An extension to multi-species models would similarly require the use of additional states, the biomass B_{it} for each species i. Model 1 has a classical extension in this direction, where the Lotka–Volterra differential equations extend model 1 with $\gamma = 1$ to a predator–prey relationship between two species (Pauly and Christensen, Chapter 10, this volume). Quinn and Deriso (1999, p. 9) discuss the generalization to an arbitrary number of species. Similar extensions could, of course, be incorporated into model 2. For example, consider two independent versions of this model, one for the predator and the other for the prey species. Additional equations could link these models by relating the natural mortality, growth and recruitment of each species to the abundance of the other. Unfortunately, as discussed by Hilborn and Walters (1992, pp. 437–8), realistic data generally lack the contrast needed to estimate all the necessary parameters.

For simplicity, we have suggested a sum of squares objective function to estimate parameters in the examples above. More generally, likelihood (Edwards 1972; Schnute 1994) or Bayes posterior (Gelman et al. 1995; Punt and Hilborn 1997) analyses give a complete description of parameter estimates and their uncertainty. The process of converting parameters to states fits particularly well into the Bayes framework of conditional distributions and hierarchical models (Gelman et al. 1995, chap. 5). Two recent papers (Meyer and Millar 1999a,b) illustrate the Bayes approach in contexts similar to models 2 and 1, respectively. Schnute et al. (2000) use Bayes methods to examine management options for a fishery modelled with the stock–recruitment relationship (T6.6.2). Freeman and Kirkwood (1995) and Reed and Simons (1996) investigate Kalman filters as more classical estimation tools in various production models intended for use with CPUE data.

Statistical theory cannot circumvent fundamental limitations in the observed data. Fisheries data sets are notoriously noisy, leading to ambiguous inferences. Meaningful conclusions about a dynamic system require observations from periods of substantial change, such as the biomass shifts illustrated in Fig. 6.7. Fishery data often lack this contrast. Many fisheries begin to operate on a pristine biomass and progress along a one-way trip downward towards economic collapse (Hilborn and Walters 1992, pp. 312–19). Do the data allow managers to recognize the problem soon enough to avert disaster? According to Walters (1998, p. 284), 'the sad fact is that most stock assessment systems are just not up to the task of providing accurate enough stock size estimates to be safe in the face of fishing technologies that can get the quota even if stock size is much lower than estimated'.

6.11 CONCLUSIONS

Despite the known limitations of fishery models, we have developed them here in mathematical detail. We have also described a design philosophy that allows models to be tailored to specific circumstances. Fishery models begin with an arithmetic that tries to capture the essential concept of surplus production. Schnute and Richards (2001) coin the word 'fishmetic' (rhymes with arithmetic) to represent uncertainty in the conversion of arithmetic to practical fishery models. That paper, written concurrently with this chapter, identifies key reasons why models can fail. Readers may wonder how the same authors can present the elaborate mathematics of this chapter and yet, in another forum, identify severe problems with its application. We believe that the surplus production paradigm, portrayed by example in Fig. 6.1, lies at the heart of any rational theory of fishing. Without surplus production, no fishery could be sustained. Anyone interested in pursuing criticisms or variations of this paradigm should understand it fully. The sceptical modeller uses production models as tools for understanding and communicating the inevitable limits to fishery harvest.

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7 Dynamic Pool Models I: Interpreting the Past using Virtual Population Analysis

J.G. SHEPHERD AND J.G. POPE

7.1 INTRODUCTION: THE DYNAMIC POOL CONCEPT

The concept of the dynamic pool as a model for fish populations is very simple. The population consists of all individuals alive at any time. This population is continuously reduced in size by deaths, due to natural mortality or to fishing, and is augmented by recruitment of young fish. This constitutes the dynamic pool. The concept was implicit in the earliest attempts to model their dynamics quantitatively, but it was developed to fruition in the work of Beverton and Holt (1957). It is generally regarded as distinct from the picture underlying stock-production models (Schnute and Richards, Chapter 6, this volume), although these too involve a dynamic balance between production (due to recruitment and individual growth) and depletion due to mortality, because more attention is paid to the fate of individuals within the 'pool', and the consequent structure and dynamics of the population.

This description naturally focuses attention on the processes of reproduction with its consequent recruitment of young fish to the population, individual growth and maturation, and death. These are usually described as a function of the age of the individuals involved, and there is therefore a close correspondence between the dynamic pool concept and age-structured methods of analysis and prediction. The natural description of the population is therefore in terms of the population number $P(y,a)$ of fish in each age class, usually measured in years, and denoted by the index a, as a function of time, also usually expressed in years, and denoted by the index y. Dynamic pool methods seek to estimate $P(y,a)$ from available data, and predict its future evolution under various assumptions about natural and anthropogenic effects, especially levels of fishing. The data to be analysed are generally some estimates of catch-at-age $C(y,a)$, possibly disaggregated between fleets and indexed by f (Sparre and Hart, Chapter 13, this volume), one or more indices of abundance $u(y,a,f)$ such as CPUE (catch per unit effort) estimates for a number of fleets and/or research vessel surveys. Estimates of the rates of mortality due to natural causes, $M(a)$, which is often expressed as a function of age and sometimes also of time, and that due to fishing, $F(y,a)$, as well as their sum, the total mortality rate $Z(y,a)$, are the natural variables used to describe the fate of the fish.

7.2 THE DISTINCTION BETWEEN RETROSPECTIVE ANALYSIS AND FORECASTING

Within the general class of dynamic pool methods, there tends to be a fairly clear separation between the techniques for the analysis of past data, to estimate the current state and structure of the population, and those for forecasting its future evolution. The former are exemplified by the ubiquitous technique known as Virtual Population Analysis (VPA), which is the subject of this chapter. The latter include both short-term catch forecast methods, and long-term analyses such as that of yield-per-recruit (introduced by Beverton and Holt 1957), which are the subject of Chapter 8. There is no essential reason for this separation, and methods certainly exist in which both analyses are conducted together within a unified framework (for an up-to-date account of such methods see Quinn and Deriso 1999). There are advantages and disadvantages in both approaches. However, it is a regrettable but undeniable fact that fish stock assessments sometimes go wrong, or at least become the subject of intense debate, and it is not unusual for assessment scientists to spend considerable time trying to figure out what happened, and why, either in reality, or in their analysis, or both. It is therefore usually helpful to have as clear a picture as possible of the actual (estimated) current state of the stock, and the information on which this estimate is based, as well as of its expected future evolution, and the principal factors determining this in both the short term and in the long term. Moreover, it is often necessary to include in the analysis some assumptions about changes, either those to be imposed as a result of management action such as reductions of fishing mortality, or changes of the exploitation pattern given by the set of values of F on all ages in any year, or to be expected from natural causes such as changes of climate regimes. It is helpful if such assumptions are exposed as clearly as possible for critical evaluation and debate. Both of these purposes, as well as the explanation of the workings of the analyses, are assisted to some extent by treating the retrospective analysis and the forecasting process separately. We have therefore adopted this approach, which also reflects the structure of much of the software available for these analyses, in the descriptions of these methods given here and in Chapter 8. However, there are also advantages in using a unified approach to analysis and forecasting, and our approach is not intended to detract from these, except in so far as critical features of the analysis may sometimes be more difficult to discern in such unified procedures. This applies especially when the retrospective analysis and the forecast are themselves integrated within a formal management procedure. These too have undoubted advantages, but when they are applied it can become very difficult to figure out what is actually going on, when surprising or controversial results are obtained.

7.3 VIRTUAL POPULATION ANALYSIS (VPA): THE BASICS

7.3.1 The virtual population and cohort analysis

The original concept of the virtual population – a minimum estimate of the size of a year class at any age, obtained by summing all the catches subsequent to that age – was introduced by Fry (1949). The idea did not become popular, however, until the 1970s, following the demonstration by Gulland (1965) that one could also allow for natural mortality to obtain a more realistic estimate. Gulland's working paper was not generally available for many years, but is now included in the compilation by Cushing (1983).

Gulland's method depended on the iterative solution of the conventional catch equation for each age and year (equation 13.19 in Sparre and Hart, Chapter 13, this volume), i.e.

$$C = (F/Z)[1 - \exp(-Z)]P \tag{7.1}$$

where we have omitted the indexes y and a for clarity. This was a laborious and expensive calculation when done on an electromechanical calculator, and it was not trivial even on an early digital computer. The so-called 'cohort analysis' approximation introduced by Pope (1972) – also reprinted in Cushing (1983) – was therefore a significant advance. It is in fact a remarkably good approximation – good enough for all practical purposes. Now that computation is much cheaper, however, its main virtue is that it exposes very clearly indeed the essence of virtual population analysis (VPA)

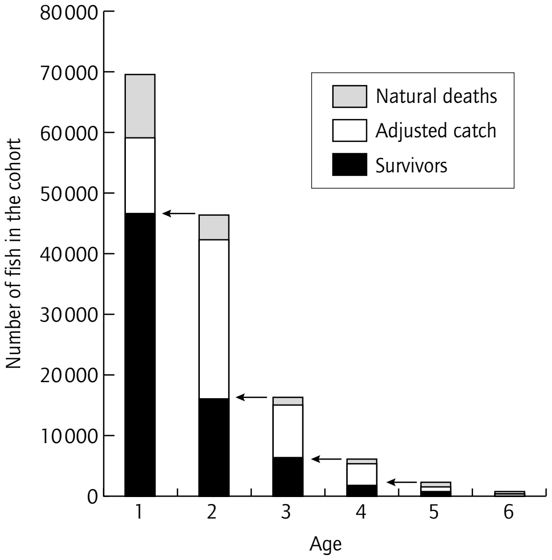

Fig. 7.1 Accumulation of the virtual population.

as a technique, and for that reason we employ it throughout this chapter.

Pope's formula

$$P(y,a) = \exp[M(a)/2]C(y,a) + \exp[M(a)]P(y+1,a+1) \quad (7.2)$$

can be derived, using a little ingenious algebra, as an approximation to (7.1). It is, however, also the obvious result of assuming that all the catch is taken instantaneously half-way through the year. One is simply raising the number of survivors to allow for natural mortality over a full year, and the number of fish caught to allow for natural mortality over only half the year. Clearly, multipliers other than exp($M/2$) could also be applied if the catches were concentrated at some other time of year. In any case, this formulation shows that VPA is no more and no less than a method for estimating the population size of a cohort at any age, by accumulating the subsequent catches, with adjustment for natural mortality. The process, which is normally applied sequentially for all age groups belonging to the same cohort, is illustrated in Fig. 7.1.

The fishing mortality values can of course be calculated immediately once the populations have been estimated, since

$$Z(y,a) = \ln[P(y,a)/P(y+1,a+1)] \quad (7.3)$$

and

$$F(y,a) = Z(y,a) - M(a). \quad (7.4)$$

Clearly also, in order to estimate the total populations, we need to have and to use the total international catch numbers for $C(y,a)$ – partial data from a few fleets is not enough, although the possibility of relaxing this restriction is discussed at the end of this chapter. Finally, it is clear that one needs some estimate for terminal population size at the end of the final year for which a catch estimate is available, in order to start the calculation, which is carried out retrospectively, as implied by equation (7.2).

'Exact' VPA, based directly on the solution of equation (7.1) (with equations (7.3) and (7.4)) can of course be carried out instead of the cohort approximation, and this is in fact the usual operational practice. A large number of algorithms for the iterative solution of this equation have been proposed, including the standard Newton–Raphson method (see for example Stephenson 1973).

Given the terminal population, all the other population-at-age estimates can thus be computed immediately. And given these, all the fishing mortality values can then also be calculated. There are no fitting procedures involved, no residuals, no lack of fit, and no degrees of freedom. VPA is therefore in no real sense a statistical modelling procedure (G. Gudmundsson, personal communication). The catch data are accepted as though they were exact, and entered directly into the calculation. VPA is therefore best thought of as a transformation of the data. The catches are converted into a set of equivalent population estimates, which may in turn be converted into the equivalent fishing mortalities. Any errors in the original catch-at-age data feed through directly into the population and fishing mortality estimates.

Thus understood, VPA is a very quick and convenient procedure for turning indigestible catch-at-age data into things that are more easily understood, at least by those who have been suitably trained, namely fishing mortalities and estimates of year-class strength. Its virtues and vices will be discussed in more detail later on. Here it is necessary to stress one vital point: the transformation performed by VPA is not unique. For every choice of terminal population, and there are infinitely many such choices, there is a resultant and different transformation: a few of the possibilities are illustrated in Fig. 7.2. In addition, with no residuals and no lack of fit, there is no way to choose among them. All are equally good (exact) fits to the data. This is the central problem of VPA, that there are infinitely many possible 'solutions' for each and every cohort. To select among these the user must supply an estimate of the terminal population, or, equivalently, the terminal fishing mortality, and there is no objective way of doing this based on the catch-at-age data alone.

Additional information is therefore required. This may take the form of additional assumptions, or additional data. In the former case one is in effect specifying a stronger and less highly parameterized model. This is the approach adopted by separable VPA, discussed in Section 7.4. It is, however, only partially successful, since serious indeterminacy remains. The second approach, adducing more data, is typified by the use of CPUE and survey abundance data for 'tuning' the VPA, and is discussed in Sections 7.5 and 7.6.

Before leaving the subject of 'conventional' (untuned) VPA, it is important to recognize some of its essential features. A first important point is that natural mortality, *M*, is taken to be known, and is not and cannot be estimated by the analysis. *M* is usually taken to be given as a constant or as a function of age, but the analysis is easily generalized should values of *M* as a function of both year and age be available. VPA is also essentially a retrospective technique, not only because that is the most convenient way in which to carry out the calculations, but because estimates of fishing mortality and population size for earlier years and younger ages become progressively less sensitive to the starting assumptions about terminal *F*. This is usually referred to as convergence of the VPA, and is discussed in detail by Pope (1972). As a rule of thumb, estimates may be regarded as more or less converged if the cumulative fishing mortality, from the oldest age in the cohort back to that in question, is greater than one, but not otherwise.

The converse is also true, that running a VPA calculation forwards in time leads to divergent estimates for the older ages and years. In practice this means that estimates of terminal *F* or population obtained in this way are highly variable, and very sensitive to the initial estimates of year-class strength used to start the calculation. They may in fact easily become infeasible (zero or negative) for what are a first sight quite plausible initial assumptions. Given sufficient precision in the calculation, forwards and backward VPA are of course exactly equivalent calculations, but in practice, because of the sensitivity to starting assumptions, the retrospective calculation is robust, whereas the prospective one is not, and it is useful only as a technical device in some special circumstances.

7.3.2 Exploratory analysis using trial VPAs

The retrospective 'convergence' property of VPA means that, even without additional information, it may often be used to obtain some idea about fishing mortality a few years ago, and the size of all but the most recent year classes, provided fishing mortality is not too small. Indeed, there are few professional analysts who, given a suitable set of catch-at-age data, would not carry out some form of trial VPA just to get some rough idea of what is, or rather was, going on. Such a trial analysis must usually be based on rather arbitrary assumptions concerning terminal *F*. We recommend setting trial terminal *F*s to a high value (of the order of 1) in such an analysis, to ensure rapid convergence. This can conveniently be achieved, especially when using cohort analysis, by setting the terminal population equal to the terminal catch number, or some fraction thereof. The value of terminal *F* so created depends on the level of natural mortality, but is satisfactorily high (0.644 when *M* is taken as 0.2). Examples of such a trial analysis, for a

Table 7.1 North Sea cod: catch number at age, 1990–5.

Age	Year					
	1990	1991	1992	1993	1994	1995
1	11 841	13 628	27 967	4 814	16 173	16 465
2	54 692	23 571	32 216	55 560	25 195	63 654
3	11 994	16 840	8 697	11 409	21 118	12 932
4	4 360	3 319	4 995	3 211	3 078	5 296
5	2 462	1 393	1 057	1 578	862	800
6	304	1 032	479	430	513	283

Table 7.2 North Sea cod: population estimates from trial cohort analysis with high terminal *F* (0.644).

Age	Year						
	1990	1991	1992	1993	1994	1995	1996
1	69 619	87 699	163 175	84 215	198 758	38 307	0
2	97 245	46 285	59 471	108 291	64 593	148 096	16 465
3	21 301	30 130	16 567	19 540	38 389	30 087	63 654
4	8 361	6 587	9 431	5 695	5 675	12 322	12 932
5	5 654	2 901	2 390	3 202	1 757	1 861	5 296
6	707	2 401	1 114	1 000	1 194	658	800
7		304	1 032	479	430	513	283

Table 7.3 North Sea cod: fishing mortality estimates from trial cohort analysis with high terminal *F* (0.644).

Age	Year					
	1990	1991	1992	1993	1994	1995
1	0.208	0.188	0.210	0.065	0.094	0.644
2	0.972	0.827	0.913	0.837	0.564	0.644
3	0.974	0.962	0.868	1.036	0.936	0.644
4	0.859	0.814	0.880	0.976	0.915	0.644
5	0.656	0.757	0.671	0.787	0.781	0.644
6	0.644	0.644	0.644	0.644	0.644	0.644

set of ICES data for the North Sea cod (*Gadus Morhua*) stock from 1990 to 1995 (Anon. 1991) are given in Tables 7.1, 7.2 and 7.3, using the fairly high estimate of terminal *F* obtained in this way.

The results of an alternative trial analysis, using a lower estimate of terminal *F*, obtained by setting the terminal populations equal to *double* the final catch number, are given in Tables 7.4 and 7.5.

The time trends of average fishing mortality and year-class strength from these analyses are plotted in Figs 7.2 and 7.3, which illustrate the considerable difference between these equally feasible interpretations of the same data, particularly (but not only) for recent years.

7.3.3 The Judicious Averaging Method (JAM)

If (and only if) one is prepared to assume that things such as fishing mortality and the exploitation pattern have not changed very much recently, a trial analysis can also give some idea of what is going on now, as well as in the past, but the validity of the interpretation depends entirely on the assumption of constancy. One is really relying on additional

Table 7.4 North Sea cod: population estimates from trial cohort analysis with low terminal *F* (0.373).

Age	Year						
	1990	1991	1992	1993	1994	1995	1996
1	70 558	89 874	174 962	107 779	293 719	58 417	0
2	98 639	47 054	61 251	117 941	83 886	225 843	32 930
3	22 258	31 272	17 197	20 998	46 289	45 882	127 308
4	9 234	7 371	10 366	6 210	6 869	18 790	25 864
5	7 193	3 615	3 032	3 967	2 179	2 838	10 592
6	1 079	3 662	1 699	1 526	1 820	1 004	1 600
7		608	2 064	958	860	1 026	566

Table 7.5 North Sea cod: fishing mortality estimates from trial cohort analysis with low terminal *F* (0.373).

Age	Year					
	1990	1991	1992	1993	1994	1995
1	0.205	0.183	0.194	0.051	0.063	0.373
2	0.949	0.807	0.871	0.735	0.403	0.373
3	0.905	0.904	0.819	0.917	0.702	0.373
4	0.738	0.688	0.760	0.847	0.684	0.373
5	0.475	0.555	0.487	0.579	0.575	0.373
6	0.373	0.373	0.373	0.373	0.373	0.373

information from a stronger model, based on the assumption of more or less constant fishing mortality, as described above. This procedure can of course be automated quite easily. One can iteratively rerun the VPA, inserting terminal *F*s based on the average over several (usually about five) previous years, for each age in the last year, and the average over (say) the five next younger age groups for the oldest age group in each year.

This formalizes the assumptions being made, i.e. approximate constancy of *F* in recent years, and approximate flatness of the exploitation pattern on the oldest ages, and creates a workable method of analysis sometimes known as the JAM method. The acronym may be expanded either informatively as the Judicious Averaging Method, or cynically as Just Another Method, according to taste. An example of such an analysis on the same North Sea cod data set is given in Tables 7.6 and 7.7, and the resulting fishing mortality and year-class strength estimates are included in Figs 7.4 and 7.5. This third interpretation of the data is less

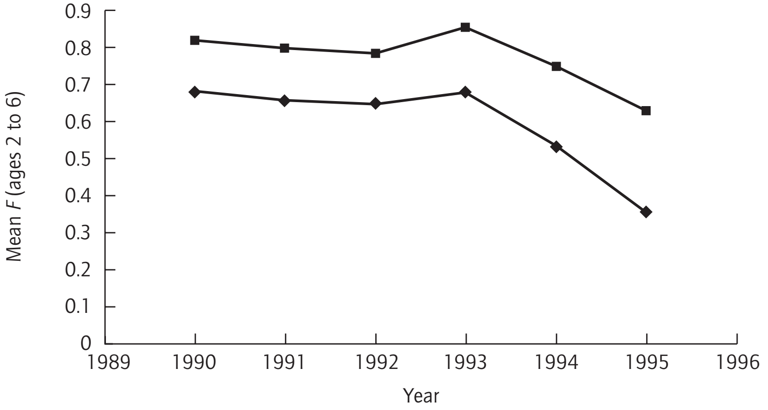

Fig. 7.2 Fishing mortality estimates from two trial VPA analyses. ■ represents higher *F*; ◆ represents lower *F*.

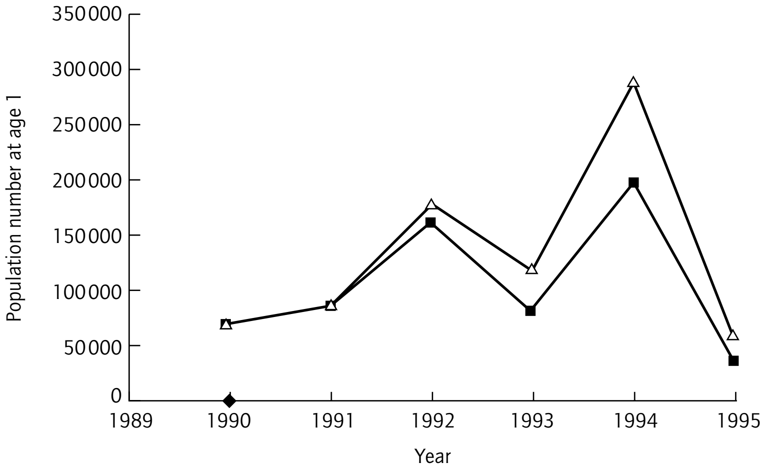

Fig. 7.3 Year-class strengths from two trial VPA analyses. △ represents low *F*; ■ represents high *F*.

Table 7.6 North Sea cod: population estimates from JAM method.

Age	Year						
	1990	1991	1992	1993	1994	1995	1996
1	69 619	87 329	158 575	73 055	165 790	122 050	
2	97 245	46 285	59 167	104 524	55 456	121 103	85 028
3	21 301	30 130	16 567	19 292	35 305	22 607	41 554
4	8 361	6 587	9 431	5 695	5 472	9 797	6 807
5	5 654	2 901	2 390	3 202	1 757	1 695	3 229
6	707	2 401	1 114	1 000	1 194	658	664
7		304	1 032	479	430	513	283

Table 7.7 North Sea cod: fishing mortality estimates from JAM method.

Age	Year					
	1990	1991	1992	1993	1994	1995
1	0.208	0.189	0.217	0.076	0.114	0.161
2	0.972	0.827	0.921	0.885	0.697	0.861
3	0.974	0.962	0.868	1.060	1.082	0.989
4	0.859	0.814	0.880	0.976	0.972	0.900
5	0.656	0.757	0.671	0.787	0.781	0.730
6	0.644	0.644	0.644	0.644	0.644	0.644

arbitrary than the two trial analyses, since it is based on clearly stated assumptions about the behaviour of fishing mortality. It depends on a rather more restrictive model for fishing mortality, but is not thereby guaranteed to be closer to the truth. This will only happen if the assumptions made happen to be correct. The validity of these assumptions is not known and cannot be tested on these data alone.

In the absence of any other relevant information, however, these assumptions may be reasonable null hypotheses, to be accepted until disproved. They are in fact weaker than the assumptions made in some alternative analyses of the same data. If one were to average over years, and plot and analyse the resulting catch curve (see Gulland 1983, Section 4.3.3), then one would be implicitly assuming that fishing mortality is constant over the whole period in question, that the exploitation pattern is flat for all fully recruited ages, and that recruitment has been constant, or at

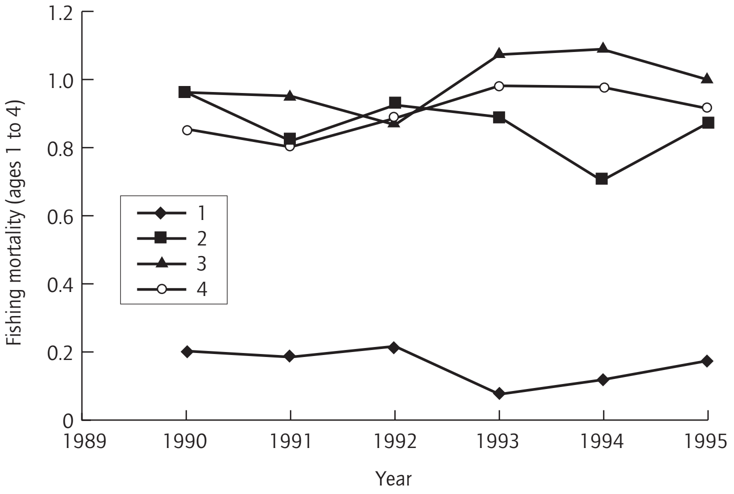

Fig. 7.4 Fishing mortality estimates from the JAM method.

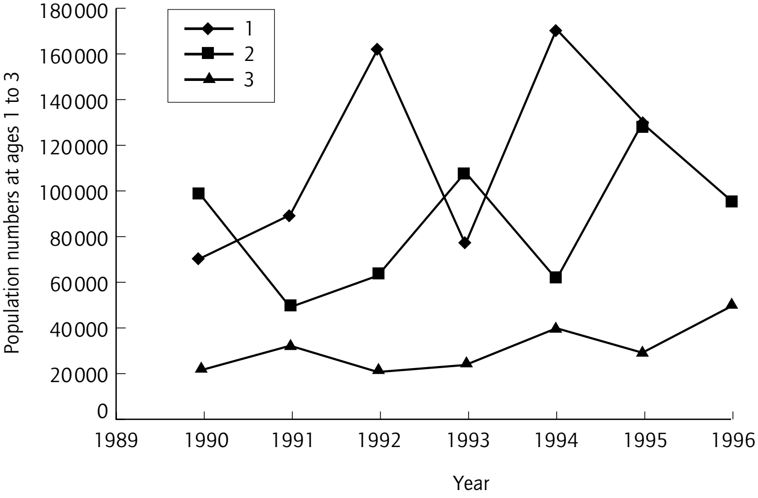

Fig. 7.5 Population numbers from the JAM method.

least trend-free for the whole period. These are much stronger assumptions, which most analysts would, however, probably make quite cheerfully in sufficiently desperate circumstances.

The strong assumptions implied by the JAM method need not therefore forbid its use as an exploratory tool. However, one should remember that it is based on assumptions concerning the things one would really like to determine, particularly the recent trend of fishing mortality, and provides no evidence about them. As will be discussed below, it is also a method which is very sensitive to errors in the catch data, which may seriously affect the population estimates obtained. A similar interpretation of the data, based on similar assumptions, which is less sensitive to these errors can in fact be constructed using separable VPA, and this is preferable, particularly if the analysis is to form the basis of a catch forecast. Finally, it should be noted that it is *not* appropriate to carry out a catch

Table 7.8 North Sea cod: population estimates from cohort analysis with implausible terminal *F*.

Age	Year						
	1990	1991	1992	1993	1994	1995	1996
1	72 438	86 612	198 535	72 433	483 640	28 252	
2	96 548	48 593	58 581	137 241	54 947	381 337	8 233
3	24 172	29 559	18 456	18 812	62 091	22 190	254 616
4	7 925	8 938	8 964	7 242	5 078	31 727	6 466
5	10 272	2 543	4 315	2 819	3 023	1 373	21 184
6	522	6 182	822	2 576	880	1 695	400
7		152	4 128	240	1 720	257	1 132

curve analysis to determine starting assumptions for a VPA, whether using the JAM method or otherwise, because the assumptions made are substantially stronger than those needed for the VPA itself, and are not more likely to be true.

7.3.4 *Trial VPA – its virtues and its vices*

A trial VPA is a very simple procedure enabling a quick preliminary analysis of a set of catch-at-age data to be carried out. Even the Judicious Averaging Method for setting the terminal *F* values relies on weaker assumptions than alternative methods such as catch curve analysis, and the whole thing can easily be set up using a spreadsheet program on a microcomputer, particularly if one makes use of Pope's cohort analysis algorithm (equation 7.2). The calculation can be done with only (say) 10 years and 10 ages – only 100 numbers – and survey or fishing effort data are not necessary. One should not, however, allow oneself to be seduced by all this convenience. Regarded as a statistical procedure, a simple trial 'untuned' VPA is completely underdetermined, and can at best be thought of as a non-unique transformation of the data. The catch data are also treated as though they were exact, and any sampling and measurement errors feed through directly into the fishing mortality and population estimates obtained, especially of the survivors at the end of the final year, which is an undesirable feature.

Table 7.9 North Sea cod: fishing mortality estimates from cohort analysis with implausible terminal *F*.

Age	Year					
	1990	1991	1992	1993	1994	1995
1	0.199	0.191	0.169	0.076	0.038	1.033
2	0.984	0.768	0.936	0.593	0.707	0.204
3	0.795	0.993	0.736	1.109	0.471	1.033
4	0.937	0.528	0.957	0.673	1.108	0.204
5	0.308	0.930	0.316	0.964	0.378	1.033
6	1.033	0.204	1.033	0.204	1.033	0.204

7.4 SEPARABLE VPA

7.4.1 *Separability of fishing mortality*

The 'solutions' of ordinary VPA, based on different assumptions about terminal *F*, all fit the data equally well (exactly), and cannot therefore be distinguished on the basis of their goodness-of-fit. There is no doubt, however, that some of the possible solutions would be regarded by any reasonable person as more plausible than others. An example of an implausible interpretation is given in Tables 7.8 and 7.9. This was constructed by inserting alternately high and low estimates of the survivors, leading to values of approximately 1.0 and 0.2 alternately for terminal *F*. The oddity of this interpretation is obvious even in Table 7.9,

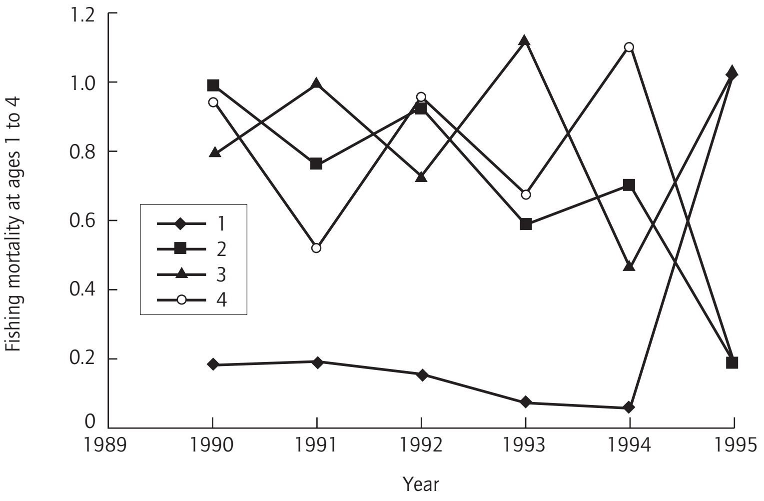

Fig. 7.6 Fishing mortality estimates for implausible terminal *F* assumptions.

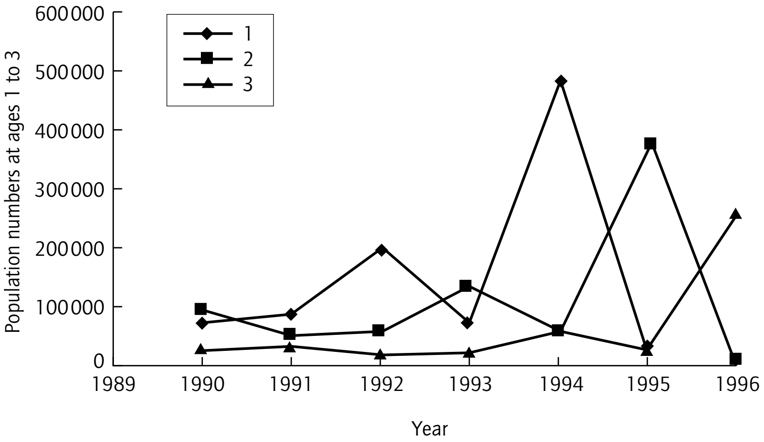

Fig. 7.7 Population numbers for implausible terminal *F* assumptions.

but may be more easily appreciated graphically, as in Figs 7.6 and 7.7.

This shows that the exploitation pattern implied by this analysis is very 'rough', alternating between high and low values on adjacent ages and cohorts, and that the positions of the highs and lows are reversed each year, creating a 'checkerboard' or diagonally banded pattern. This may be compared with the equivalent diagram derived from the JAM analysis, shown in Fig. 7.4. Here the exploitation pattern is more or less flat, and has a similar shape in each year. One feels instinctively that Fig. 7.4 represents a more plausible interpretation of the data than Fig. 7.6. Why?

Fishing mortality is a function of both time and age – we usually write it as $F(y,a)$. However, once fish have reached a certain age and size, they mature, their growth slows down and they tend to behave as a group, so that fish of similar ages are found together, and are of similar size. Even if they deliberately tried to do so, fishermen would have difficulty in applying a much different fishing mortality to adjacent age groups of the same stock – and there is no obvious reason why they should try to do so. One would therefore suppose that fishing mortality should not change very much between adjacent age groups in the same year, at least once the fish are mature and fully recruited. One would also expect that the exploitation pattern created by fishing should not normally vary haphazardly between one year and the next. Progressive changes over time are quite possible, as are sharp changes, for example if and when a new larger or smaller minimum mesh size is enforced. These changes should, however, be systematic rather than haphazard. It is for these reasons that one feels that the smoother and less structured pattern of fishing mortality of Fig. 7.4 is more plausible than that of Fig. 7.6. The argument is based on the internal consistency of the interpretation – one is favouring the interpretation in which adjacent values of fishing mortality are more or less similar, and in which the exploitation pattern is fairly consistent from year to year.

This argument can easily be formalized. Let us seek an interpretation in which the exploitation pattern (the *relative* fishing mortality on each age group), denoted by $S(a)$, is the same each year, although it is still an unspecified function of age. The overall level of fishing mortality, denoted by $F_s(y)$, where the subscript s is used to identify this as the overall F, subject to the assumption of separability (see below), may change as required from year to year. This constitutes a separable model for the behaviour of fishing mortality:

$$F(y,a) = F_s(y)S(a). \tag{7.5}$$

This technique, of representing a function of two variables by the product of two functions of one variable, is known mathematically as separation of variables. Hence the common name, separable VPA, used for the method of analysis based on this model (Pope and Shepherd 1982). It should be noted that in equation (7.5) there is a degree of arbitrariness in the definition of F_s and S. One could take any set of values for them, multiply all the F_s values by a constant, and divide all the S values by the same constant, and have exactly the same set of values for $F(y,a)$. To remove this ambiguity it is necessary to apply some normalization constraint. There are many possible ways to do this, but the simplest and most common is simply to specify that S is defined to have the value 1.0 at some age, the *age of unit for selection*, denoted by $a^\star$. All the other S values are then defined relative to that on this age, and the F_s values are then conditional on the exploitation pattern so defined. The choice of $a^\star$ is in principle completely free, but some practical considerations are discussed below.

7.4.2 Indeterminacy of terminal F and terminal S

There are many possible ways of fitting such a model to a set of catch-at-age data. A number of methods based on direct least squares fitting have been proposed (Pope 1974; Doubleday 1976; Gray 1977), but were not very successful. The reason for this was elucidated by Pope and Shepherd (1982). One can remove the effect of varying year-class strength in the catch-at-age data by taking ratios of adjacent catches for the same cohort, i.e.

$$C(y,a)/C(y+1,a+1). \tag{7.6}$$

According to the separable model, the logarithms of these ratios should be well approximated by a two-way analysis of variance based on the main effects, a year effect and an age effect, only. In practice one finds that such an analysis of variance can indeed explain a very large part of the variance of the log : catch ratios, leaving residuals which are usually quite consistent with expected sampling errors.

The consequence of this is that one can only determine, from such an analysis of variance, a set of values for the ratios $F_s(y)/F_s(y+1)$ and $S(a)/S(a+1)$. One has, from the row and column means (the main effects) of the log : catch ratio matrix, just enough constraints to specify and determine all these ratio uniquely. Given catch data for t years and g age groups there are only $(t-1)$ column means and $(g-1)$ row means, and these are not all independent because the grand mean of both sets is the same. One therefore has enough constraints (equations) to determine only $(t+g-3)$ parameters. The normalization constraint $S(a^\star) = 1.0$ provides an additional equation, leaving just enough to determine the $(t-1)$ ratios of F_s and the $(g-1)$ ratios of S only.

The solution in terms of the $F_s(y)$ and $S(a)$ values themselves is therefore twofold indeterminate. This means mathematically that attempts to determine these parameters directly, for example by least squares, are likely to fail, because the problem is singular, involving the inversion of a matrix which is rank-deficient of order two, or three if no normalization constraint on S is used. The argument above is based of course on several approximations, and is not exact. For this reason the singularity will not prove to be exact in practice, but the system is likely to have two very small eigen-values (three if $S(a^\star)$ is not fixed). The problem is very similar to that of multiple regression using correlated (co-linear) explanatory variables. The solution of such ill-determined systems is notoriously difficult. In practice all this means that in spite of the very strong model of separability, as expressed by equation (7.5), and the consequent reduction in the number of parameters to be determined, to many fewer than the number of data points, the problem of determining fishing mortality *still* has no unique solution. The number of undetermined parameters has in fact been reduced from $(t+g-1)$, the number of terminal F values required for conventional VPA, to 2 for separable VPA, assuming that natural mortality is known, throughout, which is certainly progress, but not enough. The problem is structurally underdetermined.

There are still therefore infinitely many possible interpretations based on separable VPA. It turns out that, because the separable model is only an approximation, these alternative solutions are only approximately equally good fits to the data, and of course none of them are exact. If one had exact data, it would be possible to choose among them on the basis of goodness-of-fit. In practice the differences are completely swamped by sampling errors, and goodness-of-fit is generally useless as a guide to the correct solution. To obtain a completely specified solution, it is therefore necessary to supply two additional pieces of information, usually by means of extra assumptions. Because of the convergence property of VPA, and by analogy with conventional VPA, it is usual to require the analyst to provide assumptions for terminal F and terminal S. This means values for $F_s(t)$ and $S(g)$ are required where t is the last year and g the oldest age group. Notice that because S has been normalized to unity, the value $S(g)$ is relative to that on the reference age $a^\star$, whilst the value of $F_s(t)$ is absolute, and of approximately the same size as the actual individual fishing mortality on age $a^\star$ in the last year. The analyst therefore again has to assume precisely those things he would most like to determine, namely the actual level of fishing mortality in the most recent year, and a parameter which controls the overall shape of the exploitation pattern. In spite of the strong assumption of separability, we are still left with an analysis which can determine the details, but not the overall underlying patterns.

7.4.3 *Practical implementation of separable VPA*

Given the indeterminacy of the solutions discussed above, it may be questioned whether there is any point in carrying out separable VPA rather than, say, the JAM analysis based on averaging, as discussed above. We believe that there is, for several reasons. First, separable VPA provides a simple and convenient method for generating trial analyses, by specifying only two numbers which represent clearly defined and stated assumptions. Second, the fact that the analyst is required to make these explicit choices forces the recognition of ignorance. Third, it turns out that the surviving populations determined by separable VPA are less sensitive to measurement errors than those of the JAM and similar methods. Finally, separable VPA proves to be a most useful tool for examining and determining exploitation patterns, over several fairly short periods of time required. By contrast, in the more heuristic methods such as JAM, the assumptions are less clear and less explicit. Why take the average itself? – why not 1.2 or 1.5 or 0.6 times the average? Why average over five years or ages – why not three or 10 instead? Also, if these choices are made automatically instead of explicitly, the analyst may be seduced into believing that he has determined something which he has actually assumed.

A surprisingly efficient simple algorithm for separable VPA, invented by Pope, was described by Pope and Shepherd (1982). This algorithm has been implemented several times, and is provided as part of the Centre for Environment, Fisheries and Aquaculture Sciences (CEFAS) Lowestoft and ICES VPA program suites. It can also be executed perfectly well using a spreadsheet package on a microcomputer, if required. To run separable VPA, the analyst must of course supply a complete set of catch-at-age data, for a minimum of about five years and five age groups in practice, together with data or, more likely, conventional assumptions about the level of natural mortality. The first choice to be made is the age for unit selection. This is in principle arbitrary and may be chosen freely as it will not affect the essential results. In practice it is recommended to choose the youngest age group that is likely to be fully exploited, which can usually be guessed adequately as that age which usually contributes most to the catch in numbers, or the next older age group. This is advisable because it helps to make the results for the exploitation pattern relatively independent of the choice of fishing mortality, and vice versa.

7.4.4 Interpretation of results and the calculation of year-class strength

Once values for terminal F and terminal S have also been selected, the essential results of separable VPA are a set of overall fishing mortalities $F_s(y)$, and a set of selection factors $S(a)$, normalized to $S(a^*) = 1$. These may immediately be used to generate a full matrix of fitted separable fishing mortalities using the underlying model equation

$$F'(y,a) = F_s(y)S(a). \tag{7.7}$$

The result of separable VPA is in fact an interpretation of the data which is as far as possible consistent with this separable model, but not forced to fit it exactly. The closeness with which the solution conforms to the model depends on a number of factors, and in some part of the matrix, such as in the earlier years, the fit may be quite slack. The fishing mortalities given by equation (7.7) are of course rather smooth and well-behaved, and represent some sort of averaged values.

The fitting procedure itself is based on the log : catch ratios, and leaves year-class strength undetermined. Once $F'(y,a)$ has been determined, the correspondence between it and the catch data may, however, be used to determine year-class strength. Every pair of values $F'(y,a)$ and $C(y,a)$ implies a value for the current population size (in numbers), using the catch equation (7.1), and each of these may be converted using conventional VPA or cohort analysis to a value of either initial year-class strength or terminal population.

Using this procedure one should not be surprised that the fishing mortality estimates in the final year are just as noisy as those in previous years and include occasional odd high or low values. This is a natural consequence of the procedure, since such values are the result of catch data in the final year which are somewhat inconsistent with previous data for the cohort, presumably as a result of sampling and ageing errors. These anomalous values are not usually carried forward into the catch forecast or other subsequent calculations, and need not be caused for great concern, although they may bear further investigation since they may be due to data processing or transcription errors (see commentary on measurement error in Chapter 13, this volume).

An example is given in Tables 7.10 and 7.11, for the same North Sea cod data set, using $F_s(t) = 1.0$ and $S(g) = 1.0$, and these results are illustrated in Figs 7.8 and 7.9. The exploitation patterns of Fig. 7.9 may be compared with those of Figs 7.2 and 7.3: they are clearly similar to those from the JAM method, which is to be expected since they are, in this instance, based on similar assumptions.

7.4.5 Discussion

Separable VPA is a very convenient way of generating exploratory VPAs, and very effective in forcing the analyst to come to terms with ignorance concerning estimates of terminal F and terminal S. It is also a useful objective way of estimating exploitation patterns over limited periods of time, for example before and after an expected change: three years in the absolute minimum period of time for this, but four or five would be more preferable as minimum periods in practice. Finally, the usual (e.g. CEFAS, Lowestoft and ICES) implementations include the estimation of weighted average terminal populations, which is a most useful feature, particularly with data of poor quality.

Table 7.10 North Sea cod: fishing mortality estimates from separable VPA.

Age	Year					
	1990	1991	1992	1993	1994	1995
1	0.211	0.193	0.221	0.082	0.128	0.180
2	0.977	0.835	0.931	0.898	0.774	1.044
3	1.016	0.976	0.885	1.087	1.117	1.295
4	0.916	0.909	0.915	1.024	1.043	0.997
5	0.886	0.881	0.859	0.864	0.882	0.880

Against this, the method does not permit external data such as CPUE from commercial fleets or surveys to be incorporated directly, and it really exposes the analyst's ignorance, rather than helping him to overcome it. Furthermore, the method is based on the assumption of a constant exploitation pattern, for the total international fishery, for some period of time, and some range of ages. The results are not, of course, forced to fit this model exactly, but it does nevertheless underpin the solutions obtained. In the case of changes of exploitation pattern on the youngest ages, there is little

Table 7.11 North Sea cod: population estimates from separable VPA.

Age	Year						
	1990	1991	1992	1993	1994	1995	1996
1	68 369	85 590	155 264	67 535	147 955	109 885	0
2	95 232	45 317	57 804	101 949	50 951	106 557	75 138
3	20 399	29 346	16 099	18 664	34 011	19 243	30 710
4	7 900	6 045	9 055	5 438	5 155	9 112	4 314
5	4 555	2 588	1 995	2 968	1 599	1 487	2 754

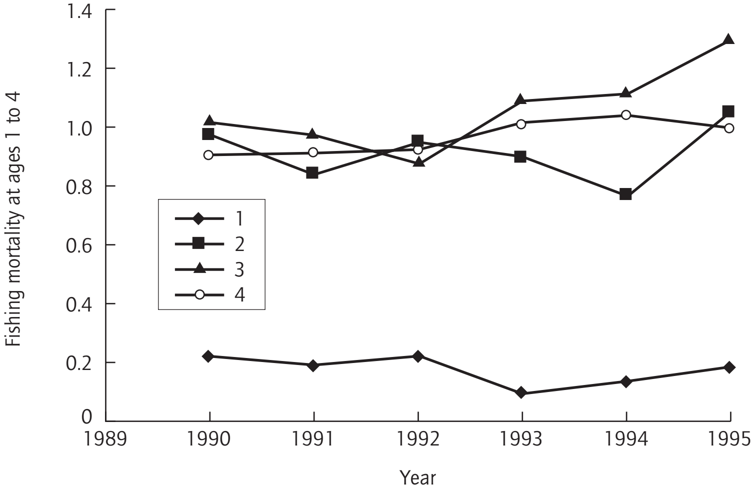

Fig. 7.8 Fishing mortality estimates from separable VPA.

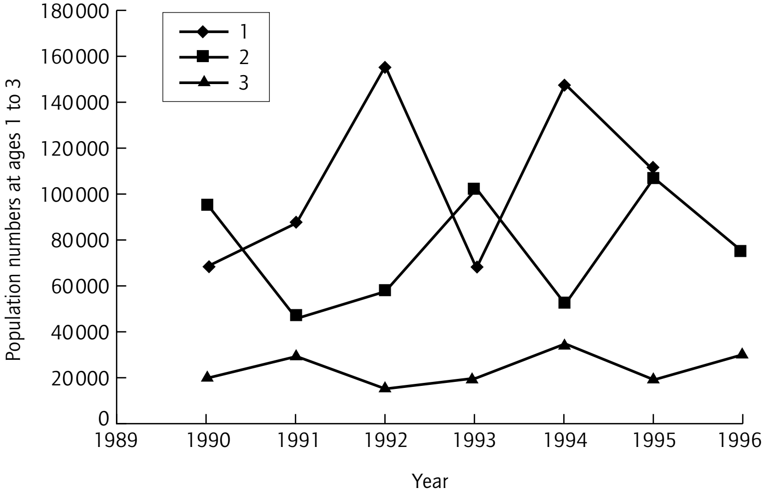

Fig. 7.9 Population estimates from separable VPA.

doubt that such changes are a priori quite likely, because of differing spatial distributions of juvenile fish from year to year. They are, however, also confounded with higher sampling errors on younger ages. It is, indeed, not at all clear how much larger residuals on the younger ages are due to process errors through changes of exploitation pattern and how much to sampling errors (Sparre and Hart, Chapter 13, this Volume). In any case, any unexpectedly high or low catches of young fish due to either process in recent years will be interpreted by separable VPA as being due to large or small year classes, and since no long run of data exists for these recent year classes there is no prospect of deciding which is the correct interpretation.

The estimates of newly recruiting (recent) year-class strengths obtained by separable VPA should therefore be treated with appropriate scepticism. They are based on the application of 'normal' levels of *F* to the few catch data available, but may be due either to a real large or small year class, a shift of exploitation pattern, or simple sampling error. An analysis of the variability (log standard error) of historic fishing mortality on the age in question gives a rough idea of the probable imprecision of the estimates. The true interpretation cannot be deduced from catch-at-age data alone: independent information, such as indices from a series of recruit surveys, is vitally important for this purpose. In the absence of such information the estimates from separable VPA may, however, give some rough indication of recruiting year-class strength, but these should be handled with extreme caution, and alternative explanations sought, especially if they are outside the historic range of the data.

On balance, we consider that separable VPA is a useful tool, if carefully applied, and preferable to more heuristic methods such as those discussed above, including the JAM method. When total catch-at-age data is the only thing available, it may indeed be the method of choice, but in this situation the risk of an incorrect interpretation is high, and independent CPUE and/or survey data are greatly to be desired. Their analysis is discussed below.

7.5 TUNING OF VPA USING CPUE AND SURVEY DATA

7.5.1 The analysis of catchability

The need for additional information to resolve the indeterminacy of VPA has been stressed above.

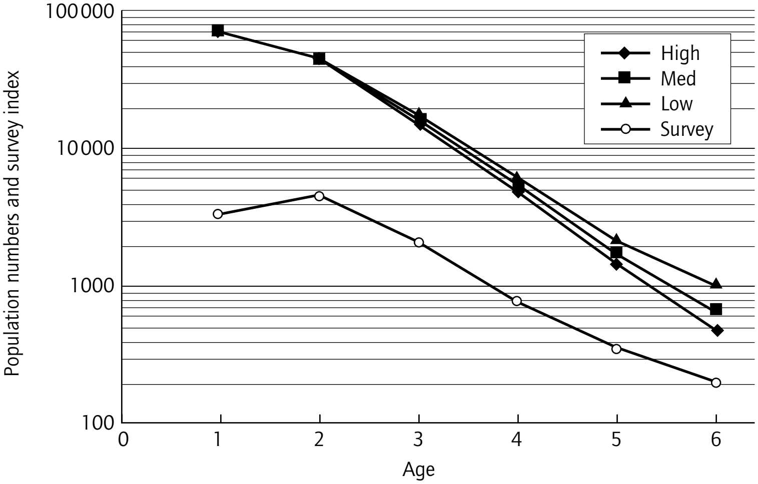

Fig. 7.10 North Sea cod: the 'tuning' problem. The method changes the terminal *F* value in an attempt to make the trend line for population numbers parallel the trend line found in the survey data. High, medium and low *F* values are used.

Common forms of information suitable for this purpose are indices of abundance such as catch per unit effort (CPUE) from commercial fleets or research vessel surveys, or indices derived from acoustic surveys. It will be assumed here that age composition information is available to go with these data, although this is not always the case, and that a reasonable time series of say five or more years of data are available.

Such data therefore provide estimates of the relative abundance of each year class through time, and may therefore be used in principle to choose the VPA interpretation in terms of absolute abundance most closely in accordance with them. This process is usually referred to as 'tuning' the VPA, by analogy with the process of tuning a musical instrument to the correct absolute pitch. The process is essentially a synthesis of two different sorts of information, the estimates of *relative* abundance from abundance indices, and the estimates of *absolute* abundance from VPA applied to catch data. In the interpretation of the former we have an unknown *multiplicative* calibration constant, which is the catchability, and in the latter an unknown *additive* constant, the terminal population. By putting the two data sets together we can in principle determine both of these unknowns, and thus the full sequence of absolute population size, as illustrated in Fig. 7.10.

The use of CPUE data on its own to provide indices of abundance, and hence estimates of total mortality, using the log:catch ratio method, i.e. $Z(y,a) = \ln[u(y,a)/u(y+1,a+1)]$, has a long history (see e.g. Gulland 1983). Its use for VPA tuning is, however, relatively recent. Many methods have been invented, particularly by assessment working groups during the 1970s, when VPA became widespread, and as its indeterminacy became understood (Ulltang 1977). The reason for the multiplicity of methods is that there are many possible choices to be made, even assuming that one uses some sort of regression method. Should one regress *F* on effort or CPUE on population size? What type of regression is appropriate – predictive, functional or calibration? Should the regression be forced through the origin? Should a logarithmic transformation be applied? What criterion of best fit should be used? Different answers to these questions all generate different methods of analysis which, given the quite substantial sampling errors of catch-at-age and CPUE data, can easily generate results which differ from one another by amounts which are of considerable practical significance, even if the differences are not statistically significant! This is a classic example of the need to exercise more care in choosing methods for the analysis of poor data than is required if one has good (precise) data. However, Laurec and Shepherd

(1983) showed that many of the doubts and confusions can be clarified if one takes care to treat the problem as an exercise in statistical modelling, and if one regards the whole process as an exercise in the analysis of catchability. The reasons for this are as follows.

The use of fishing effort or CPUE data relies on the assumption that fishing mortality should be strongly related to fishing effort, preferably proportional to it, and that CPUE should be similarly related to abundance. It is perhaps not quite obvious that the constants of proportionality are the same. If E is fishing effort, u is CPUE and q is the catchability coefficient, we may write

$$F = qE \tag{7.8}$$

or alternatively,

$$u = q'\overline{P}, \tag{7.9}$$

where $\overline{P}$ is the population averaged over the year in the same way as is the CPUE, and we allow the possibility that q' may possibly be different from q. However, by definition, $u = C/E$, and $C = FP\,[1 - \exp(-Z)]/Z$, so $C = F\overline{P}$, since $[1 - \exp(-Z)]/Z$ is just the ubiquitous averaging factor relating the average of an exponentially declining quantity to its initial value. Thus, from equation (7.9)

$$q'\overline{P} = u = C/E = F\overline{P}/E \tag{7.10}$$

and thus $q' = F/E = q$. The models (7.8) and (7.9) are therefore precisely equivalent, and involve the same catchability coefficient, so that in principle it should not matter which of these is used as the basis of the analysis.

However, in practice, different results may arise because of fitting procedures. The basic 'observable' quantities may be regarded as C and E (raw data), and P which are simply derived from cumulative catches by VPA. Using model (7.8), one would naturally fit the relationship

$$C/P \approx qE, \tag{7.11a}$$

for example, by fitting a regression of C/P against E.

Similarly, using model (7.9) one would naturally apply the same procedure to

$$C/E \approx qP, \tag{7.11b}$$

However, the results of these analyses would not generally be the same. Firstly, use of standard predictive regression formulae to fit these equations would imply different assumptions about the nature of the errors, and therefore lead to different results. In case (7.11a), effort (E) would implicitly be treated as exact, and uniform additive errors would implicitly be assumed for the ratio C/P. In case (7.11b), P would be treated as exact, with uniform additive errors in C/E. The effects of these different assumptions would usually be greatly increased if one permitted non-zero intercepts for the regressions, which might seem to be a normal and natural thing to do.

Secondly, the effects of variations of effort and year-class strength on these two possible relationships are quite different. Consider a typical situation where effort does not change very much, but year-class strength does. The first model (F versus effort) leads to a plot like Fig. 7.11(a), whilst the second (CPUE versus population) leads to a plot like Fig. 7.11(b).

The first plot exhibits no convincing relationship between F and effort. One has a cloud of points some way away from the origin. The correlation coefficient will be very small and probably not even statistically significant, and the usual predictive regression coefficient will likewise be very small. With no convincing evidence of any relationship, the faint-hearted analyst could easily give up and conclude that the CPUE data are worthless. Contrast this with the situation shown in Fig. 7.11(b). Here one sees a good spread of points tracing a fairly convincing linear relationship. The correlation coefficient will be high, with a highly significant regression coefficient, and an intercept near zero. Yet these are simply different presentations of the same data! And the position could in fact be reversed if one had a stock where year-class strength was rather invariable, but effort had

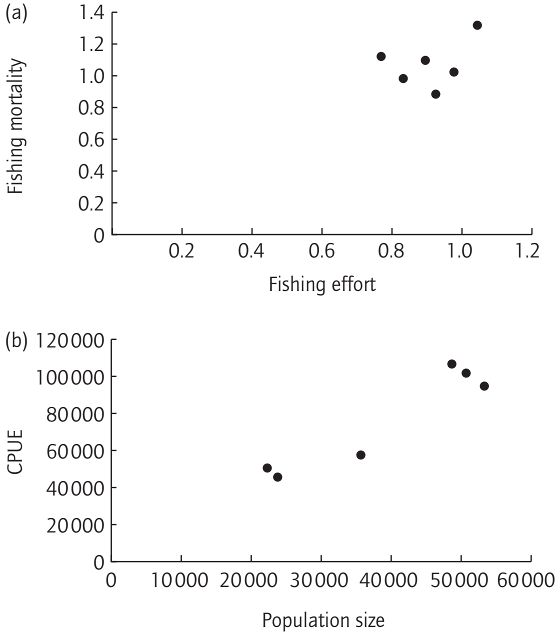

Fig. 7.11 (a) Relationship between fishing mortality and effort; (b) relationship between CPUE and population size. The graphs illustrate the relationship implied by (a) equation 7.8 and (b) equation 7.11(a).

changed considerably during the period covered by the data.

This confusion is reduced considerably if one realizes that allowing a non-zero intercept in these regressions is in principle inconsistent with the postulated models (equations 7.11(a) and 7.11(b)). If one forces the regressions through the origins the discrepancy between the results using these two alternative models is much reduced: the correlation coefficients based on deviations from the origin will be similar, as will the regression coefficients, which are the estimates of catchability, though they will still not be quite the same.

Even then, however, there is still scope for considerable confusion and argument. One could make an excellent case for doing the regressions the other way round, which would mean using a calibration rather than a predictive regression (see Shepherd 1997). Furthermore, when working with model equation (7.11b), it would be very reasonable to apply a logarithmic transformation to the data, since both u and P are fundamentally non-negative quantities, and both are probably measured with something approaching a constant coefficient of variation, rather than with constant additive errors.

Most of this confusion can, however, be avoided if we remember that the whole analysis is founded on the presumption of a more or less constant catchability, which is of course given by

$$q = u/\overline{P} = (C/E)/\overline{P} = \left(C/\overline{P}\right)/E = F/E. \qquad (7.12)$$

Thus q is just the slope of a straight line joining each of the points to the origin, in *both* Figs 7.11(a) and 7.11(b). Given the statistical properties of C and P, mentioned above, it would be reasonable and preferable to work with the logarithm of this equation, i.e.

$$\ln(q) = \ln(C) - \ln(P) - \ln(E). \qquad (7.13)$$

This has the incidental benefit of circumventing any argument as to whether one should in fact try to estimate the reciprocal catchability $(1/q)$, since after log transformation this becomes an equivalent procedure. If one is prepared to treat catchability as a constant, for each fleet and age, then one needs to do no more than estimate the mean of $\ln(q)$ from applying equation (7.13) to the data. This is equivalent to estimating and using the geometric mean slope of the lines joining the points to the origin in either of Figs 7.11(a) and 7.11(b). This commonsense approach was suggested by Laurec and Shepherd (1983), and leads to a VPA tuning method often known as the Laurec–Shepherd method.

The approach implied by this procedure can, however, be extended. One can treat the individual estimates of log catchability from equation (7.13) as a derived quantity, whose variation with time, population size, effort and weather can potentially be examined, and tested against the underlying default null hypothesis that it should be a constant. This constant will be different for each fleet, although preferably not varying with age for older fish. We are therefore led to consider the statistical modelling of log catchability, rather than any other quantity. We expect that it should be approximately normally distributed and homoscedastic, assumptions which can be tested, and we shall, in the absence of evidence to the contrary, treat it as a constant, because that is the underlying model based on our understanding of the nature of the catching process, at least for demersal fish.

For operational use, however, well-automated methods of analysis and processing are required. All possible variations of catchability cannot be considered, but it is very important to check for trends with time. This is because, regrettably, much fishing effort and therefore CPUE data are not well standardized for possible changes of fishing power. Such standardization is not easy to do well (see e.g. Gulland 1983), and even if one had done a good job of allowing for changes in the composition of the fleet, in the engines and gears used by the different vessels and so on, there is still the problem of changes of catchability caused by natural shifts in the spatial distribution of the fish, or shifts in the spatial distribution of fishing effort within the strata of the sampling scheme in use.

Because of the irregularity described, abundance indices from carefully controlled series of surveys by research vessels, covering the whole distribution of the stocks, are much the preferred form of data. However, the sampling levels attained on surveys may not be sufficient to keep the level of sampling errors low enough for very reliable analysis, especially on the older and less abundant age groups. It is therefore usually necessary also to use and analyse data from commercial sources, in which changes of catchability are more likely.

A useful practical procedure is to examine such data for changes of catchability with time, not just because such changes are the likely consequence of imperfect standardization of the effort data, but because other changes, such as those due to climatic changes or changes of distribution and abundance, which include density-dependent changes (Myers, Chapter 6, Volume 1) are likely also to show up as time trends, even if time itself is not the underlying causal variable.

7.5.2 **Ad hoc** ***methods for tuning VPA***

This approach to the analysis of catchability leads directly to practical procedures for tuning VPA. Starting with a trial VPA, one iteratively computes catchability, analyses it by means of regressions and/or averages, uses these estimates to predict terminal F, and repeats the procedure until it has converged. Such methods are generally referred to as *ad hoc* tuning methods, because they are not directly based on fitting a formal statistical model. They should not, however, be confused with even more *ad hoc* approaches which have sometimes been used, based on regressions of F on fishing effort, possibly raised in some way to the total fishery, or correlations of some measure of biomass with CPUE. These are fraught with problems and not recommended.

The *ad hoc* tuning method of analysis, for each fleet and age, proceeds as follows: past estimates of log catchability over the available time period are used to make an estimate of the current value. If one is assuming constant catchability, this estimate is just the average. Otherwise a regression against time is calculated, and used to make the prediction. A conventional predictive regression is appropriate here, since all the errors are in the catchability estimates: the explanatory or independent variable, time, is known exactly. In either case, an estimate of the standard error of the prediction is also made, either from the standard deviation of the observations about the mean, or the standard three-term formula for the standard error of a further prediction from a regression. Note that the standard error of the mean, or the two-term formula for the standard error of the fitted value, are not what is required here. Any prediction based on the estimate will be fully affected by the usual level of error in the observations, so this residual error must be included via the three-term formula.

The estimation of these standard errors is important, because one often has several sets of abundance indices. Each may be analysed in this way, each may be used to make a prediction, and these results will invariably be in conflict with one another. Some way of reconciling these conflicting estimates is needed, and a weighted mean, with weights based on the inverse variances of the individual estimates, is an obvious and attractive candidate. This overall estimate can in fact be shown to be the minimum variance estimate, and can be justified as a maximum likelihood estimate under suitable and not unreasonable assumptions. It clearly makes sense, too, to give greatest weight to these estimates which have historically given the most precise predictions. Prior estimates of the quality of the various data sets based, for example, on the number of stations worked, the proportion of the total catch taken, or the area covered, may in fact be quite misleading: the acid test should be the actual performance based on the historic data set.

The full VPA tuning algorithm may therefore be written in pseudo-code as follows:

Pseudo-code for ad hoc tuning of VPA

```
Initialize: Set terminal $F = 1.0$ (for oldest ages and last year)
    Do VPA
        For each age
            For each fleet
                For each year
                    Calculate $\ln(q)$
                Next year
                Fit model to $\ln(q)$ (by regression)
                Predict terminal $\ln(q)$ (and standard error thereof)
                Calculate terminal partial $\ln(F)$
                Raise to terminal total $\ln(F)$
            Next fleet
            Combine to get weighted average terminal total $\ln(F)$
            Retransform
        Next age
    Repeat (VPA et seq.) until converged
Print results etc.
```

As mentioned above, in the past, numerous variations on this preferred procedure have been used. For example, a similar calculation can be carried out without using the logarithmic transformation, or regressing q (or $ln(q)$) against population size, or fishing effort. It is also possible to perform similar analyses on CPUE data which have been aggregated over fleets in some way. All these variants should now be regarded as relatively inappropriate and inferior, and only of historical interest. Readers interested in these aspects are referred to the reports of the ICES working group on the Methods of Fish Stock Assessment for the period 1983 to 1988 for more details. Some computer packages may still offer these variants as options, but we would recommend that they be avoided. The ICES working group also recommended that other possible variants which are still virgin should be left intact! Simulation tests of various methods have been carried out (Pope and Shepherd 1985; Anon. 1988; Sun 1989) and confirm that the procedures described above work about as well as anything else which was then available, and as well as could be expected, given the inevitable imperfections in the available data.

These methods are often referred to as the Laurec–Shepherd method, where catchability is treated as constant and its average is used, and the Hybrid method when a time trend of catchability is fitted. A Mixed method is also possible where trends are fitted for some fleets but not others. The methods may be available as options in standard computer packages such as the Lowestoft and ICES VPA packages.

7.5.3 Practical aspects

In carrying out VPA tuning and similar analyses, a number of practical details have to be decided, which may have significant effects on the results. The most important of these are discussed below, and these issues are still relevant when more advanced methods are used.

7.5.3.1 Inclusion or exclusion of data

Firstly, if one has an abundance of data, one must decide how much of it to use. It is not obvious that it is best to use all of it. Firstly, the data for the youngest and oldest age groups may be poorly sampled, with very high sampling errors, and at best may add little to the analysis, and at worst may confuse it or even cause it to crash. Prior estimates of precision are not usually available, but the occurrence of numerous zeroes is almost always diagnostic of severe sampling problems (for more on sampling see Evans and Grainger, Chapter 5, this volume). Practical computer programs have to trap zeroes and handle them as best they can, but this is usually a rather simple-minded procedure, and should not be relied upon to any great extent. Age groups with more than the occasional zero in either total or individual fleet catches should be excluded from the analysis, if necessary by deleting them from the data files.

Secondly, there is no doubt that in fisheries things change, for reasons which are not always understood. Old data may therefore no longer be representative of current conditions. There may have been some unrecorded changes in the manner of fishing, by either commercial or research vessels, or in the spatial distribution of the stocks because of climatic or multi-species effects, or the way in which the data is worked up may have changed. In general, therefore, one usually wishes to place greater reliance on recent data than on old data. In practice a VPA can be carried out quite satisfactorily on five to 10 years' data, and data more than 20 years old may be regarded as ancient history. A convenient way of taking account of this is to apply a *tapered* weighting to the data before regression or averaging, the terminology being borrowed from spectral analysis.

Finally, it is necessary to decide whether data for all available fleets should be included in the analysis. In principle the method of analysis is itself testing the quality of the various data sets, and allowing for this as far as possible, so that all available data may indeed be used. In practice, however, there is little point in including bad data along with good data – it will be down-weighted, and merely increase the labour of the data preparation and the volume of the output with little or no benefit. Furthermore, although modern tuning methods do attempt to allow for data of varying quality, they cannot do so perfectly. They are not completely impervious to bad data, and may be adversely affected by it – particularly by outliers in the data for the most recent year. It is therefore advisable to remove poor-quality data sets once these have been identified. Here the provision of good diagnostic information is most helpful (see below). No hard and fast rule can be given, but we would certainly regard any data set which consistently gives log standard errors of one or more, on significant age groups, with grave suspicion – that means that the prediction is not even good to within a factor of 3 either way, meaning that it is barely yielding even an order-of-magnitude estimate.

7.5.3.2 *F* on the oldest age

A second important choice in practice is what to select for *F* on the oldest age groups. This is, of course, not determined by the tuning procedure, and must be specified in some other way. At one time it was common practice to set these *F* values arbitrarily, or by trial and error, or simply to choose a value, and not subsequently ever change it. When overall levels of *F* are high at around 1.0, these choices are adequate: the resultant *F* values on other ages are little affected, because of the strong convergence of the VPA. At moderate and low levels of *F*, however, the effects are more serious, and arbitrary or careless choices of *F* on the oldest ages can lead to very strange results and odd exploitation patterns. This is in fact the key to a practical solution of the problem, which is addressed in a more fundamental way by the integrated and 'survivors' methods of analysis discussed later on.

Bearing in mind that the results of separable VPA show that the shape of the exploitation pattern on the older ages is undetermined, and that we have added nothing in the *ad hoc* tuning methods to determine it, it seems reasonable to choose *F* on the oldest age group so that the shape of the exploitation pattern is internally consistent – for example, terminally flat, meaning that it levels off on the oldest ages. This can be done by setting each *F* value to some proportion of the average over a few of the next younger age groups. A proportion of 1.0 and an average over about five age groups will usually achieve terminal flatness, and these are suitable default choices. It is, however, still very important not to choose low values for *F* on the oldest ages without strong reasons, since this can destroy the convergence property of VPA, and drive one to the ever-present trivial interpretation of low *F*, and large populations, everywhere. If in doubt, one should err on the side of higher *F*s on the older ages rather than low ones. It occasionally happens that an initial tuning analysis gives surprisingly low *F*s. In such a case it would be desirable to test the effect of increasing the oldest age *F*s, by increasing the proportion above 1.0, to see if this removes the problem.

7.5.3.3 Diagnostic information

Even if one is using an analysis package which is fairly well automated, it is important that as much statistical examination of the data, and the fit of the model to it, as possible should be carried out. This requires that good statistical diagnostics be made available. There are, of course, a large number of potential diagnostics which could be calculated, including correlation coefficients between variates, tests of normality and so on. In practice the most important and useful ones, when using a regression method, are probably the estimated slope and its standard error, the standard error of the estimated log catchability, and the highlighting of possible outlying observations. It is important to know the size of the slope and its standard error, so that one can judge both the practical and the statistical significance of the slope, when deciding whether or not to fit a trend of catchability, as discussed in Section 7.5.4 below.

The standard error of prediction of $\ln(q)$ is the best final arbiter of the quality of the result from a particular data series, at a particular age. It controls both the weight attached to each individual estimate, and the overall error of the final weighted estimate of F, which can and should be calculated. As mentioned above, high prediction standard errors indicate problems with a data set, and should never be ignored. Similarly, highlighting of possible outliers helps quality control of the data, as it may pick up data processing errors before it is too late, and will bring unusual results to the analyst's attention for further investigation. These should be regarded as a minimum set of diagnostics. In principle, the more diagnostics examined the better, but it is in practice necessary to strike a balance, because of the psychological disincentive attached to the study of large volumes of output. There is, however, no doubt that there is room for further development of useful diagnostics. This approach has at present been taken furthest in the integrated statistical methods (see Quinn and Deriso 1999).

7.5.4 *Fitting and suppressing trends*

At first sight there seems to be no reason why one should not fit trends of catchability to the data from all fleets in an *ad hoc* tuning analysis, and this approach has indeed been used in practice in the past. In the present context this leads to the so-called Hybrid method. However, it has been known for some time that indiscriminate fitting of trends of catchability is a dangerous procedure (see, for example, Anon. 1983). Qualitatively it is obvious that allowing much variation in catchability must be undesirable – the whole idea of CPUE tuning rests on the assumption that CPUE is an indicator of abundance, and any variation of catchability weakens that foundation. In fact, if one allowed catchability to vary with abundance, rather than with time, CPUE could in fact become independent of abundance, when catchability is inversely proportional to abundance, and therefore lose all utility as an indicator. A similar but less severe problem arises with variations with time. In fact, we now know that allowing for an arbitrary exponential trend of catchability with time causes linearized versions of the equations one is trying to solve to become singular, meaning that they acquire a zero eigen-value, and this makes the solution indeterminate again.

The conclusion from this is therefore that one should not fit trends of catchability unless this is inescapable. Indeed, one may state quite firmly that it is highly undesirable to fit trends to the catchability for all fleets. If one does, the solution will be at best very poorly determined, and at worst effectively a random number. This rules out in practice the Hybrid method in its pure form, which applies to variable catchability on all fleets. One should in fact keep catchability constant for as many fleets as possible. Results of simulation tests (Anon. 1988; Sun 1989) show that paradoxically one may in fact obtain more precise results by *fixing* catchability on all fleets, even when this is an erroneous assumption, than by fitting the trends, even when one only fits the trends where they really exist. This is because the expected reduction of bias by fitting the trends is outweighed in the final prediction error by the associated increase in variance, manifest as sensitivity to noise.

Nevertheless, it would be unreasonable to just fix catchability uncritically by using the Laurec–Shepherd method, for all and any data sets: one needs to start with fixed catchability on 'at least one reliable fleet' – meaning one where there is a high probability of little or no trend in catchability. But this can only be based on a prior assumption, or more commonly prejudice, since there is no way to test the assumption made. Indeed, selecting different fleets to be the standard in this way will usually lead to different results – all the trends are just determined with respect to one another, and all ultimately depends therefore on which subset of fleets are taken as the standard. One may, however, have quite strong grounds for the choice: in general a research vessel survey would be preferred to a commercial data series, and one where it is known that great care has been devoted to standardization of gear and fishing practice would be preferred to one which is known to be conducted in a more haphazard way. Nevertheless, this remains a potential weak point of this and all similar methods of analysis, and if one finds a discrepancy between the results of what should be well-standardized data series, one may be left in doubt about the correct result.

This also serves to emphasize that standardization of effort data remains vitally important, since otherwise one can never have any confidence that a data series may be taken as a standard. Indeed, at first sight it seems that one might as well just discard any data from unstandardized fleets, since one would be able to fit any necessary trend of catchability for them, and they will add little or nothing to the determination of terminal *F*. This would, however, be hasty and undesirable, for two reasons. First, survey data is (one hopes) unbiased with respect to trends of catchability, but it is often quite variable in that it has a high sampling error. Conversely, commercial data may be biased by trends of catchability, but may be based on higher levels of sampling, and hence have lower sampling error although this is not guaranteed. If this is the case, however, including both sets of data should improve the analysis. The surveys will control the absolute size of terminal *F* determined, but the commercial data will help to reduce the variability of the estimates. Secondly, it is often found that surveys give good (precise) results for younger fish, not fully recruited to the commercial fisheries, but poor results for older fish of which relatively very few are caught. The surveys therefore dominate the results for younger fish, and the commercial data dominate for old fish, where the reduction of estimated variance may be substantial. There is therefore still some point in including even unstandardized commercial data, but it would be much more valuable if it were properly standardized.

7.6 THE EXTENDED SURVIVORS METHOD (XSA)

7.6.1 Introduction

Fully integrated statistical methods such as those described by Quinn and Deriso 1999 and briefly outlined by Sparre and Hart (Chapter 13, this volume) are in principle the most desirable methods to use for the analysis of catch-at-age and CPUE data. The models so fitted are as accurate a representation of the dynamics of populations as possible, and they can allow for errors in all measured quantities. They do, however, usually have a large number of parameters to be estimated, and this makes them computationally relatively quite demanding, and sometimes less robust.

These is in fact a middle way between the known crudities of the *ad hoc* tuning methods, and the full integrated statistical methods. This is the 'Survivors' method, which was devised by Doubleday (1981). The original implementation by Rivard (1980) has, however, not been very widely used, partly because it was written in the APL programming language, which is not universally available, and is quite impenetrable to the uninitiated, and partly because it did not always give reliable results (D. Rivard and S. Gavaris, personal communication). The original implementation also allowed for only one set of survey/CPUE data, which is a considerable disadvantage in practice. A development of the original method (Shepherd 1999), known as Extended Survivors Analysis, overcomes these difficulties, corrects an inconsistency in the original formulation, and has given excellent results in simulation tests.

The essential idea of these Survivors methods is that they focus on determining the surviving population for each cohort, and use VPA, or in practice, the cohort analysis algorithm of Pope (1972), for the estimation of past population abundance. Thus, they are expressed directly in terms of the survivors, the variable for which results are really required, avoiding the error-prone projection through the final year characteristic of *ad hoc* tuning procedures. Second, they treat the catch data as error-free in the calibration (VPA) phase of the calculation, but allow for deviations from the resulting population estimates when determining survivors. This reduces the number of parameters to be determined considerably, and permits the use of simple iterative algorithms rather than direct search minimization methods. By treating the catch data as exact during a non-critical phase of the calculation (the VPA), one gains a substantial conceptual and computational saving. The imprecision introduced is unlikely to be severe unless the total international catch-at-age data are subject to larger errors than are the data for individual fleets. This is not impossible, but it seems not to be the usual situation. The method is therefore useful and practical, and achieves some of the benefits of the integrated methods, without incurring the major extra costs.

7.6.2 Description of the method

In this section we outline the method as formulated by Doubleday (1981), in a rather simplified manner, since the original description allows for a number of confusing complications which either were not implemented by Rivard (1980), or are rarely used in practice. The aim is to explain the basis of the method, and to prepare the ground for the account of the Extended Survivors method which follows. The notation used is as follows. Firstly, suffix k is used to index cohorts (year classes). Thus

$$k = y - a. \tag{7.14}$$

Suffix i is used to index ages within a cohort, and the range of i within a summation usually runs from the current age a to the maximum observed within the cohort, $a_{\max}$, where

$$a_{\max} = \min(g, t - k) \tag{7.15}$$

(where g is as usual the greatest true age group, and t is the final year). The notation *cum* (short for cumulative) is used to denote the operation of accumulating something over all subsequent ages within a cohort, so

$$cum = \sum_{i=a}^{a_{\max}}. \tag{7.16}$$

Later, the notation *cum′* will be used to denote accumulation over all previous ages, i.e. over the range $i = a_{\max}, a - 1$. The mnemonic symbol *ECZ* denotes Exponential Cumulative Z or total mortality, i.e.

$$ECZ(y,a) = \exp\{cum[Z(y,a)]\}. \tag{7.17}$$

Similarly, *ECM* denotes Exponential Cumulative (Natural) Morality:

$$ECM(y,a) = \exp\{cum[M(y,a)]\}. \tag{7.18}$$

The symbol $P_t(k)$ is used to denote the terminal population at the end of the final year, i.e. the survivors for each cohort

$$P_t(k) = P(y_{\max} + 1, a_{\max} + 1), \tag{7.19}$$

where we recall that $a_{\max} = \min(g,t - k)$ from equation (7.15) and similarly

$$y_{\max} = \min(k + g, t). \tag{7.20}$$

With this notation, Pope's cohort analysis equation

$$P(y,a) = \exp[M(y,a)]P(y+1,a+1) + \exp[M(y,a)/2]C(y,a) \tag{7.21}$$

may be rewritten for the final age group in each cohort (k), for which the survivors are $P_t(k)$

$$P(y,a) = \exp[M(y,a)]P_t(k) + \exp[M(y,a)/2]C(y,a). \tag{7.22}$$

Then, applying equation (7.21) repeatedly

$$P_{vpa}(y,a) = ECM(y,a)P_t(k) + P_c(y,a), \tag{7.23}$$

where $P_c(y,a)$ is the contribution to the population arising from the raised and accumulated catches,

$$P_c(y,a) = \sum_{a'=a}^{a_{\max}} ECM(k+a',a')C(k+a',a') \times \exp[-0.5M(k+a',a')]. \tag{7.24}$$

Equation (7.23) is a simple explicit expression for the population-at-age in terms of the key variables to be determined (the survivors) and some constants (including the $P_c(y,a)$ array), which depend only on the data and on natural mortality which is taken is taken to be known or, at least given.

The second main ingredient of the method is a model for the relationship between CPUE and the population abundance. Doubleday uses the same model as that which underlies the *ad hoc* tuning procedures, i.e.

$$u(y,a) = q(a)P(y,a) \tag{7.25}$$

where u has no suffix f (for fleet) since for the moment we assume that there is only one fleet or survey. In practice it is convenient to reverse this equation, and write

$$P(y,a) = r(a)u(y,a) \tag{7.26}$$

where $r(a)$ denotes the reciprocal of catchability, which is assumed to be a function of age, but to be constant with respect to time. Now, the catch data are treated as exact in the VPA, and the estimates of population so obtained using equation (7.22) are regarded as the best available estimates of the unknown true abundances, and will be treated as error-free estimates thereof. The survey CPUE data, however, also provide, through equation (7.25), a relatively error-prone estimate of these same abundances, once the survey has been calibrated by determining the reciprocal catchability. We seek therefore to determine both the survivors and the incidental variables $r(a)$ by minimizing the discrepancies between the VPA estimates of population P_{vpa}, and those determined from the CPUE, P_{est}, which are

$$P_{\text{est}}(y,a) = r(a)u(y,a). \tag{7.27}$$

Since the errors in P_{vpa} are assumed to be small, the main source of errors will be those in the CPUE data. These are assumed to be log-normal, but of variable size $\sigma^2(y,a)$, so that

$$P_{\text{est}}(y,a) = P_{vpa}(y,a)\exp[N(0,\sigma^2(y,a))]. \tag{7.28}$$

Under the assumptions of normality and independence (etc.) maximum likelihood estimation of the parameters reduces to weighted least squares estimation, and we therefore seek to minimize

$$S = \sum_y \sum_a \frac{\{\ln[P_{\text{est}}(y,a)] - \ln[P_{vpa}(y,a)]\}^2}{\sigma^2(y,a)}. \tag{7.29}$$

The magnitude of the errors $\sigma^2(y,a)$ cannot usually be taken as known a priori, and they must usually be estimated from the data. Taking them to be constant with respect to time, so as to avoid estimating as many parameters as we have data points, and substituting equation (7.27), we have

$$S = \sum\sum [\ln r(a) + \ln u(y,a) - \ln P_{vpa}(y,a)]^2 / \sigma^2(a). \tag{7.30}$$

Differentiating with respect to $\ln r(a)$ and setting this to zero, and rearranging, allows $\ln[r(a)]$ to be written explicitly as

$$\ln[r(a)] = \frac{\sum_a \ln[P_{vpa}(y,a)/u(y,a)]/\sigma^2(a)}{\sum_a 1/\sigma^2(a)}. \qquad (7.31)$$

Since the terms $P_{vpa}(y,a)/u(y,a)$, may be regarded as individual estimates of reciprocal catchability, this simply states that the best estimate of $r(a)$ is a weighted geometric mean of the available estimates of it. Doubleday then used equation (7.27) to estimate the population $P(y,a)$ at all ages, and a subtractive algorithm corresponding to VPA done forwards in time (rather than retrospectively) to estimate the survivors corresponding to each of these estimates, and combined these by a weighted arithmetic average procedure. There are a number of difficulties with this procedure in practice. First, as is well known, the subtractive forward VPA algorithm can, and often does, lead to negative estimates of survivors. These infeasible estimates could be included in the weighted mean, since this is an arithmetic mean, but they were in practice replaced by zeros, and it is not clear whether these zeros were, or should be, included in the mean, or not. Tests with a Fortran re-implementation of the procedure showed that this was a severe problem on a number of data sets which had been analysed without difficulty by *ad hoc* tuning procedures.

Generation of infeasible negative estimates of survivors is clearly an undesirable feature, which undermines confidence in the results produced. It can in fact be overcome without difficulty by using the logarithm of survivors as the estimation variable, and determining it by the same least squares procedure adopted for $r(a)$, as described below. The use of the subtractive algorithm is in fact inconsistent with the least squares approach, and this is the source of the problem.

The performance of the original Survivors method has indeed been found to be rather variable in practice. It gives plausible results on some data sets, and thoroughly implausible ones on others. It performed very poorly in the simulation tests conducted by the ICES 'Methods' Working Group in 1988 (Anon. 1988), failing to give usable results on several of the more demanding data sets. The essential process is well conceived, but some important technical details need to be handled more carefully.

7.6.3 Extended survivors analysis

It is quite straightforward to extend the Survivors method to allow for multiple CPUE data sets, and to derive a non-negative estimator for the survivors themselves using least squares. We refer to the method so obtained (Shepherd 1999) as the Extended Survivors Analysis (XSA for short). The basic procedure, involving iterative use of VPA, calibration of reciprocal catchability, calculation of estimated populations, and computation of weighted mean estimates of survivors, is the same, but there are important differences of detail.

In particular, a different algorithm is used for the estimation of survivors, while the VPA phase of the procedure (equations 7.14 through to 7.24) remains the same. Equation (7.25) is, however, generalized to allow for several 'fleets' (or indices of abundance):

$$u(y,a,f) = q(a,f)P(y,a), \qquad (7.32)$$

and similarly $r(a)$ becomes $r(a,f)$. The least squares procedure for determining r generalizes without difficulty, and the final estimate or r, corresponding to equation (7.31), is given by

$$\ln[r(a,f)] = \frac{\sum_a \ln[P_{vpa}(y,a)/u(y,a,f)]/\sigma^2(a,f)}{\sum_a 1/\sigma^2(a,f)}. \qquad (7.33)$$

The interpretation of this as a weighted geometric mean of all available estimates is unchanged. The analogue of equation (7.27) is

$$P(y,a,f) = r(a,f)u(y,a,f). \qquad (7.34)$$

Each survey/CPUE datum now generates an estimate of the true population, and thus an estimate of the survivors of the appropriate cohort. If now one differentiates S (as generalized for multiple fleets) with respect to the logarithm of survivors, in order to obtain a non-negative estimate of that parameter, one can show (leaving out the indices for clarity) that

$$\sum_f \sum_i [w(\ln P_{est} - \ln P_t - cum\,Z)/ECF] = 0 \qquad (7.35)$$

and thus

$$\ln P_t = \frac{\sum_f \sum_i w'(\ln P_{est} - cum\,Z)}{\sum_f \sum_i w'}, \qquad (7.36)$$

where $w' = w/ECF$. The interpretation of equation (7.36) is again quite straightforward. It simply asserts that the best estimate of survivors is a weighted geometric mean over all available data of the populations estimated from the CPUE/survey data, reduced by the estimated cumulative total mortality to the end of the final year. This is a commonsense result, except that the weights are modified by division by ECF. This term progressively reduces the weight attached to estimates based on older, earlier data, in addition to any explicit downweighting of old data, and reflects the reduced utility of older data for determining the terminal population. This is not surprising, as the forward projection of the population is closely related to, but much more robust than, forward VPA, which is of course very sensitive to observation errors in old data.

7.6.4 Practical considerations

This completes the description of the Extended Survivors Analysis. The calculation of reciprocal catchability and survivors is of course carried out iteratively, with a new VPA at each step, so there is always a current estimate of *cum Z* for use in equation (7.36). The algorithm may be summarized by the following pseudo-code:

Pseudo-code for Extended Survivors Analysis

```
Read data
Set prior weights, etc.
Set terminal $F$s (e.g. to 1.0)
Begin iterative loop
  Do VPA (or cohort analysis)
  Calculate $Z$, $ECZ$, etc.
  For each fleet and age
    calculate weighted mean reciprocal catchability (7.33) and variance thereof
  Next fleet and age
  Adjust weights (using estimated variance of $r$)
  For each fleet, age and year
    calculate estimated population (equation 7.34)
  Next fleet, age, and year
  For each cohort
    calculate weighted mean survivors (equation 7.36)
  Next cohort
Repeat loop
Print results, residuals, diagnostics, etc.
```

In fact, it turns out that, as usual, catchability on the oldest age is extremely ill determined, and some restriction must be imposed. In practice it is usual to assume that catchability for each fleet is constant above a certain age, so that the values estimated for that age are used for all subsequent ages, in estimating the populations. This removes the need to make an *ad hoc* assumption about fishing mortality on the oldest ages, but may lead to rather extreme estimates for these *F* values. A further technical detail is that, since surveys are carried out at different times of the year, and commercial fleets may catch fish mainly during one season or another, it is desirable to relate the CPUE/survey indices to the population estimates at the appropriate time of year. The most convenient way to do this is in fact to correct the indices to the beginning of the year using the appropriate proportion of *Z*. This is, however, almost an unnecessary refinement, since these adjustments would otherwise be allowed for in the calibration of the catchability values.

A more substantial refinement is to allow a more complicated model for the catchability on the youngest recruiting ages. As discussed by Shepherd (1997), there is good evidence that CPUE is *not* linearly proportional to eventual year-class strength for these youngest age groups. This is easily allowed for in this method, since any procedure, such as a regression, which permits population to be estimated from CPUE may be substituted for the use of the simple weighted mean. The calibration regression procedure described by Shepherd (1997) is fully compatible with this, and may be used for any desired range of ages, provided that the oldest age is less than that above which one wishes to set catchability to be constant. All the technical refinements proposed by Shepherd (1997), such as shrinkage to the mean, setting minimum variances, forecast/hindcast variance inflation, etc., may also be incorporated without difficulty.

7.6.5 Example

An example of the results of analysis by XSA is given in Tables 7.12 and 7.13 below. For this analysis the CPUE data from only two surveys (the English and Scottish Groundfish Surveys) were used.

Table 7.12 North Sea cod: fishing mortality estimates from XSA.

Age	Year					
	1990	1991	1992	1993	1994	1995
1	0.209	0.190	0.213	0.074	0.091	0.164
2	0.982	0.835	0.930	0.857	0.679	0.613
3	1.018	0.989	0.887	1.089	0.993	0.938
4	0.922	0.910	0.947	1.032	1.049	0.735
5	0.813	0.893	0.861	0.938	0.898	0.889
6	0.901	1.029	0.932	1.134	0.960	0.875

The results are also illustrated in Figs. 7.12 and 7.13. From these it can be seen that the XSA interpretation differs in important details from those presented before. Firstly, it indicates a moderate reduction of fishing mortality rates over the period, particularly on the 2-year-old fish, which are among the most important age groups for this stock. The mean *F* on ages 2 to 6 is in fact also estimated to have fallen from 0.93 to 0.81. Secondly, the estimated abundance of the survivors at age 3 is much higher than for either of the other two credible analyses given above using the JAM and separable VPA methods. This is because both survey indices indicate a high abundance for these fish, and the survivors estimate is adjusted accordingly. Evidence-based estimates for features such as a secular trend in fishing mortality and the abundance of survivors of individual age classes, can only be obtained with any confidence when CPUE estimates are included in the analysis.

7.6.6 Discussion

The Survivors methods effectively combine the better features of the separable VPA and the *ad hoc* tuning methods. The underlying model assumes that fishing mortality is separable at the fleet level only, and the CPUE/survey data are incorporated in a consistent way, while data for the final year are correctly treated as subject to similar errors as those for other years. The final estimates are appropriately weighted averages over all available data. This is achieved using a simple but efficient iterative algorithm, derived from a simplified but plau-

Table 7.13 North Sea cod: population estimates from XSA.

Age	Year						
	1990	1991	1992	1993	1994	1995	1996
1	69 300	86 900	161 000	74 400	205 000	120 000	
2	96 600	46 000	58 800	107 000	56 500	154 000	83 700
3	20 800	29 600	16 300	19 000	37 100	23 500	68 100
4	8 000	6 140	9 020	5 510	5 240	11 200	7 520
5	4 890	2 610	2 020	2 870	1 610	1 500	4 410
6	566	1 770	873	701	919	536	505

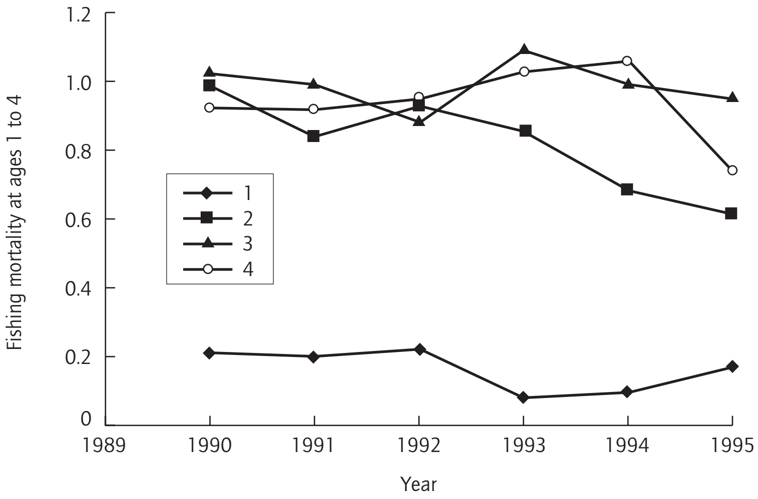

Fig. 7.12 Fishing mortality estimates from XSA.

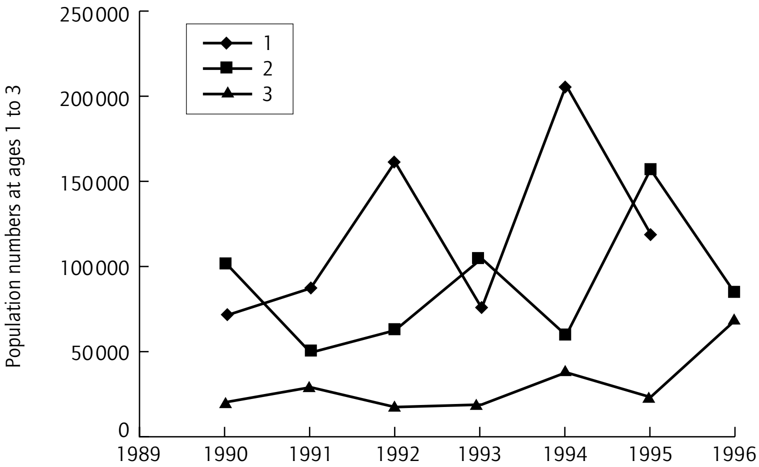

Fig. 7.13 Population numbers from XSA.

sible statistical model. The main simplifying assumption used is that VPA provides, once tuned, the most precise estimate of population abundance, so that total international catch data may be treated as exact in the VPA or calibration phase of the calculation. This seems to be a reasonable assumption for stocks where the major catches are well sampled, but would be inappropriate where the catch data are poorly sampled or otherwise defective, but one or more sets of reliable survey data are nevertheless available. Such situations may occur, and in these cases a full integrated analysis, with suitable low weight attached to the catch data, would be more appropriate.

Nevertheless, there are many practical situations where the Survivors type of method is quite appropriate, and it often seems to provide adequate computational speed, robustness and precision of the results. The Extended Survivors Analysis is an improvement over the original implementation in three ways, namely:

- allowance for multiple CPUE/survey data sets;
- consistency and robustness of the calculation of survivors;

- incorporation of non-constant catchability for recruiting age groups.

It has performed well in simulation trials and practical use, and can be recommended as a useful and practical tool, unless the catch-at-age data are of very poor quality relative to the CPUE/survey data.

7.7 MULTISPECIES VIRTUAL POPULATION ANALYSIS

We saw in section 7.3 that single-species virtual population analysis requires the assumption that natural mortality rate is a known value, often thought to be both constant with year and with age. But in practice we might well expect that natural mortality rate would vary by age, because smaller fish are more vulnerable to predation than larger fish. We might also expect levels of predation mortality to vary from year to year because numbers of fish predators are known to vary from year to year. For example, if the numbers of cod in the North Sea doubled then we might expect as a first approximation that the amount of food they ate would double. We might also expect the predation mortality to vary if the total amount of prey available to the predators varied from year to year. For example in the North Sea, saithe eat mostly Norway pout and herring, hence if in a particular year there was more herring we might expect predation mortality on Norway pout to decrease. Clearly, such changes in natural mortality would influence the results of VPA and so might have profound effects on our perception of the numbers of fish in the sea. It is also likely that realizing that natural mortality could vary would also influence our perception of how the fish stock should be managed.

Such considerations persuaded Andersen and Ursin (1977) to make a model of the North Sea fisheries, which included a variable predation mortality. Their model worked using a forward simulation of fish stocks based upon the solution of simultaneous differential equations. Their most important innovation was to partition natural mortality rate (M) into two components, $M2$, due to predation mortality, and M1, due to other forms of natural mortality.

$$M = M1 + M2 \tag{7.37}$$

This idea was carried into multispecies versions of virtual population analysis (Helgason and Gislason 1979; Gislason and Helgason 1985) and cohort analysis (Pope 1979; Pope and Knights 1982). The strength of these two, essentially similar, approaches, were that they showed how the existing catch-at-age data from a number of predator and prey species could be combined to estimate predation mortality rate. However, it was clear that in addition to the catch-at-age data, additional data would be needed to characterize the feeding of each age of each predator. Thus these early papers led to the establishment of a working group of ICES, which undertook to make a comprehensive study of the feeding of the major predatory fish of the North Sea during one year, to provide suitable inputs to these models.

This study was first conducted in 1981 and was known unofficially as 'the International Year of the Stomach'. The predator species considered in the study were cod, whiting, haddock, saithe and mackerel. Stomach samples from size-stratified ranges of these species were taken from all parts of the North Sea for all quarters of 1981 because, as shown for example by Daan (1973), the stomach contents of species such as cod were known to vary by size by area and by season. Analysis of the contents of the stomachs of the five predators were undertaken by five designated laboratories to ensure consistency of their interpretation. The contents of the stomachs of each predator were analysed to provide, where possible, estimates of how much of each species was eaten; not an easy task with partially digested remains. In particular, their feeding on species for which catch-at-age data were available were carefully reconstructed, as ingested weight by prey size range. There were nine species of particular interest as prey: these were the five predators themselves and the prey species herring, sprat, Norway pout and sandeel, for which catch-at-age data were also available. Thus the data on these predators and prey species were in a form that could be converted to estimate how many fish, of each age, of each prey species, were eaten by each age of each predator species. These data became available in 1983 (Daan 1983; Daan 1989) and the ICES multispecies assessment working group was then established to analyse the data using Multispecies Virtual Population Analysis (MSVPA). The early history of this working group is summarized in Pope (1991) while more recent approaches can be seen in ICES (1997).

The actual analysis made by the working group was based on the Helgason and Gislason MSVPA model, but since the Pope multispecies cohort analysis model is easier to understand, it is used here to explain the approach. However, the formulation of feeding relationships used by Helgason and Gislason (1979) is more robust than that of Pope (1979) and so is adopted in the following.

The single-species cohort equation (7.2) can be modified quite simply to include a term due to feeding, by all quantified predators on the prey species age in question. We may call this term $D(y,a,s)$, the numbers of prey species (s) of age a eaten by all quantified predators in year y (or perhaps in some other portion of the year such as a quarter).

$$P(y,a,s) = \exp[M1(a,s)/2][C(y,a,s)+D(y,a,s)] + \exp[M1(a,s)]P(y+1,a+1,s). \qquad (7.38)$$

Note that not only does this equation contain the amount of the prey species eaten by all predators included on the analysis, but it also uses $M1$ instead of M. In effect it treats predation deaths as just another form of catch. Notice also that once we have successfully performed a multispecies cohort analysis and estimated population sizes then we can estimate the predation mortality rate ($M2$) and the fishing mortality rate (F) by solving:

$$\begin{aligned} &\ln[P(y+1,a+1,s)/P(y,a,s)] \\ &= Z(y,a,s) \\ &= F(y,a,s)+M1(a,s)+M2(y,a,s) \end{aligned} \qquad (7.39)$$

and

$$F(y,a,s) = M2(y,a,s)^{*}C(y,a,s)/D(y,a,s). \qquad (7.40)$$

Equation (7.38) shows how we would include predation, if predators provided catch statistics in the same way that fishermen do. If this were the case the multispecies cohort analysis equation would suffice to solve the problem. However, since predators do not provide catch statistics, we must find other ways of estimating $D(y,a,s)$. We can do this by considering the quantity $d(y,A,S,s,a)$, the numbers of prey species (s) of age (a) eaten by a particular predator species (S) of age (A) in year (y). Thus:

$$D(y,a,s) = \sum_{all\ A}\sum_{all\ S} d(y,A,S,a,s). \qquad (7.41)$$

Of course we do not know what $d(y,A,S,s,a)$ is either, but we can write an equation for it in terms of the ration $R(y,A,S)$ of all the predators of age A and species S in the year y, and the diet proportion $DP(y,A,S,a,s)$ that the predator obtains from prey of age a and species s. Thus:

$$d(y,A,S,a,s) = R(y,A,S)^{*}DP(y,A,S,a,s)/Wt(y,a,s) \qquad (7.42)$$

where $Wt(y,a,s)$ is the average weight of the prey in the predator's stomach. Note that this may differ from the weight of the prey in the sea, but can be obtained from stomach samples.

Ration may also be written as the average population sizes of the predator, times the average annual (or quarterly) diet $r(y,A,S)$. Average values in the equations are denoted by an over-bar:

$$R(y,A,S) = \bar{P}(y,A,S)\bar{r}(y,A,S). \qquad (7.43)$$

Average population size is estimated from the results of VPA or MSVPA, while average ration is provided by the results of feeding experiments. If necessary, ration may be modified from year to year in response to the size and growth of predators.

Diet proportion $DP(y,A,S,a,s)$ may be written in terms of the populations of the prey species and of the predator, and a factor called the 'suitability' $Suit(A,S,a,s)$. Suitability expresses how much a predator of a certain age would eat of a certain prey, relative to the total prey biomass available, of all possible ages a' of all prey species s'. Note that in this formulation it is considered to be constant for all years, though it may be allowed to vary between quarters, or other divisions of the year, to reflect changing diet preferences/availabilities with season:

$$DP(y,A,S,a,s) = \frac{\overline{P}(y,a,s)^{\star}Wt(y,a,s)^{\star}\,Suit(A,S,a,s)}{\sum_{all\ a'}\sum_{all\ s'}\overline{P}(y,a',s')^{\star}Wt(y,a',s')^{\star}\,Suit(A,S,a',s')}. \tag{7.44}$$

This equation can be solved, if we know the numbers of predators and of prey, and also the suitability of each prey for each predator. Population numbers will of course ultimately be obtained from the multispecies cohort analysis equation. Suitabilities, however, need to be estimated using additional data. For prey species whose numbers are not known, Helgason and Gislason (1979) adopted the approach of including an additional group of 'other prey' whose joint biomass was considered, in the absence of any information, to be constant through time. This turned out to be a very stabilizing assumption, and moreover the biomass of these prey could actually be set at any arbitrary level without affecting the model. This is because the model effectively estimates the product of the biomass and suitability for these prey and hence an assumption of a higher biomass would be balanced by an estimation of a lower suitability.

Suitabilities are estimated by first guessing their values for each predator age and prey age combination, and using these guesses in combination with population sizes of predator and prey age groups obtained from singles-species cohort analysis. This gives initial values of $d(y,A,S,a,s)$. A multispecies cohort analysis run with these values provides new estimates of population size for each predator and prey species. The proportion that the various prey items that the MSVPA predicts to form of the diet of each age of each predator species in a particular year, in our case 1981, can then be compared with the proportions that were found in stomach samples for that year. This allows the estimates of suitability to be corrected. The corrected estimates of suitability may then be used to estimate new values of $d(y,A,S,a,s)$, and the process is repeated until the estimated values of suitability converge to a stable value. An exactly similar procedure can be adopted using the 'exact' multispecies virtual population analysis if required.

In pseudo-code we can write this as an iterative loop, as follows:

Pseudo-code for multispecies VPA

```
Choose initial values of $Suit(A,S,a,s)$.
For all species for which catch-at-age data are available . . .
    carry out single-species cohort analysis to obtain estimates of $P(y,a,s)$.
Begin iterative loop
    estimate $d(y,A,S,a,s)$
    perform a multispecies cohort analysis
    calculate estimated feeding $EF(y',A,S,a,s)$ of predators
    compare with actual feeding $AF(y',A,S,a,s)$ obtained from stomach samples
    recalculate $Suit(A,S,a,s,new) = Suit(A,S,a,s,old)^{\star}AF(y',A,S,a,s)/EF(y',A,S,a,s)$.
Repeat until values of population and suitability converge.
```

When this procedure was first used concern was raised that even if the process converged, the results might not be unique. Studies by Magnus and Magnusson (1983) indicated mathematically sufficient conditions for uniqueness which appeared to be robust enough to ensure convergence in most cases. However, these sufficient, but not necessary, conditions excluded the possibility that a predator could eat conspecifics of the same age. Since this phenomenon is observed from time to time, for example small 1-year-old cod are eaten by large 1-year-old cod, the possibility of non-uniqueness of the above procedure cannot be entirely ruled out. However, it has yet to be observed in practice.

In principle it is possible to tune MSVPA to trends in CPUE or survey data, in a similar fashion as described in single-species assessments, and such results could be used for setting quotas. However, the ICES multispecies assessments working group found that for the predator species, at least, there was little to be gained from calculating multispecies-based quotas rather than those based upon single-species analysis. This is because the predation mortality on the larger species occurs mostly on prerecruitment ages. Thus, while this affects the long-term yield, it has much less impact on short-term predictions. This is because these are typically made using estimates of the numbers of prerecruitment ages obtained from the results of surveys, often using results from ages older than those on which the majority of the predation has occurred. Multispecies effects might well affect quotas set for prey species, since predation affects all ages of the species, but in the case of sandeel and of Norway pout in the North Sea these were usually set on an average basis. In other areas, however, multispecies effects are considered in the setting of quotas for prey species such as capelin, and in these cases tuning of some sort becomes important. For more details of the behaviour and ecology of age-specific predation, see Chapters 11, 12, 13, Volume I, and Chapter 16, this volume).

In the North Sea the more interesting features of the analysis relate to the changes observed in natural mortality rate with age and with time, and the consequent effects this has on recruitment estimates. This is illustrated in Fig. 7.14, which shows the cumulative predation mortality of North Sea cod at age, estimated by MSVPA. The figure clearly shows that predation mortality rate can vary with both year and age and that thus the assumption of constant natural mortality rate typically used in single-species models is violated. The figure indicates that the cumulative predation mortality to age 3 varied by nearly 1.0 between a high value in 1980 and a low value in 1992. This is equivalent to a change in survival and hence of apparent recruitment over these ages by a factor of 2.7.

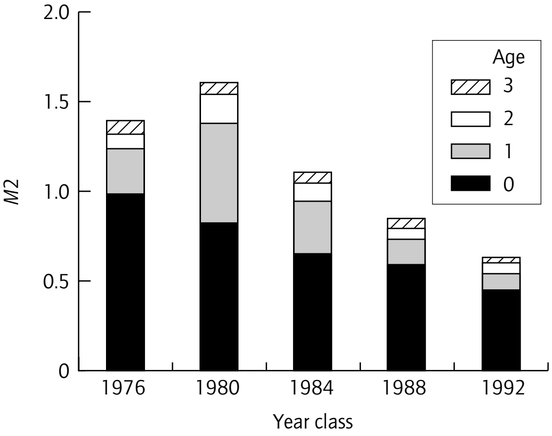

Fig. 7.14 North Sea cod predation mortality rate by age, for selected years, from MSVPA. M2 (1980)–M2 (1992) = 0.99, equivalent to a exp(0.99) = 2.7 change in recruitment.

Inevitably, multispecies virtual population analysis, and multispecies cohort analysis, are heavily over-parameterized, since not only do they estimate the population and the fishing mortality terms of the single species VPA models, but they also estimate predation mortality and suitability. As with the single-species models there is no goodness-of-fit measure. This is because all the degrees of freedom in the data are absorbed by the model. At the time the models were developed, more restrictively parameterized, least-square-fitted models would not have been practical, due to limitations in computer power. It was, however, possible to fit more restrictive models to the results of MSVPA using simple statistical packages. This was performed for both estimates of $M2(y',A,S,a,s)/[P(y',A,S)^{*}Wt(y',A,S)]$ and of $Suit(A,S,a,s)$. Quite reasonable fits of both outputs can be obtained using predator–prey species interaction terms $int(S,s)$ and an Ursin (1973) log-normal predator weight/prey weight food-preference model, $N\{\ln[Wt(A,S)/Wt(a,s)],\mu,\sigma\}$.

$$Suit(A,S,a,s) = \mathrm{int}(S,s)^{*}N\{\ln[Wt(A,S)/Wt(a,s)],\mu,\sigma\}+\varepsilon. \quad (7.45)$$

These statistical models can absorb up to half of the variation in estimates of suitability or of $M2$. The remaining variation ε is probably what one should expect from what must be rather variable data on stomach content data broken down by age of both predator and prey.

Clearly, simple MSVPA is dependent on the assumption that suitability is constant through time. If this assumption were not made it would not be possible to base it upon one year's stomach content data. Historical estimates might still be obtained if stomach content data were collected each year and suitability estimated on an annual basis. However, since in the North Sea the stomach content data collected in 1981 required a large sampling effort and the dedicated work of five stomach-content analysis teams for two years, this would scarcely be practical. Moreover, if suitability changed from year to year it might prove difficult to make forward predictions. Thus, it was considered important to test the hypothesis of constant suitability. This was attempted by collecting partial stomach samples in 1985, 1986 and 1987. Analyses of these are given in Rice et al. (1991). However the partial nature of these samplings made the tests incomplete and it was decided to repeat the full sampling in 1991. This allowed equations of the form of (7.45) to be fitted jointly to estimates of suitability based upon the 1981 data and the 1991 data.

For most predator species the joint model captured about 40% of the variation, and a smaller but significant fraction of the variation (between 6% and 29%) could be captured by allowing suitability to change with year. Thus, from a strictly statistical point of view the null hypothesis of no-year effect has been disproved. This suggests that assumption of constant suitability is also disproved, though one might note that an alternative explanation might be a drift in stomach-sampling procedures over a 10-year period. It is also worth bearing in mind the point made by ICES (1994) that rejection of constant suitability implies a more complex model, but not a return to single-species dynamics. While the differences found were statistically significant, the high number of degrees of freedom of the fits meant that in many cases the differences were not large, and not necessarily of practical significance, as may be judged from Fig. 7.15. This shows the differences of the fitted suitability of cod (as prey) for cod (as predator) by ln(size ratio), estimated from the 1981 and 1991 data respectively. Analyses of these data may be found in the 1993 and 1997 reports of the ICES Multispecies Assessment Working Group (ICES 1994, 1997).

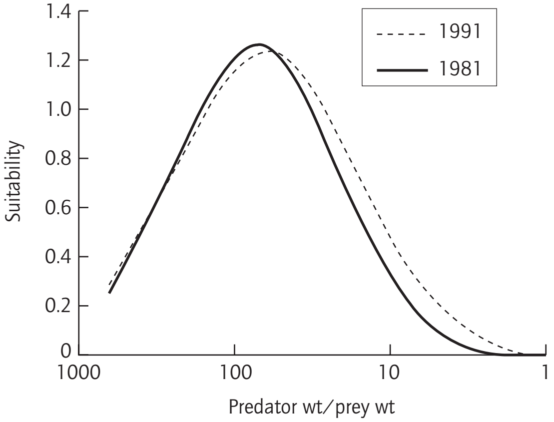

Fig. 7.15 Suitability of cod as prey for cod as a function of predator weight/prey weight.

In the North Sea the comparison between 1981 and 1991 was quite testing because the herring, which is an important prey, had gone from low abundance in 1981 to high abundance in 1991, and other species abundances had also shifted. Given the problems of sampling the North Sea, it is difficult to carry investigations of the constancy of suitability further there. Clearly, one might expect suitability to be a function of size ratio, of species overlap and of the behaviours of predator and prey. One might also speculate that the diet proportion function described by equation (7.44) might be in higher powers (positive switching) of prey biomass or lower powers (negative switching) rather than in unit powers.

It is rather easier to investigate changes in suitability and thus the applicability of MSVPA in areas where there are fewer species. Work in the Baltic (ICES 1999) and at Iceland and the Barents Sea (Stefansson and Pálsson 1997; Tjelmeland and Bogstad 1998) has this benefit and the challenge has been taken up. The latter areas have also seen developments of forward simulation models that fit to data using more statistical principles. Again this is more simply achieved in areas with fewer species to consider.

7.8 CONCLUSIONS

There can be no doubt that VPA is a useful and quite widely applicable technique. It has both virtues and vices, and some care is needed in its application to ensure that useful results rather than misleading results are obtained. However, it is least able to determine the things that one most wishes to know – the recent trends of overall fishing mortality and stock size, and year-class strengths. The details, such as the sequence of highs and lows of year-class strength, and the ups and downs of fishing mortality, especially in the past, emerge quite clearly: it is the underlying large-scale patterns which are undetermined. The only possible conclusion is that VPA alone is not enough. To have any reasonable chance of assessing the true state of the population, more information is needed than is contained in the array of total catch-at-age data. Only when combined with good-quality CPUE or survey data can it be regarded as a reliable technique. These fundamental problems, together with many of the more technical difficulties discussed in this chapter, also affect other related methods of analysis, and here the relative simplicity and transparency of the VPA calculation can help, as it is easier to understand what is going on than it is for more elaborate methods of analysis.

In all analyses of fisheries data, including catch-at-age data, one should beware of stocks which are subjected to low fishing mortality, and more especially of arriving at such an interpretation of the data for stocks where F is in reality quite high. This problem arises because VPA and most related analyses always have a trivial 'solution' corresponding to infinitesimal values of fishing mortality everywhere. This is obvious, because if one starts with small enough terminal F values, corresponding to very large surviving populations, all the catches will be trivially small compared with the populations, and correspond to very small Fs. This is connected with the previously mentioned fact (Pope 1972) that the convergence of the VPA depends on the size of the *estimated* fishing mortality, not the true fishing mortality. There is always a danger that any iterated VPA interpretation may drift into this trivial solution, which is why small assumed terminal F values should be avoided wherever possible. Clearly, however, this is no help if the fishing mortality really is very small. This is just one example of the extreme difficulty of estimating the absolute size of a lightly exploited population, especially in the absence of fishery-independent data.

The other main difficulty with VPA is that natural mortality is taken to be known, and usually constant with time, which is not a very plausible assumption in a system where it is mostly due to predation, and the abundances of the predators vary with time. This issue is addressed by the multispecies VPA technique, but at the cost of a much greater burden of both sampling and computational effort. Thus, whilst in principle MSVPA should be the preferred technique, in practice most assessments are still conducted primarily on a single-species basis. This is not a serious problem for short-term forecasting, but can lead to substantial problems for long-terms assessments. These issues are discussed in detail in Chapter 8, this volume.

Finally, it is interesting to observe that VPA, being in essence an additive procedure based on accumulated catches, can in fact be applied to data pertaining to some fraction of the whole population. Suppose one systematically had data for just half the total catches. Assuming that one started with the correct total terminal F, one would start the calculation with just half the true population, and thereafter repeatedly raise this, and add in half the true catches. At all stages the estimated population would be half the true population, but the fishing mortalities (from equations 7.3 and 7.4) would be correct. This is obviously a highly idealized situation, and in practice any available partial catch data would be likely to derive from some of many fishing fleets, or from one area representing only part of the distribution of the stock, or from one season of the year, and would not be a fixed and constant fraction of the total. Nevertheless, it seems that the main errors involved in applying VPA to partial catch data would be in the estimated populations, and that the fishing mortalities would still be a reasonable first approximation to the truth. This approach has not often been applied in practice (not deliberately, at any rate), and it would be interesting to explore the conditions under which it could be used without incurring serious errors.

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8 Dynamic Pool Models II: Short-term and Long-term Forecasts of Catch and Biomass

J.G. SHEPHERD AND J.G. POPE

8.1 SHORT-TERM FORECASTS OF CATCH AND BIOMASS

8.1.1 Introduction

An essential task in fish stock assessment is the preparation of short-term forecasts of catch and biomass. Whenever management is based on Total Allowable Catches (TACs) and quotas, such calculations are a necessary part of the provision of management advice. Indeed, so important had this task become in certain areas, such as the North Atlantic, that it had until recently almost overshadowed the other essential ingredients of an assessment – and regrettably had received higher priority than the provision of long-term advice, such as that based on yield-per-recruit and biomass-per-recruit analysis, and the stock–recruitment relationship, which is discussed later in this chapter in Section 8.2.

A number of methods are used for the preparation of short-term catch forecasts, depending on the data available, and the type of assessment that has been carried out. The 'classical' dynamic pool method, which is based on estimates of population and fishing mortality for each age group, is the subject of this chapter. Methods based on simpler multiplicative models and on length compositions are also possible, but are not treated here (see Pitcher, Chapter 9, this volume). Methods based on stock-production models are discussed by Schnute and Richards (Chapter 6, this volume).

The essential ingredients of a dynamic pool short-term forecast are:

1 an estimate of the current population size;
2 an estimate of the likely exploitation pattern;
3 estimates of the sizes of newly recruiting year classes;
4 some assumptions concerning future overall levels of fishing mortality.

Note that the first three ingredients are all actual estimates of the current or future situation, whereas the last is just a set of assumptions of what may possibly occur, rather than an estimate or prediction of what will actually occur. These assumptions are usually used to generate a range of catch options, from which managers are expected to choose an appropriate course of action. In doing so it is to be hoped that they will also have some idea of the long-term strategy which they are attempting to implement, and some guidance on the probable consequences, in both the short- and longer-term, of the options presented. In some parts of the world the options are more constrained by management policy and strategic decisions which have already been taken, so that it may be necessary to carry out calculations for only one option, for example, that corresponding to the $F_{0.1}$ level of fishing mortality. The nature of the calculation is, however, the same.

The distinction between ingredients 2 and 4 is not very precise, because the future exploitation pattern may sometimes be expected to differ from that of the recent past, if one is about to implement a mesh change, for example. We have separated them in order to stress that the exploitation pattern can be estimated from recent data, and often can reasonably be assumed to remain the same for the immediate future. The future level of overall fishing mortality is, however, not only uncertain, and not necessarily similar to recent levels – it is, moreover, just this which man-agement action normally seeks to control. At the stage of preparing catch option calculations, it must therefore be treated as unknown, and can only be fixed by assumption, not from the data.

8.1.2 The basic method

An age-based catch forecast is very simply carried out using two of the fundamental equations of fish population dynamics (see e.g. Sparre and Hart, Chapter 13, this volume). First, we use the catch equation

$$C(y,a) = F(y,a)P(y,a)[1-\exp(-Z(y,a))]/Z(y,a) \tag{8.1}$$

where C represents catch in number of fish of age a in year y, and similarly F denotes the fishing mortality rate per year, P the population in number at the beginning of each year, and Z represents the total mortality rate. Next, we also use the usual population evolution equation

$$P(y+1,a+1) = P(y,a)\exp[-Z(y,a)]. \tag{8.2}$$

These, of course, are the discrete forms of the underlying differential equations, integrated over a finite time step which is usually one year as shown here. They would therefore be exact, provided that F and Z remained constant during the time period in question. The total catch in weight (or yield, Y) is simply calculated by summation over all the age groups:

$$Y(y) = \sum_a C(y,a)W_c(a) \tag{8.3}$$

where W_c represents the average weight at age of fish in the catch, which is often different to that of those in the stock, W_s, because fishing is a biased size-selective process.

The summation extends over all ages, from that of first recruitment to the fishery, up to and including that of the greatest age (g), which is usually a plus group. This means that it includes fish of age g and older simply so that no fish are 'lost' from the calculation. A modified form of equation (8.2) is thus required to take account of the plus group. This is just

$$\begin{aligned} P(y+1,g) = {} & P(y,g)\exp[-Z(y,g)] \\ & + P(y,g-1)\exp[-Z(y,g-1)]. \end{aligned} \tag{8.4}$$

In practice, the two values of Z in this equation are usually taken to be the same, giving a small simplification.

The calculation defined by equation (8.3) is clearly a simple sum-of-products, which can easily and conveniently be carried out using a spreadsheet. An example of the calculation is given below, but first it is necessary to be explicit about the source of the estimates of $F(y,a)$ and $P(y,a)$ needed as a starting point.

The estimates of $P(y,a)$ required for these calculations are generally obtained from virtual population analyses (VPA) (see Chapter 7 this volume), or a related calculation such as an Integrated or Survivors analysis. They are in fact the estimates of terminal population (survivors) obtained from these analyses. They will therefore be averaged over the available data to some extent, at least for separable VPA, any multi-fleet-tuned VPA, Survivors analysis and most more complex methods (see Chapter 7, this volume). This is a Good Thing.

The estimates of $F(y,a)$ required to apply equation (8.1) may be obtained in various ways. These generally involve the application of assumed levels of future overall fishing mortality $F^*(y)$ which are usually based on estimates from the recent past, to a specific exploitation pattern, $S(a)$, where $S(a)$ is just the fraction of the overall F^* suffered by fish of each age:

$$F(y,a) = F^*(y)S(a). \tag{8.5}$$

Methods for estimating these recent levels of fishing mortality, and thus the exploitation pattern, are discussed in detail in Chapter 7 (this volume). There are several possible ways of constructing estimates of overall fishing mortality. The most usual is just to take an arithmetic mean over a suitable, but not too large, range of older and fully exploited age groups.

A second, almost precisely equivalent, procedure is to apply multiplicative scaling factors known as F-multipliers (F_{mult}) to some reference array of fishing mortalities:

$$F(y,a) = F_{mult} \times F_{ref}(a). \tag{8.6}$$

The F-multipliers are in practice usually just a set of standard numbers representing a range of increases and decreases of fishing mortality, relative to the most recent level, chosen to reflect various possible options for future management of the stock. The reference fishing mortalities at age $F_{ref}(a)$ are usually obtained by averaging over the estimates for a few (typically 3 to 5) recent years,

$$F_{ref}(a) = mean_y[F(y,a)], \tag{8.7}$$

where the required estimates of recent values for $F(y,a)$ are again usually obtained from some form of VPA (see Chapter 7, this volume). The stock biomasses are, of course, also calculated by a simple weighted sum of products

$$B(y) = \sum_a W_s(a) f_x(a) P(y,a) \tag{8.8}$$

where $W_s(a)$ is the appropriate weight-at-age of fish in the stock, and $f_x(a)$ is the appropriate fraction of the population to be included at each age. This would be the fraction of mature fish at age a if spawning stock biomass is required, or the fraction of fully exploited fishing mortality suffered by fish of age a, if exploited stock biomass is required.

In both cases, the estimates of future $F(y,a)$ involve a substantial element of averaging. This is also a Good Thing, because by convention almost all methods of analysis in current use allow any errors in the catch-at-age data to appear in the output estimates and tables of fishing mortality. Such errors, whatever their origin, are by definition not expected to be repeated systematically in the future: they should therefore be suppressed so far as possible before they appear in forecast calculations. Such suppression cannot, of course, ever be achieved perfectly, and averaging is usually just the best blunt instrument available for the purpose.

It is therefore usually highly undesirable to simply take the last year's values, $F(t,a)$ and use those for a forecast. One exception to this rule is if the Judicious Averaging Method (see Chapter 7, this volume) is being used, since in this case the $F(t,a)$ are already averages, and are therefore relatively stable estimates. However, this does not make this a desirable method, because, as noted in Chapter 7 (this volume) any errors are simply transferred to the population estimates.

The third main ingredient, estimates of the strengths of forthcoming year classes, which have not yet been observed in the catch-at-age data, is, however, often among the most important. Ideally such estimates should be based on rigorous analysis of suitable survey indices, and methods for doing this are discussed by Shepherd (1997). Where suitable survey data are not available, less satisfactory methods must be applied. These boil down to intelligent guesswork, deliberate cautious underestimation, and the use of averages, or estimates from stock-recruitment analyses (see Chapter 6, Volume 1). None of these has useful short-term predictive ability in practice, and none can be considered satisfactory unless recruitment to the fishery is a very gradual process, and recruitment, expressed as year-class strength, is itself a rather stable quantity. The use of averages for the strengths of any year classes which will contribute substantially to the fishery during the period covered by the forecast should be considered to be a desperate measure, and such forecasts should be heavily qualified with suitable health warnings.

One important question in practice is how many year-class strengths, as estimated by VPA or other methods, should be replaced by independent estimates from surveys? In principle the use of integrated methods, which combine the analysis of catch-at-age and survey data for both recruited and recruiting year classes, should reduce or eliminate this problem. In practice, however, available methods for estimating recruitment from survey data are mostly distinct from those based on VPA used for analysis of catch data. A sensible rule of thumb seems to be to replace, if possible, any estimates for year classes on which the cumulative fishing mortality to date is less than about 0.7, so that we have seen less than half the year class in the catches. If one wished to be more scientific, one could instead replace any estimates for which the estimated standard error of the terminal *F*, as estimated from the VPA tuning procedure or elsewhere, exceeds that for the year-class strength, derived from the recruit index analysis.

The simple sums-of-products calculation described here is, of course, ideal for implementation as a spreadsheet, and for the simplest form of forecast considered so far there is little need to seek anything else. An example of a spreadsheet implementation for three options concerning the future level of fishing mortality is given in Table 8.1. For simplicity and clarity, this illustrates a catch forecast only for a single year, although a two-year catch forecast is usually required when an operational assessment is carried out. This is because an assessment is usually carried out in year $(t + 1)$ using data up to and including the last full year t, and a forecast is required of catches in the next full year $(t + 2)$. It is also usually necessary to calculate the stock biomass at the *end* of year $(t+2)$, which is of course the beginning of year $(t + 3)$, in order to illustrate the full effect of choosing any particular catch option. The extension of the calculation to more years is straightforward.

The results of this forecast are also illustrated in Figs 8.1 to 8.3. These show how the catch-at-age increases as the forecast fishing mortality is increased by increasing the *F*-multiplier (Fig. 8.1), whilst the future population number at each age decreases (Fig. 8.2). Note how the catches are dominated by the strong year-class contributing at age 3 in these data, which also makes a major contribution to the future population at age 4. The VPA results indicate that the subsequent year class is weak, and it makes an unusually small contribution to the catches at age 2 and the population at age 3. The contributions to the catches at age 1, and to the future population at ages 1 and 2, are due to year classes whose size has been assumed to be 50 000. The overall effects (Fig. 8.3) are therefore a progressive increase of total catch weight, and a decrease of future spawning stock biomass, as the fishing mortality is increased. This figure summarizes the information on the short-term evolution of the stock under the three selected management options, expressed as $F_{mult} = 0.75$, 1.00 and 1.25, which would be considered when selecting the level for a recommendation for the Total Allowable Catch (TAC) for the stock.

This information would also usually be summarized in an option table, such as Table 8.2, and the usual procedure would simply be to pick as the TAC the catch weight corresponding to whichever option was considered to provide the best compromise between allowing continued fishing at an acceptable level, whilst still preserving an adequate biomass for the future (see also Table 1.1, Chapter 1, this volume). Such a selection is often the subject of considerable uncertainty and controversy. In general the assessment scientists are likely to take a long-term view and argue on behalf of the fish, for a low *F*, high SSB option, whereas the fishing industry is likely to take a short-term economic view and argue for a high *F*, high-catch option.

8.1.3 Complications

A spreadsheet implementation is perfectly satisfactory for such simple forecasts for a couple of years. However, there are a number of additional factors which need to be considered in most real-life situations, which can lead to considerable complication of this fundamentally straightforward procedure. These include, in particular:

- calculation of a large number of management options;
- medium or long-term forecasts extending over a longer time horizon;
- allowing for discards;
- calculations for multiple fleets;
- simultaneous calculations for several species in a mixed fishery;
- allowing for changes of exploitation pattern.

Some observations on each of these aspects follow:

Table 8.1 Catch forecast spreadsheet.

Age	Weight at age	Maturity at age	Current population (from VPA)	Current SSB	Recent F at age	Expected F at age	Forecast catch (numbers)	Forecast catch (weight)	Forecast population (numbers)	Forecast SSB
	$M=0.20$					$F_{mult}=0.75$				
1	0.69	0.01	50 000	345	0.09	0.07	2 961	2 043	50 000	345
2	1.08	0.05	16 465	889	0.64	0.48	5 734	6 193	38 265	2 066
3	2.29	0.23	63 654	33 527	0.83	0.62	27 011	61 854	8 341	4 393
4	4.30	0.62	12 932	34 477	0.81	0.61	5 390	23 178	27 965	74 555
5	6.64	0.86	5 296	30 242	0.76	0.57	2 105	13 979	5 767	32 934
6	8.38	1.00	800	6 704	0.81	0.61	333	2 794	2 452	20 549
7+	9.80	1.00	283	2 773	0.87	0.65	124	1 218	477	4 679
Total								Catch 111 259		SSB (new) 139 521
			B (old) 108 957			$F_{mult}=1.00$				
						0.09	3 906	2 695	50 000	345
						0.64	7 129	7 699	37 413	2 020
						0.83	32 982	75 528	7 108	3 744
						0.81	6 594	28 353	22 725	60 585
						0.76	2 587	17 180	4 710	26 896
						0.81	408	3 418	2 028	16 993
						0.87	151	1 482	388	3 807
								Catch 136 356		SSB (new) 114 390
						$F_{mult}=1.25$				
						0.11	4 831	3 333	50 000	345
						0.80	8 326	8 992	36 581	1 975
						1.04	37 884	86 755	6 057	3 190
						1.01	7 587	32 623	18 467	49 232
						0.95	2 990	19 852	3 847	21 966
						1.01	469	3 933	1 677	14 052
						1.09	173	1 696	316	3 097
								Catch 157 185		SSB (new) 93 858

Notes: F = fishing mortality; F_{mult} = potential F values relative to the most recent F; M = natural mortality; SSB = spawning stock biomass.

Table 8.2 Catch forecast option table.

Option	F-multiplier	Catch weight (ktonne)	SSB (new) (ktonne)
A	0.75	111	140
B	1.00	136	114
C	1.25	157	94

1 Multiple-option calculations need usually only be provided in one year of a multi-year forecast, preferably the final one. Allowing for several 'option years' leads to an explosion of alternatives, and these are usually difficult to understand, as well as tricky to organize.

2 There is no reason why the forecast calculation may not be continued indefinitely, provided that the output is suitably organized. A suitable way of supplying the future fishing mortalities and recruitment estimates is, of course, required. In practice recruitment in the unforeseeable future can only realistically be supplied as an average or from a stock–recruitment relationship (see below and Myers, Chapter 6, Volume 1). Allowing for indefinitely long catch forecasts can be quite useful because it provides a cross-check on yield-per-recruit calculations (see also below).

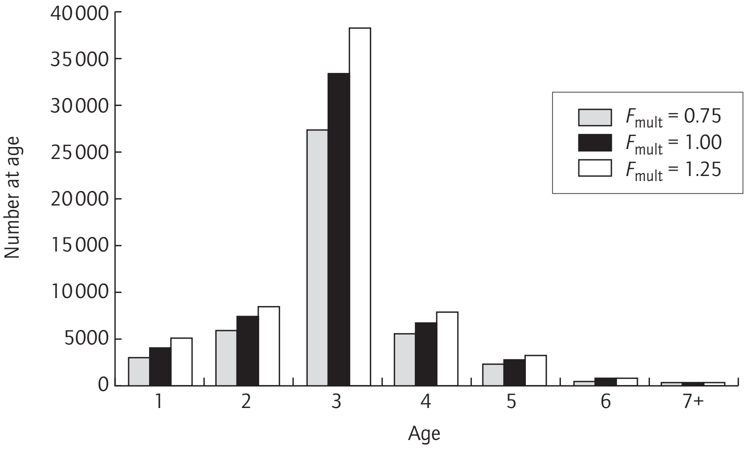

Fig. 8.1 Forecast catch numbers: *F*-multiplier is used to modulate fishing mortality.

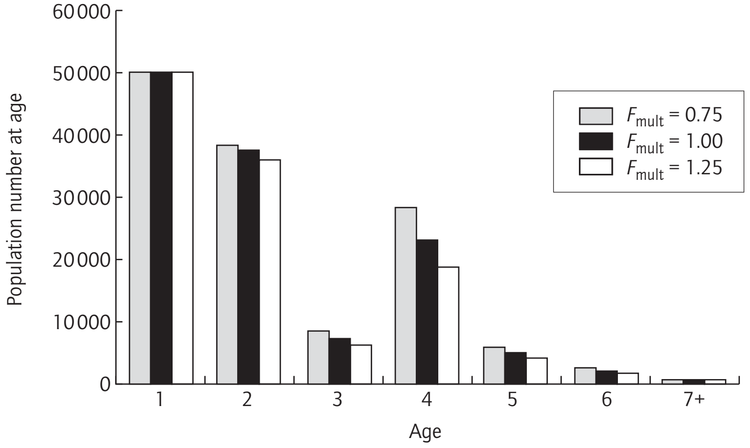

Fig. 8.2 Forecast population number at age.

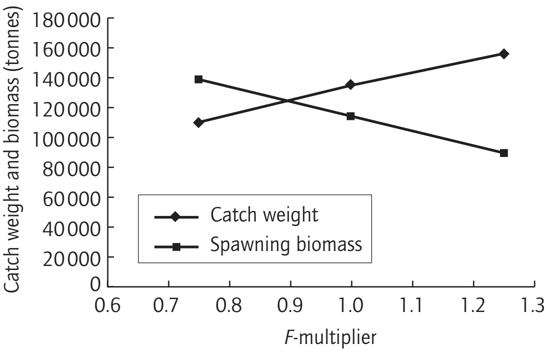

Fig. 8.3 Forecast catch weight and spawning stock biomass.

The specification of these future fishing mortalities is not trivial, because there are numerous possible scenarios which could be considered. The mortality rates associated with these are often most conveniently provided as '*F*-multipliers' rather than absolute values, as discussed above. Experience has shown that it is thoroughly confusing to use year-on-year multipliers which accumulate, and that it is preferable for all *F* values to be expressed as multipliers relative to a single historic reference *F*-pattern. Changes in the exploitation pattern cause further complications (see item 6 below).

3 Discarding at sea of fish because they are too small, unmarketable, or over quota, is a fact of life (see Kaiser and Jennings, Chapter 16, this volume). Sometimes it is a major factor in assessing the state of a stock and its prognosis for the future. In principle there is no particular difficulty in including it in assessment calculations, whether retrospective (see Chapter 7 this volume) or prognostic, as here. In practice there may be some problems, because the sampling errors associated with discard data are usually high. For a forecast, one needs to specify the rate of discarding, and this is most easily done by supplying estimates of the fraction of fish caught which are discarded, as a function of age or size (Sparre and Hart, Chapter 13, this volume). To a first approximation, these fractions may be taken to be constant over time, and for medium/long-term forecasts this is likely to be the best available assumption. In practice the fraction discarded is likely to vary with a number of factors, including the size of the year class concerned. If a statistical analysis of the data were carried out to establish a satisfactory predictive model for this variation, then it could of course be included in the calculation.

The catch equation is easily modified to incorporate discards, as

$$C_L(y,a) = F(y,a)P(y,a)[1 - f_D(a)] \times \{1 - \exp[-Z(y,a)]\}/Z(y,a) \tag{8.9}$$

where the subscript$_L$ implies those fish caught and landed. The symbol $f_D(a)$ denotes the fraction discarded of each age group. The numbers discarded are then, of course

$$C_D(y,a) = F(y,a)P(y,a)f_D(a) \times \{1 - \exp[-Z(y,a)]\}/Z(y,a). \tag{8.10}$$

The equation for the evolution of the population (8.2) needs no modification, because the usual convention is that fishing mortality (and therefore total mortality) includes all deaths due to fishing, whether or not the fish are landed. Finally, looking forward to the next paragraph, discarding practices often vary considerably between different fleets, so that f_D may require another suffix (f, for fleet), as do C and F, when several fleets are considered.

4 The extension of the calculations to several fleets is straightforward. One uses the partial fishing mortality $F(y,a,f)$ and calculates the catch (or landings) for the fleet $C(y,a,f)$ using

$$C(y,a,f) = F(y,a,f)P(y,a) \times \{1 - \exp[-Z(y,a)]\}/Z(y,a) \tag{8.11}$$

with or without the extra term for discarding, as required. Again the population equation (8.2) needs no change, since $Z(y,a)$ is always taken to refer to the total of all mortality rates, and therefore includes the sum of all the partial fishing mortality rates. The symbol $F(y,a)$ (without the extra index f) normally refers to this total fishing mortality rate, unless otherwise specified. Equation (8.3) for the yield (catch-in-weight) by each fleet of course becomes

$$Y(y,f) = \sum\nolimits_a C(y,a,f)W_c(a,f) \tag{8.12}$$

since the weight-at-age of fish in the catch (or landings) may be expected to vary from fleet to fleet, and these must then be summed to get the total yield.

5 The extension to several species caught simultaneously in a mixed fishery is also conceptually straightforward. Multispecies forecasts which include biological interactions (such as the effects of predation) are discussed in more detail in Section 8.3 below. For the technical interactions caused only by the occurrence of mixed fisheries, the equations just get duplicated for each species, acquiring yet another suffix (s, for species) on all relevant quantities. The only real complication is in the generation of the partial fishing mortalities. We now have an array of reference fishing mortalities, $F_{ref}(a,f,s)$, obtained by time-averaging over a few recent years of the historic data for $F(y,a,f,s)$. The future fishing mortalities are obtained by applying F-multipliers for each year and for each fleet which represent modulations of the fishing effort exerted by those fleets in the past, so that

$$F(y,a,f,s) = F_{mult}(y,f)^{*} F_{ref}(a,f,s) \tag{8.13}$$

where $F_{mult}(y,f)$ is just specified as a set of numbers representing the assumptions about the future activity of each fleet, which are not directly dependent on species (s). This is consistent with the simplifying assumption that both effort and fishing mortality vary in the same way for all species caught. This implies that there is a time-invariant set of 'bycatch ratios', or species-specific selection patterns, i.e. $S(a,f,s)$, where

$$F(y,a,f,s) = F(y,f,s^*)S(a,f,s), \tag{8.14}$$

where $F(y,f,s^*)$ is determined for a target or reference species s^*, and

$$S(a,f,s) = mean_y[F(y,a,f,s)/F(y,f,s^*)]. \tag{8.15}$$

Thus the values of $S(a,f,s)$ are likely to be close to 1.0 only for fully exploited ages of the reference species. They will usually be substantially less than one for all ages of the 'bycatch' species. Equation (8.14) provides an alternative, although in practice less convenient, way of generating the partial fishing mortalities.

6 Things get even more complicated than this if the exploitation pattern is permitted to change with time, as, for example, when one is assessing the consequences of a change of mesh size. Here again, to avoid confusion, it is important that the new exploitation patterns $S'(a,f,s)$ are expressed relative to the same reference fishing mortality arrays $F_{ref}(y,f,s^*)$, rather than by applying multipliers cumulatively.

8.1.4 Discussion

Catch prediction is mathematically rather simple, but computationally it can become rather complicated and tedious. Whilst spreadsheets are adequate for simple situations, dedicated computer programs are generally preferable for operational use, not least because compiled programs are much more secure against the introduction of accidental errors. They can also be constructed to provide output organized according to the layout required by the subsequent users of the information, such as the fishery management authorities. For these reasons such programs are often provided and maintained by the international bodies responsible for stock assessments, such as ICES (see www.ices.dk).

There are numerous practical details to be taken into account when executing catch forecasts, especially concerning the selection of the basic data representing the state of the stock, and the assumptions to use for its future development. In particular, we recommend that the calculations should always be started from the best possible estimates of the current surviving populations for each age group, as free as possible from sampling errors. In practice, this means taking great care, especially when using *ad hoc* tuning methods which treat the total international catch data in the final data year as exact, when projecting forward to the end of that year, and thus to the beginning of the next, as required. If the data are less than adequate, with coefficients of variation for important age groups larger than 20%, say, it may well be worthwhile switching to an Integrated or Survivors method, or even using a separable VPA (as discussed in Chapter 7) on the last five years' data, just to get a stabilized estimate of the survivors and the exploitation pattern for the forecast. Similarly, the reference F array should be calculated in a stable way, by appropriate averaging over time. 'Raw' final-year F estimates from VPA should not be used because they contain the full sampling errors of the catch and CPUE data.

Finally, great care should be taken over estimates of discard proportions and weights-at-age. Both often contain real changes with time, as well as discrepancies due to poor-quality data, and careful scrutiny of these data is necessary, preferably by statistical modelling, such as age-by-year multiplicative modelling (see Shepherd and Nicholson 1986). This can help to avoid major errors which may otherwise creep unnoticed into the calculation. A 30% error in the weight-at-age for an important age group could vitiate all of the effort devoted to careful tuning of the VPA calculation, and such errors can easily arise if there are trends in the data, or if growth depends on year-class size or prey abundance, and this is not recognized and allowed for (see Jobling, Chapter 5, Volume 1).

8.2 LONG-TERM FORECASTS OF CATCH AND BIOMASS

8.2.1 Introduction

In Chapter 7 (this volume), we stressed the importance of having good-quality estimates of the size of newly recruiting year classes when making short-term catch forecasts. Unless fishing mortality is less than about 0.3 and the variability of recruitment is also low, the accuracy of the forecast is largely controlled by the accuracy of the estimates of these recruitment estimates. Recruitment is, however, not usually determined until around the end of the first year of life, and it may not be possible to actually observe it until the following year, or even later, even in a research survey with a small mesh net. In temperate waters, most fisheries begin to exploit fish of two or three years old, and three- and four-year-old fish often constitute the major part of the catch. Thus, it is often only just possible to get the observations of recruitment which are required in time to make informed forecasts of the catches one or two years ahead. When no research survey data are available, so that one must rely on catches of young fish in the fishery itself, the situation is even worse.

Forecasts are, however, often required for more than two years ahead. This may, for example, be necessary so as to provide advice on the time-scale of recovery of the stock after a management measure has been implemented. This may require a forecast extending five to 10 years into the future – a medium-term forecast. In addition, the selection of appropriate management measures, such as the selection of a mesh size, or a target level of fishing mortality, usually requires the comparison of the state of the stock and the fishery under the new management regime, with that which would have occurred had nothing been done, after everything has settled down to its final state, after 10 years or even more.

The provision of sensible estimates of recruitment for such calculations is obviously a major problem (Myers, Chapter 6, Volume 1). In principle, the state of the stock, particularly the size of the spawning stock, would be expected to have some effect on recruitment. In practice, the relationship is almost never clear, and has little predictive utility, because of the very large fluctuations of recruitment, presumably due to the vagaries of weather and currents. This problem of determining the stock–recruitment relationship is discussed in detail by Myers. Even in the unlikely event that a useful predictive relationship could be found, this would not solve the problem, because this would predict only the expected (deterministic) size of the future year classes. These would in practice be perturbed by other events – notably the weather. Even if the effects of the weather were understood and quantified, this would not help us until the happy day when our meteorological colleagues were able to provide accurate and detailed weather forecasts up to a decade ahead. The prediction would therefore still only be of expected average recruitment, and would not include the inevitable perturbations, except in so far as one could calculate confidence regions for recruitment, and make stochastic forecasts.

Thus, medium- and long-term forecasts are at best only forecasts of average catch and biomass, where the average must be understood to be taken over hypothetical ensembles of all possible outcomes, or over enough years, which usually means five or more, to prevent fluctuations from dominating the result. In fact, it is common practice to use some recent average of actual recruitment as the estimate for those year classes for which no information is available. This bold assumption can perhaps be justified as the least implausible one available, but one should always be aware that it may be quite unrealistic in practice. There are in fact at least four reasons why such a recent average may not be a good estimate for the future:

1 if a stock–recruitment relationship exists, even though it cannot be demonstrated statistically to exist, then the expected level of recruitment will change as the stock size changes;

2 if climatic changes occur, as they seem to do on decadal and longer time-scales, the expected level of recruitment may also change;

3 if multispecies effects are important, recruitment to one stock may be modulated by changes in the size of other stocks;

4 if recruitment is determined by a stochastic process, as discussed below, this may be non-stationary, so that the mean for one period is not a reliable estimate of that for another period.

Nevertheless, even if these problems were understood, only in cases 1 and 3 would there be any realistic hope of allowing for them. In practice, there is usually little that can be done but to use some ensemble average recruitment, and try to ensure that the Health Warnings which should be attached to the results do not get forgotten. Most assessment scientists learn to attach these automatically. Their customers, however, do not, and may need to be reminded at regular intervals.

Despite this, it may sometimes be necessary to present the results of medium-term forecasts in absolute terms such as tonnes of fish, but long-term calculations can often better be presented in relative terms, as percentage gains or losses, either compared with the past or relative to another management option. This is a big help, because it automatically suggests that the calculation assumes that 'other things remain equal', as it does. Furthermore, since the quantities of interest are catch and biomass, which usually scale proportionally with the level of recruitment, it means that exogenous changes of recruitment, such as those due to chance events, or to processes 2 and 4 above, are cancelled out at least to a first approximation. This is not, regrettably, true for the endogenous processes 1 and 3, where the absolute size of the stocks affects the results in a non-linear fashion. Even so, a result expressed in percentage terms is still probably less likely to be misunderstood or misused than one in tonnage terms.

The proportionality of catch and biomass to recruitment, in the absence of non-linear processes such as 1 and 3 or density-dependent growth, mortality or fecundity, was recognized by the early workers in the field, as allowing for a major simplification of some assessment problems (see Beverton and Holt 1957). This led to the adoption and popularity of yield-per-recruit type calculations, and these are discussed below. These are often referred to as 'steady-state' or 'equilibrium' calculations, and this is a source of some unproductive semantic argument, since it may rightly be argued that fish stocks are never in a steady state, but invariably subject to substantial fluctuations, and that we have no basis for assuming that an equilibrium state ever exists. Whilst true, these objections are not helpful, since the calculations merely produce estimates which would apply if there were a steady or equilibrium state, and do not assume that such a state actually occurs. The results are in any case best presented as averages, even if this is statistically inexact, since this term carries the clear and correct implication that there are fluctuations too, whilst 'steady-state' and 'equilibrium' unfortunately suggest the opposite.

More recently, attention has also been focused on biomass-per-recruit estimates, in attempts to make some allowance for the possibility of stock collapse. The methods for computing yield and biomass-per-recruit are discussed in the following section of this chapter. This is followed by a brief discussion of the stock–recruitment problem, and the risk of stock collapse, and the use of stock–recruitment relationships in long-term forecast calculations to allow for this.

8.2.2 Yield- and biomass-per-recruit

The calculation of yield-per-recruit is probably the best-known procedure described in the classic monograph of Beverton and Holt (1957). The method they describe is, however, adapted to the computational facilities of their day, and is not often used today. The simplest way to compute long-term average yield and biomass is often just to insert an arbitrary constant value for recruitment into one of the short-term forecast calculations described in Chapter 7 (this volume), and step it forward in time until the results have stabilized. This typically requires a few more annual time steps than there are age groups in the calculation (the extra ones are required to let the plus group settle down properly). Whilst inelegant, the computations involved are trivial by modern standards, and this method is often useful. If density-dependent processes such as stock–recruitment relationships or density-dependent growth are involved, this method may well be the best, since time-stepping is just as good a way of reaching a steady state as any other iterative process, and has the advantage that the intermediate steps are also interpretable and may be useful. The time-stepping calculation is, of course, just a brute force method for carrying out a sum-of-products integration with fairly large (usually annual) age increments. If applied unthinkingly, this may lead to non-trivial truncation errors, but even these are not often troublesome, since the main purpose of such calculations is most often to compare one calculation with that for another related option, so such errors tend to cancel out to some extent. In addition, the standard short-term catch forecast procedures actually involve an implicit analytical integration of numbers within each year, thus overcoming the most serious possibility for error, due to significant changes of this quantity.

The main disadvantage of this approach is the practical difficulty of organizing and displaying the results for a wide range of fishing mortalities and, for this reason, the calculations are in practice often carried out by distinct programs written for the purpose. Nowadays, these invariably employ the discrete sum-of-products method of Thompson and Bell (1934). This is very simple, and has been well described by several authors, including Ricker (1975), Gulland (1983) Hilborn and Walters (1992) and Quinn and Deriso (1999). The main advantages of this method are that there is no difficulty in allowing for arbitrary growth patterns and/or exploitation patterns, or variation of natural mortality or discarding practices with age, within the same computationally straightforward framework. A brief account of the method is given below. The calculations may easily be implemented using spreadsheet software if desired, and we give an example of this.

We consider the contributions to yield and biomass of each age group of a year class as it passes through the fishery. This is equivalent to an integration of the catch equations with annual age increments. The calculations may easily be generalized to permit quarterly or monthly increments if so desired.

From equation 8.3, suppressing the variation with time (suffix y), the yield is

$$\begin{aligned} Y &= \sum\nolimits_a C(a)W_c(a) \\ &= \sum\nolimits_a P(a)F(a)\{[1-\exp[-Z(a)]]/Z(a)\}W_c(a). \end{aligned} \quad (8.16)$$

The calculation may, of course, be carried out for more than one fleet: $F(a)$ would then become the partial fishing mortality for that fleet, and $W_c(a)$ the weight-at-age for the catches by that fleet. $P(a)$ still represents the total population and $Z(a)$ the total mortality on the whole stock, however. For constant recruitment, R, at whatever age is taken to be the first in the summation, and writing YPR for Y/R, equation (8.16) becomes

$$\begin{aligned} YPR = \sum\nolimits_a &\exp[-cumZ(a)]W_c(a)F(a) \\ &\times\{1-\exp[-Z(a)]\}/Z(a) \end{aligned} \quad (8.17)$$

where the notation *cum* for cumulative mortality is as defined in Chapter 7 (this volume).

Similarly, but more simply, the biomass per recruit, B/R, denoted by BPR, is

$$BPR = \sum\nolimits_a W_s(a)f_x(a)\exp[-cumZ(a)] \quad (8.18)$$

where $f_x(a)$ as usual represents the appropriate fraction of the population, in this case usually $f_s(a)$ for the fraction mature, to give the spawning stock biomass-per-recruit.

Both these quantities may easily be calculated using the following pseudo-code routine. Note that it is assumed that the calculation is carried out for a range of overall fishing mortalities, F^*_{ref} so that $F(a) = F^*_{ref}\,S(a)$, where $S(a)$ as usual denotes the exploitation pattern.

Pseudo-code for yield and biomass-per-recruit

```
For each value of $F^*_{ref}$
    Initialize: ($P = 1$, $YPR = 0$, $BPR = 0$)
    For each age $a$
        $F(a) = F^*_{ref} * S(a)$
        $Z(a) = F(a) + M(a)$
        $BPR = BPR + P * w_s(a) * f_s(a)$
        $YPR = YPR + P * F(a) * w_c(a) * Ave[Z(a)]$
        $P = P * exp[-Z(a)]$
    Next age
    Add contribution from the plus-group ($g$)
    $BPR = BPR + P * w_s(g) * f_s(g) * \{1 - \exp[-Z(g)]\}$
```

```
    $YPR = YPR + P * F(g) * w_c(g)/Z(g)$
Next $F^*_{ref}$
End
```

A spreadsheet implementation of this calculation is shown in Table 8.3, for a simple case with constant M, a single fleet, and no discards, for just one level of future fishing mortality.

The results of a more complex case, with age-dependent M, allowing for discards, and with results computed for a substantial range of F to allow the plotting of a yield-per-recruit curve, is shown in Table 8.4.

These results are illustrated in Figs 8.4 and 8.5. Also shown in Fig. 8.4 are the locations of the biological reference points known as F_{max} and $F_{0.1}$, whose use is discussed further in section 8.2.4 below. F_{max} is the value of overall F for which the yield-per-recruit is a maximum. It may be very large, or even infinite if the curve is asymptotic rather than domed. $F_{0.1}$, on the other hand, is a measure of the overall F at which a high value of yield-per-recruit can be obtained without excessive effort. It is determined by the point on the curve at which its slope is reduced to 0.1 of that estimated at the origin. Thus, at $F_{0.1}$, extra increments of effort produce only one-tenth the extra yield that they would if the stock were very lightly fished, and one is deeply into a regime of diminished returns. The concept of $F_{0.1}$, introduced by Gulland (see Gulland 1983), is therefore based on an arbitrary but commonsense rule for determining when further increases of F lead to little extra yield, and are likely to be uneconomic.

The calculation of $F_{\max}$ and $F_{0.1}$ can be carried out in various ways, including numerical solution of the equation for the slope of the curve. This is not always straightforward and such elaboration is hardly necessary, since the simplest method works perfectly well. This is to calculate *YPR* for about one hundred increments of F, between zero and some maximum value such as 1 or 2, and then to select those values of F at which the increment of *YPR* first becomes negative, or less than 10% of its initial value, respectively.

8.2.3 Incorporating the stock–recruitment relationship

8.2.3.1 Recruitment failure and stock collapse

Calculations of yield and biomass per recruit are easy to carry out, and need only very limited data. These are a growth curve, some assumption about natural mortality, and some estimates for the exploitation pattern and the maturity give. They have therefore been very popular for many decades. Their virtue is that they cancel out the

Table 8.3 North Sea cod: yield and biomass per recruit analysis. Detailed calculation for a single level of overall fishing mortality.

Age	Weight	*F*-at-age	Maturity	Population	Biomass	Catch number	Catch weight
$M = 0.2$							
1	0.69	0.09	0.01	1000	7	78	54
2	1.08	0.64	0.05	748	40	324	350
3	2.29	0.83	0.23	323	170	167	383
4	4.30	0.81	0.62	115	307	59	253
5	6.64	0.76	0.86	42	240	21	136
6	8.38	0.81	1.00	16	135	8	69
7	9.80	0.87	1.00	6	57	3	31
			Total		957		1276
NB: Divide by assumed number of recruits					BPR = 0.957		YPR = 1.276
					Both expressed as kg/recruit		

Table 8.4 Yield and biomass per recruit: North Sea cod (with discards).

Data	Age 1	2	3	4	5	6	7	8
Proportion mature	0.01	0.05	0.23	0.62	0.86	1.00	1.00	1.00
Natural mortality	0.80	0.35	0.25	0.20	0.20	0.20	0.20	0.20
Fishing mortality: human consumption	0.14	0.76	0.92	0.78	0.73	0.76	0.78	0.76
Fishing mortality: discards	0.60	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Fishing mortality: total	0.74	0.82	0.92	0.78	0.73	0.76	0.78	0.76
Proportion retained	0.19	0.93	1.00	1.00	1.00	1.00	1.00	1.00
Weight-at-age: in stock	0.63	0.93	1.93	3.63	5.94	8.10	9.92	11.31
Weight-at-age: in catch	0.63	0.93	1.93	3.63	5.94	8.10	9.92	11.31
Weight-at-age: effective	0.01	0.05	0.44	2.25	5.11	8.10	9.92	11.31

Age F	1	2	3	4	5	6	7	8	BPR	1	2	3	4	5	6	7	8	YPR
	Stock number at age									Landed weight at age								
0.00	1.00	0.45	0.32	0.25	0.20	0.17	0.14	0.61	11.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.05	1.00	0.43	0.29	0.22	0.17	0.14	0.11	0.39	8.15	0.00	0.01	0.02	0.03	0.03	0.04	0.04	0.15	0.33
0.10	1.00	0.42	0.27	0.19	0.15	0.11	0.08	0.26	6.02	0.01	0.02	0.04	0.05	0.06	0.06	0.06	0.20	0.49
0.15	1.00	0.40	0.25	0.17	0.12	0.09	0.07	0.18	4.56	0.01	0.03	0.06	0.06	0.07	0.07	0.07	0.20	0.57
0.20	1.00	0.39	0.23	0.15	0.11	0.07	0.05	0.12	3.51	0.01	0.04	0.07	0.07	0.08	0.08	0.07	0.18	0.60
0.25	1.00	0.37	0.21	0.13	0.09	0.06	0.04	0.09	2.74	0.01	0.05	0.08	0.08	0.08	0.08	0.07	0.15	0.60
0.30	1.00	0.36	0.20	0.12	0.08	0.05	0.03	0.06	2.17	0.02	0.06	0.08	0.08	0.08	0.08	0.06	0.13	0.59
0.35	1.00	0.35	0.18	0.10	0.06	0.04	0.03	0.04	1.73	0.02	0.06	0.09	0.08	0.08	0.07	0.06	0.10	0.57
0.40	1.00	0.33	0.17	0.09	0.05	0.03	0.02	0.03	1.40	0.02	0.07	0.09	0.08	0.08	0.07	0.05	0.08	0.54
0.45	1.00	0.32	0.16	0.08	0.05	0.03	0.02	0.02	1.14	0.02	0.07	0.09	0.08	0.07	0.06	0.04	0.07	0.51
0.50	1.00	0.31	0.15	0.07	0.04	0.02	0.01	0.02	0.93	0.03	0.08	0.09	0.08	0.07	0.05	0.04	0.05	0.49
0.55	1.00	0.30	0.13	0.06	0.03	0.02	0.01	0.01	0.77	0.03	0.08	0.09	0.07	0.06	0.05	0.03	0.04	0.46
0.60	1.00	0.29	0.12	0.06	0.03	0.02	0.01	0.01	0.64	0.03	0.08	0.09	0.07	0.06	0.04	0.03	0.03	0.43
0.65	1.00	0.28	0.11	0.05	0.02	0.01	0.01	0.01	0.53	0.03	0.09	0.09	0.07	0.05	0.04	0.02	0.02	0.41
0.70	1.00	0.27	0.11	0.04	0.02	0.01	0.00	0.00	0.45	0.03	0.09	0.09	0.06	0.05	0.03	0.02	0.02	0.39
0.75	1.00	0.26	0.10	0.04	0.02	0.01	0.00	0.00	0.38	0.04	0.09	0.09	0.06	0.04	0.03	0.02	0.01	0.37
0.80	1.00	0.25	0.09	0.03	0.01	0.01	0.00	0.00	0.32	0.04	0.09	0.08	0.05	0.04	0.02	0.01	0.01	0.35
0.85	1.00	0.24	0.08	0.03	0.01	0.01	0.00	0.00	0.28	0.04	0.09	0.08	0.05	0.03	0.02	0.01	0.01	0.33
0.90	1.00	0.23	0.08	0.03	0.01	0.00	0.00	0.00	0.24	0.04	0.09	0.08	0.05	0.03	0.02	0.01	0.01	0.32
0.95	1.00	0.22	0.07	0.02	0.01	0.00	0.00	0.00	0.20	0.04	0.09	0.07	0.04	0.03	0.01	0.01	0.01	0.30
1.00	1.00	0.21	0.07	0.02	0.01	0.00	0.00	0.00	0.18	0.04	0.09	0.07	0.04	0.02	0.01	0.01	0.00	0.29

biggest unknown factor, recruitment, and this is also their vice, since they thereby suppress what may be the most important factor to consider. This may be easily appreciated, since it would actually be impossible ever to fish a stock that had constant recruitment to the point of collapse, since in this case neither *YPR* nor *BPR* ever reduces to zero, however high a value is taken for fishing mortality. In real life, however, recruitment failure is always possible (see Myers, Chapter 6, Volume 1). There are a number of stocks that have collapsed at various times under heavy fishing, for example the North Sea cod (*Gadus morhua*), herring (*Clupea harengus*) and mackerel, the Atlanto-Scandian

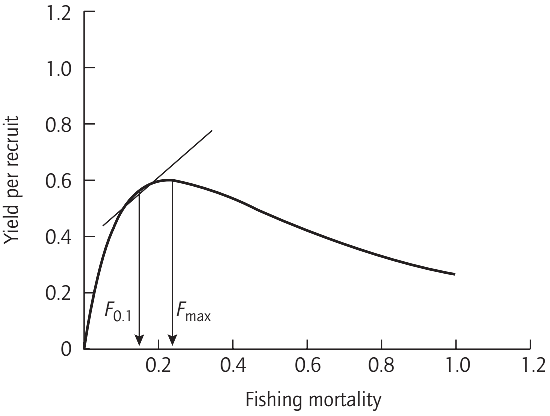

Fig. 8.4 North Sea cod: yield per recruit.

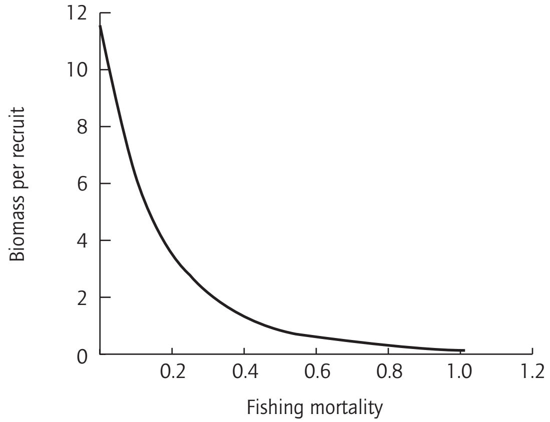

Fig. 8.5 North Sea cod: biomass per recruit.

herring and the Canadian northern cod. In each case the reduced stock size was probably only a contributory factor, since most disasters are caused by a conjunction of two or three factors, not just one. In addition, however, one should take note of the virtual elimination of large species such as halibut, turbot and ling from heavily fished areas such as the North Sea.

It is therefore imprudent to work with models which neglect the possibility of stock collapse through recruitment failure, and one must deplore the excessive attention to yield-per-recruit, and the $F_{\max}$ and $F_{0.1}$ reference points, in much traditional fisheries management. The extra ingredient which produces the possibility of stock collapse is, of course, the likelihood of reduced recruitment at reduced stock size, i.e. the stock–recruitment relationship (*SRR*).

Whether or not such relationships exist is a matter of controversy (see Myers, Chapter 6, Volume 1). Recruitment is usually subject to large fluctuations from year to year, and the relationship is thus obscured. Generally the size of the spawning stock is not a powerful determinant of recruitment. Indeed, it may not even be the major factor. However, this is one of those cases where failure to demonstrate an effect statistically does not provide a licence to ignore it, because the consequences of doing so are too great.

8.2.3.2 Fitting stock–recruitment relationships

What sort of relationship would it be appropriate to seek in a data set on spawning stock and recruitment? In the absence of processes serving to regulate the population size the expected relationship between recruitment and parent stock size would be strict proportionality – a straight line through the origin on a stock–recruitment plot. This would be the result of constant fecundity and mortality rates, and this should in principle be the most appropriate null hypothesis, to be adopted in the absence of evidence to contradict it.

The consequence of such an assumption is, however, that the stock would tend exponentially to either zero or infinite size, with a characteristic time-scale of a few years, depending on the level of total mortality on the stock, unless by chance this happened to be just sufficient to keep the stock in a state of neutral equilibrium. Simple graphical simulations (see e.g. Beverton and Holt 1957, Fig. 6.1) can easily be used to illustrate such behaviour, and the results are quite unlike anything normally observed in practice. It is for this reason that almost all fishery biologists believe that some sort of regulatory processes are at work, even though they cannot be described in any detail.

If the relationship between recruitment and parent stock is non-linear, then the possibility of regulation towards one or more stationary states exists. These may, however, be either stable or unstable equilibria, and are unlikely to be clearly observable in the presence of large variability. For single-cohort spawning stocks, these occur wherever the stock–recruit curve intersects a line of unit slope which passes through the origin on a plot of recruits against spawning numbers (Ricker 1975). The generalization of this to multiple-age spawning populations is straightforward: one simply calculates the steady-state level of spawning stock biomass per recruit for any desired regime of natural and fishing mortality, growth and maturity at age, and plots the line of the corresponding slope through the origin on the diagram of recruitment against spawning stock biomass. The intersections of these survival lines with the curve defining recruitment as a function of spawning stock size again define potential equilibrium states. In fact, for a stationary state, the ratio of recruitment (R) to spawning stock biomass (SSB) must equal the reciprocal of the spawning biomass-per-recruit (BPR) so that

$$R/SSB = 1/BPR \tag{8.19}$$

This relationship is the basis for combining a stock–recruitment relationship with yield- and biomass-per-recruit calculations to produce total yield curves (see e.g. Shepherd 1982, and Section 8.2.3.3 below). Now, biomass-per-recruit is a measure of survival and decreases as total mortality increases. The equilibrium stock size therefore decreases as F increases, as illustrated in Fig. 8.5. It is easy to see that the stock will collapse when fishing mortality is so high that $1/BPR$ exceeds the slope of the recruitment curve at the origin. This slope at the origin is therefore a quantity of great concern to fishery biologists. Regrettably it is not guaranteed to be positive definite. It could be zero, or effectively infinite, and techniques for determining this slope for real data sets are in their infancy.

In practice there has been a tendency among fishery biologists to take constant recruitment as the null hypothesis. As discussed above, this is dangerous, because a stock capable of generating constant recruitment at any stock level cannot be collapsed, however great a fishing mortality is applied. Some relationship between R and SSB should always be considered as soon as sufficient data has been acquired, using the techniques discussed by Myers (Chapter 6, Volume 1). In practice the most common and useful stock–recruitment relationships are those proposed by:

(a) Beverton and Holt (1957)

$$R = aB/(1 + B/K) \tag{8.20}$$

(b) Ricker (1975)

$$R = aB\exp(-B/K) \tag{8.21}$$

(c) Cushing (1973)

$$R = aB(B/K)^{-(1-\beta)} = aK(B/K)^{\beta} \tag{8.22}$$

(d) Shepherd (1982)

$$R = aB/\left[1 + (B/K)^{\beta}\right] \tag{8.23}$$

(e) Schnute (1985)

$$R = aB[1 + (B/K)]^{\beta} \tag{8.24}$$

As explained by Shepherd (1982), the three-parameter expressions such as (8.23) and (8.24), which are very similar in practice, can be used to approximate the effect of the three more traditional relationships. With $\beta = 1$ they are identical to the Beverton–Holt form. With $\beta > 1$ they produce a domed relationship similar to a Ricker curve. With $\beta < 1$ they lead to a non-asymptotic relationship similar to that used by Cushing, with the bonus that they avoid the infinite slope at the origin which is the major defect of that form, since it precludes the possibility of stock collapse. Some of these relationships are illustrated in Figs 8.6 and 8.7. Note that equations 8.20 to 8.24 have been written in a dimensionally consistent form: a has the dimensions of recruits per unit biomass, and represents the slope at the origin (except for the Cushing form). B and K are biomasses, and K is a threshold

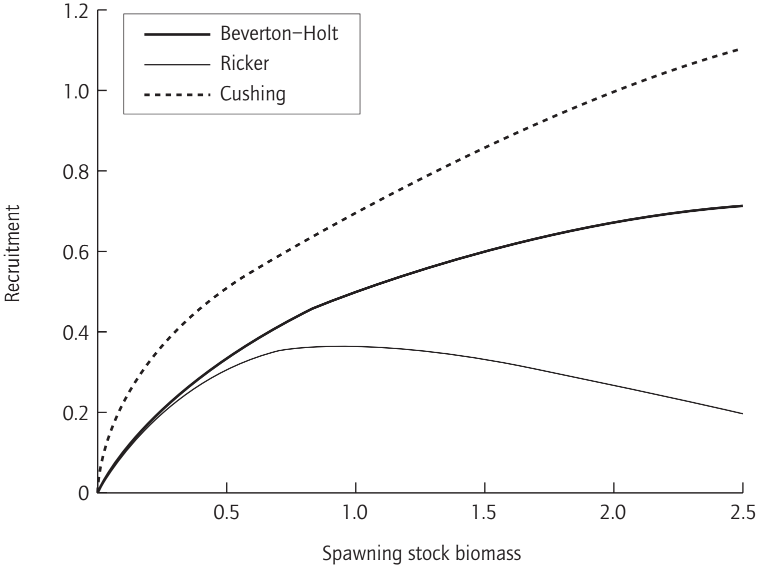

Fig. 8.6 Stock–recruitment relationships.

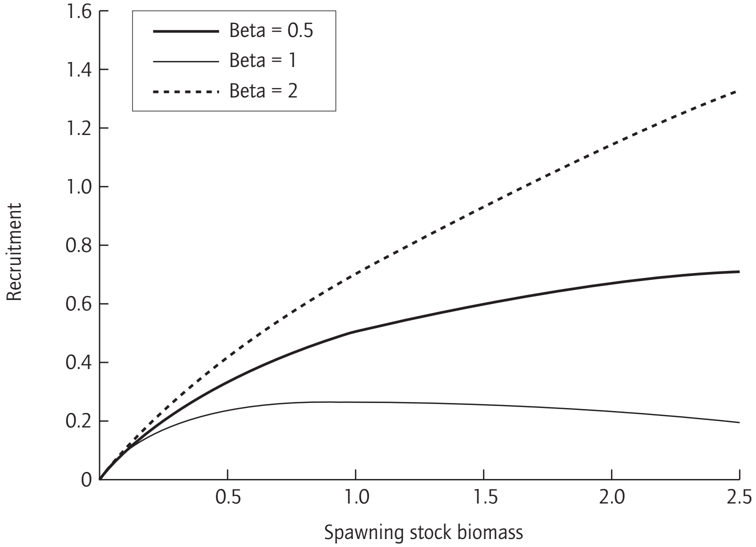

Fig. 8.7 Shepherd-type stock–recruitment relationships.

biomass above which the relationship departs considerably from linearity (again, except for 8.22). The exponent β is a dimensionless number of order 1, and is a shape parameter representing the degree of curvature.

8.2.3.3 Total yield curves and *MSY*

The calculation of total yield and biomass curves in absolute units such as tonnes, as functions of fishing mortality, is straightforward, given a suitable SRR and previous estimates of yield-per-recruit (YPR) and biomass-per-recruit (BPR) as functions of F. The procedure is as follows, using the Shepherd form of the relationship:

Pseudo-code for total yield and biomass calculations

```
For each value of $F$
    Calculate $YPR$ and $BPR$
    Calculate $B = K(a * BPR - 1)^{1/\beta}$
    Calculate $R = B/BPR$
    Calculate $Y = R * YPR$
Next $F$
```

This calculation is easily integrated with that of YPR and BPR (Section 8.2.2) if desired.

The results may be plotted as graphs of Y and B against F, or as the 'general production' curve of Y against B, as illustrated in Figs 8.8 and 8.9. These curves are, of course, only valid for a hypothetical steady state which never exists in practice. They represent the ensemble or time-averaged yield and biomass that would be obtained if fishing mortality were held constant for a long time and, of course, if the fitted stock–recruitment relationship were valid. Nevertheless, they can be quite instructive, because they do allow for the possibility of stock collapse. It is by no means uncommon for these curves to indicate that at current levels of F the stock will collapse, and this may sometimes be taken to mean that the stock should in fact have collapsed already. This can occur because these are steady-state analyses, whilst real stocks are never in a steady state. It can only be interpreted as a warning, although it does make the conclusions difficult to explain when there are still fish in the sea. In addition, the results depend crucially on the parameters estimated for the stock–recruitment relationship. These are always uncertain, and usually contentious. The utility of these calculations is in practice therefore limited, but an excellent example (Cook et al. 1997) of their use predicted the demise of the North Sea cod, which is occurring a few years later.

Several important conclusions can be drawn from such calculations:

1 The possibility of stock collapse is made explicit, and some estimate of the level of fishing mortality at which it may occur is provided.

2 An estimate of Maximum Sustainable Yield (MSY) may be made, in absolute terms of tonnes of fish, rather than as yield-per-recruit. This is normally less than the product of maximum yield-per-recruit and average recruitment, and may be used to dampen unrealistic expectations, particularly in the early years of a developing fishery.

3 An estimate of F_{msy}, the fishing mortality at which MSY would be attained, may also be made. This is almost always less than F_{max}, the fishing

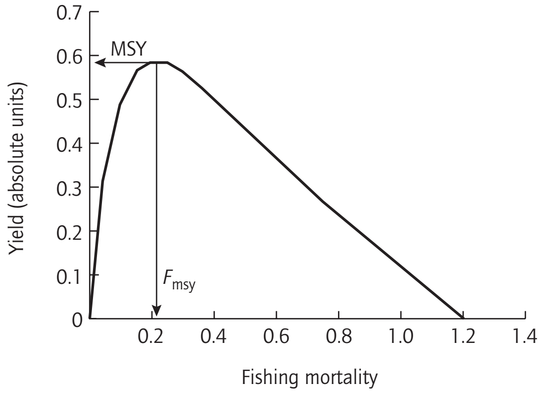

Fig. 8.8 Total yield versus F (illustrative).

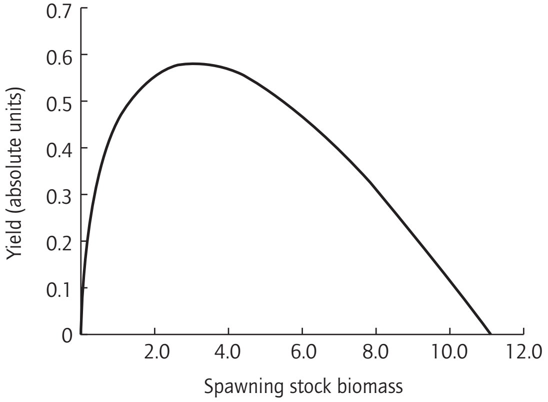

Fig. 8.9 Total yield versus spawning stock biomass (illustrative).

mortality yielding maximum yield-per-recruit, since recognizing the possibility of stock collapse leads to a more conservative interpretation.

Taken with appropriate levels of enlightened scepticism, these estimates may be useful additional guides to the appropriateness of various levels of exploitation. They still neglect economic factors (Chapter 12, this volume), but include more of the relevant biology. As is often the case, when one includes important but uncertain factors in an assessment, one hopes that it becomes less biased, but it is likely also to become more variable.

Another point of interest is that the end product of these calculations are production curves similar to those obtainable from stock-production models (Schnute and Richards, Chapter 6, this volume). The gulf between age-based and bulked stock-production models may therefore be crossed without undue difficulty. Where age-based data are available, the results of the two approaches may be compared. The important difference is that the stock–recruitment relationship, with all its uncertainties, is made explicit in the age-based approach, while in the bulked-stock methods it lies implicit, usually unrecognized and sometimes implausible. Treating it explicitly should make one aware of the limitations of the approach, and particularly of the wide confidence limits on the estimates, and thus engender a more realistic and balanced appreciation of the conclusions.

8.2.4 Biological reference points

Biological reference points are values of quantities which are indicative of the state or character of a stock, and which may be used as 'signposts' to guide the management of the stock. The traditional reference points F_{max} and $F_{0.1}$ have been discussed in Section 8.2.2. These are indicators of levels of exploitation at which maximum physical yield, or something close to it, could be achieved under the assumption that recruitment is not affected by stock size.

If a stock–recruitment relationship is estimated and allowed for, either explicitly or through a stock-production model, an equivalent reference point can be calculated, i.e. F_{msy}. Since recruitment is now specified rather than normalized out of the calculations, the associated reference points MSY and B_{msy} can also be calculated. These are, of course, the maximum sustainable yield and the spawning stock biomass at which this would be achieved. Because of the uncertainty of the stock–recruitment relationship these reference points are not widely accepted, but may be useful for convincing managers or fishermen that recent yields have been unusually high, and that the normal expectation is much less, or that stock size has fallen way below desirable levels.

F_{msy} is analogous to F_{max}, and one can also calculate reference points indicating maximum economic yield (MEY), provided that reliable cost and price information is available – $F_{0.1}$ is of course a surrogate for these. The actual physical or monetary yield (MEY) and the associated biomass B_{mey} can also be computed together with F_{mey} itself (see Hannesson, Chapter 12, this volume for further detail).

These biological reference points are sometimes regarded as targets for management, and were indeed originally intended for this purpose. The rationale for this is dubious, however, since maximum physical yield as tonnes of fish, and maximum economic return to a hypothetical monopolistic owner of the fishery, are not usually the real objectives of any of the interested parties. The real objectives are more usually sustainable positive returns to individual fishermen, the maintenance of employment, the utilization of existing fishing vessels, and the avoidance of social and political unrest (see also Hart and Reynolds, Chapter 1, this volume). Some further shortcomings of these reference points as objectives are discussed below. In the light of these reservations, they are best regarded only as signposts, or navigation markers, which highlight the consequences of moving in one direction or another.

F_{max} and $F_{0.1}$ have been quite widely used as reference points and targets of management, in the northeast and northwest Atlantic respectively, but they suffer from the serious defect that they exclude the possibility of stock collapse. Whilst this may be overcome by fitting a stock–recruitment curve, as described above, this is invariably a contentious procedure. Since the most important quantity to know is perhaps the maximum fishing mortality which the stock can withstand before being driven to collapse, it is useful to try to do this directly. A procedure proposed by Shepherd (1982) may be useful for this purpose. The fishing mortality corresponding to the upper 10th percentile of the slopes (R/SSB) given by all the data points on a stock recruitment plot is estimated. This estimate of fishing mortality was named F_{high} by the ICES Methods Working Group, when the problem was considered. Associated estimates F_{med} and F_{low} were also defined, corresponding to the median slope and that exceeded by 90% of the data points. It should be noted that F_{low} does not always exist – the biomass-per recruit obtained sometimes exceeds that corresponding to zero fishing mortality.

There is, of course, no guarantee that F_{high} is a good estimate of the slope at the origin of the stock–recruitment curve, even assuming that such a quantity is well defined: the procedure is a practical *ad hoc* procedure rather than subtle science. Nevertheless, the rationale for using F_{high} as an estimate of a level of F likely to involve an excessive risk of stock collapse is quite plausible, and may be stated as follows: given the data available, the levels of recruitment-per-unit-biomass need to maintain the stock under levels of fishing mortality exceeding F_{high} have been observed in only one year in ten, and it would be imprudent to assume that they could be generated routinely. Conversely, for F_{low} one can say that the required levels of R/SSB have been generated in most years, and these should be little risk of stock collapse. F_{med} divides the region of high risk from that of low risk. At or below F_{med} the risk should be acceptable – not more than 50%, but above F_{med} it begins to increase rapidly. This line of argument was pursued by Sissenwine and Shepherd (1987), where it was argued that F_{med} (there called F_{rep}) could serve as a target for management, whilst F_{high} is clearly an indicator of danger, to be avoided, and certainly not a target.

Several authors have pointed out that the estimates of F_{high} and F_{med} that one obtains depend to some extent on the history of the stock. If it has never been heavily exploited, yet there is indeed some compensatory stock–recruitment relationship, the estimates will be too low simply because the region where compensation is important (so that R/SSB is increased) will never have been explored. Conversely, if a stock has been on the verge of collapse for some time, so that one is seeing the straight-line relationship between R and SSB near the origin, then F_{med} is likely to estimate the critical level of fishing mortality rather than a safe level. Finally, if a stock suffers very high recruitment variability, the estimate of F_{high} will be inflated by that variability, as the 10th percentile is pushed away from the median, and may not be conservative. Finally, like the other biological reference points, these measures depend on the vital parameters of the stock, and are in fact especially sensitive to the maturity ogive. If this has changed with time, the estimates may be biased. These measures are therefore far from perfect, and are certainly not magical solutions to the problem of providing an early warning of stock collapse. They must therefore be used with caution, but they do at least attempt to address the problem in a systematic way, and are probably the best blunt instruments available at the present time (see also Myers, Chapter 6, Volume 1, for further discussion).

The problem of estimating a minimum tolerable spawning stock size is, if anything, even more difficult, and until recently relied almost entirely on subjective estimates from stock–recruitment plots. Serebryakov (1990) has, however, proposed a solution to this problem which is very much in the spirit of the F_{high} approach. He suggests that we identify the critical stock size as the smallest stock at which there is a reasonable chance of getting a good recruitment. The rationale for this is that it invariably requires one or more good year classes to initiate a stock recovery. This stock size may be estimated from the intersection of the upper 10th percentile of the slope R/SSB, as used for the estimation of F_{high}, and the upper 10th percentile of the recruitment values, representing a typical good year class. At this stock size, good survival (high *R/SSB*) can still generate a good year class (high *R*). At lower stock sizes it cannot, with reasonable probability (of the order of 1 in 10).

This provides a sensible rationale for estimating a critical stock size in a reasonably robust way. It has been used by the ICES North Sea Roundfish Working Group (Anon. 1991), and for the North Sea cod stock it gave the same result as previous purely subjective evaluations. Whether or not this constitutes support for the idea is arguable! The method has not yet been extensively field-tested, nor have the consequences of using it for management been thoroughly simulated. At the least, it provides a sensible and objective way of estimating some low-ish value of stock size, within the range observed, below which it may be imprudent to go. This is better than nothing.

8.2.5 Stochastic stock–recruitment relationships

All the discussion in this chapter so far has implicitly assumed that there is some compensatory relationship between recruitment and spawning stock size, even though this may be comprehensively obscured by the high variability of recruitment (Myers, Chapter 6, Volume 1). Even this assumption may, however, be questionable. The possibility that there is no such deterministic compensatory relationship at all has been explored by Shepherd and Cushing (1990). The somewhat subversive idea is that one might have *only* variability around a constant median level of *R/SSB*. On the face of it, this would not supply a regulatory mechanism. However, if the frequency distribution of the variability is sufficiently skewed, and if the variability increases as the stock size decreases, as has often been suggested, then the arithmetic mean recruitment would be inflated above the median level at low stock sizes, and would thus follow a compensatory relationship, of an unusual form, even though the median does not. The stock size, at fixed fishing mortality, is of course just some weighted running arithmetic mean of recruitment, and so responds like the arithmetic mean rather than the median level, and this supplies a purely stochastic mechanism for regulation, which relies entirely upon the variability for its existence. The potential efficacy of the mechanism has been confirmed by simulation. This is, in many respects, a rather plausible description of the recruitment process (see Shepherd and Cushing 1990 for a full discussion). At present it can only be regarded as hypothetical, but it may perhaps serve as a warning that strong assumptions about the nature of existence of stock–recruitment relationships are unwarranted, and that the whole subject needs to be viewed with healthy scepticism.

8.2.6 Discussion

The abundance of fish stocks is driven to two main factors: the recruitment of young fish, and mortality, which is usually dominated by the effects of fishing. If the recruitment is taken as given, it is not too difficult to assess the effects of varying the intensity and nature of fishing. Such yield-per-recruit calculations have been for many years the main tool for determining the appropriateness of various amounts and types of fishing, and remain useful for that purpose today.

However, recruitment to fish stocks is far from constant in practice, but varies on all time-scales, from years through to centuries. The reasons for these variations remain to a large extent unknown. This severely compromises the usefulness of long-term forecasts for fish stocks, which must invariably be heavily qualified with 'other things being equal'. In particular, in most cases there is no clear indication of the effects of spawning stock size on recruitment, and this is particularly important because it is intimately connected with the possibility of stock collapse under fishing. Furthermore, the interactions between species make the absolute size of recruitment important – and may make the 'other things' unequal after all. This issue is discussed further in Section 8.3 below.

Given all these problems, it is clear that long-term forecasting is a difficult area, which must be approached with considerable caution and mature judgement. The attempt is however essential, since it is only in the long-term that the effects of management are fully expressed, and any attempt to manage a fishery without the perspective of the long-term effects would be foolhardy. The assessment of the long-term effects is also the arena in which the skill and judgement of the fisheries scientist is most crucial. The short-term effects of most fishery management actions are fairly obvious to all concerned. The long-term effects are however much less obvious, more subtle, and often counter-intuitive. The assessment, and explanation of these effects is arguably the most important, and probably the most difficult task which fisheries scientists are called upon to undertake.

8.3 MULTISPECIES FORECASTS

It was noted in Chapter 7, this volume, that, while in principle changes in predation mortality might be considered in some short-term predictions, in practice for the larger species rather little is to be gained from doing so. The reason is that for these species predation mortality acts mostly on pre-recruit ages and their numbers can often be estimated from research surveys at a time after the major part of the predation mortality has occurred. In areas with important fisheries for prey species the need for considering the effect of predation mortality rate on short-term yield is likely to be greater. As an example of this, routine calculations of predation losses are made in the case of the northeast Arctic capelin TAC (ICES 2000).

Multispecies effects may, however, affect the growth of predator species and also their reproductive capability. For example, Marshall et al. (1998) showed that condition and fecundity in northeast Arctic cod was determined to a large extent by capelin abundance. Effects on growth are particularly likely in areas heavily dependent on one key prey species such as capelin in the northeast Arctic, Iceland and Newfoundland. Weight-at-age is a significant component of catch prediction so changes in growth are likely to affect short-term predictions. This was seen particularly strongly in the late 1980s when the northeast Arctic cod failed to grow as expected (ICES 1990). However, in general the use of multispecies considerations is the exception rather than the rule for short-term predictions.

In practice the same could also be said for long-term predictions. However, it is far less certain that ignoring multispecies effects is sensible for medium- to long-term predictions. Predation mortality can make considerable changes to average levels of natural mortality rate on pre-recruit ages of larger fish such as the North Sea cod depicted in Fig. 7.14, and it affects all ages of smaller species. It is well known that increasing natural mortality alters the shape of yield per recruit curves. It will also affect the number of recruits living long enough to form the spawning biomass.

The equations for multispecies cohort analysis and the equivalent equations for multispecies VPA can be reversed and long-term simulations produced, to predict how the equilibrium yield will change under various exploitation regimes for the fish stocks included. Since fishing mortality rate might alter, or exploitation patterns may be changed on any of the predator or prey stocks, a wide range of scenarios is possible and the computations are quite complex. A computer model, MSFOR, which makes long-term predictions based upon the equations and estimates of MSVPA, was written by Sparre. It was tested and used extensively by the ICES Multispecies Assessment Working Group (see ICES 1986).

The wide range of possible scenarios possible with a multispecies prediction on a number of stocks makes it rather difficult to provide understanding of how the system may behave. However, we may generalize to a certain extent. Yield-per-recruit curves typically become flatter-topped and their maximum moves to higher values of fishing mortality rate as levels of natural mortality increase on recruited ages. When natural mortality increases on pre-recruit ages the effect is to reduce the numbers of recruits entering the fishery. This would generally depress yield-per-recruit curves if the constant recruitment of the model was at a younger age than some of those that the predation mortality acted on. In either case yield would seem likely to be lower when predation mortality is high. This is likely to have occurred in periods when fishing mortality was low. Thus the predictions of single-species yield-per-recruit curves are likely to be unsound when fishing mortality rate is typically low throughout an ecosystem. We may therefore conclude that predation mortality generated from multispecies interactions leads to flatter-topped yield-per-recruit curves with maxima at higher levels of fishing mortality.

This is illustrated by Fig. 8.10. This shows the calculated change in yield per average recruit for North Sea fish stocks that would occur if fishing mortality rate was lowered by 10% on all species. The three lines show the changes expected when predation mortality rates were based upon the 1981 stomach-sampling data, the 1991 stomach-sampling data and a key run based upon both sets of stomach-sampling data. This illustrates that under a multispecies model decreasing fishing mortality decreases yield for most of these stocks. This is in sharp contrast with current long-term single-species predictions for these stocks which would predict most yields increasing with decreased fishing intensity. The figure also indicates that the predictions are affected by the stomach data set used in MSVPA and the consequent choice of suitability with which to run MSFOR. Differences are particularly large between the two runs for haddock and herring. This largely resulted from apparent changes in predation patterns of saithe between the two stomach-sampling data sets.

A further concern with such predictions is that (like single-species yield-per-recruit) they do not necessarily include stock–recruitment considerations. However, since multispecies models generally predict asymptotic yield curves because of the buffering effect of predation, it is clearly even more important that stock–recruitment effects are included in multispecies models. If these are included then it seems likely that yield curves would initially increase more slowly with increasing fishing mortality than a single-species yield curve due to predation mortality effects. However, once recruitment overfishing occurred, the decrease in yield would be far more rapid than a single-species yield-per-recruit curve would predict.

This pattern is illustrated in Fig. 8.11, which for the northeast Arctic cod shows the 7-year running average of yield plotted on the 7-year running average of fishing mortality rate, transformed to the yield/biomass ratio, expressed as the harvest percentage. This is contrasted with a single-species yield-per-recruit curve for the same stock, scaled to the same maximum yield. It is apparent that the slope of actual yield at low fishing mortality, as indicated by the running average curve, is

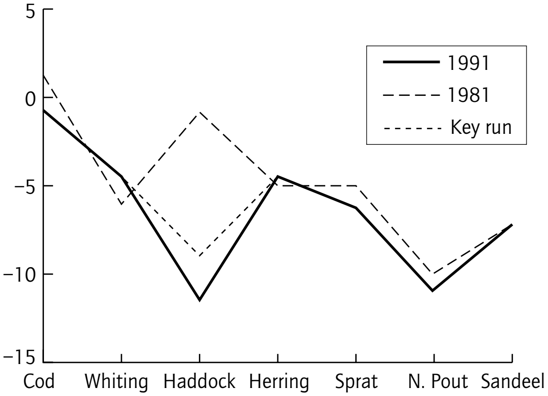

Fig. 8.10 Yield of North Sea species after a general reduction of 10% in all fishing mortality. N = Norway.

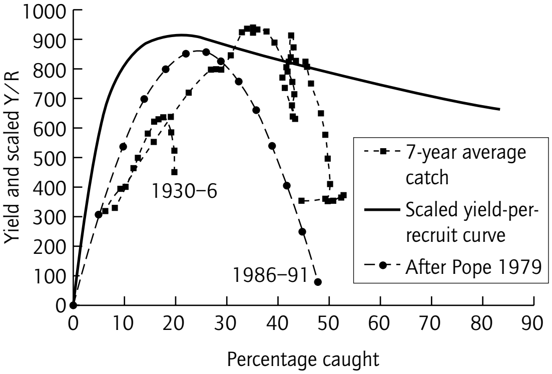

Fig. 8.11 Yield-per-recruit curve for the northeast Arctic cod compared to a 7-year running average of yield-against-harvest rate, and to an early production curve fit due to Pope (1979).

shallower than the response predicted with a single-species yield-per-recruit curve. Predation mortality (which is mostly caused by cannibalism in this case), and density-dependent growth seem the likely cause of this discrepancy. It is also apparent that the actual yield has dropped away very precipitately at higher harvest rates and this is doubtless due to stock–recruitment effects, which might have been exacerbated by reductions in prey availability. The figure also shows a surplus production curve (Pope 1979) fitted to the biomass and harvest rates estimates of VPA. While not exact, this makes more sensible management predictions than the single-species yield-per-recruit curve and it is notable that it did so before the steep decline in yield occurred in the 1980s.

Because of the likely changes in growth and stock-recruitment effects on yield functions, the ICES Multispecies Working Group has usually declined to predict long-term yield which takes the North Sea stocks far from their average situation. They have thus usually just indicated the changes that might result from changing effort by 10% on seven broadly defined fishing fleets. This produces what may be converted to a Jacobian matrix $\partial Y(s,f)/\partial E(g)$ of yield $Y(s,f)$ of species (s) by fleet (f) relative to a change of effort $E(g)$ in another fleet (g). This provides information on the local slope of the multispecies yield per average recruit surface. Interestingly this and contemporary yield provides just sufficient information to fit a multispecies production model which can be used to predict yield in the near vicinity and can also be used to predict the position of multispecies analogues to the more usual reference points (ICES 1989).

In conclusion, multispecies effects sometimes affect short-term predictions and can undoubtedly have a strong effect on long-term predictions. However, the increasing detail of multispecies models can mean that while they may improve on single-species models, particularly in the low fishing mortality range, their long-term predictions may be very variable. There may be an argument for making long-term predictions using simple production models which implicitly include many of the compensatory effects that multispecies models and stock–recruitment models attempt to provide. However, the formulation of these simpler models is helped by more detailed understanding of the biology. Moreover, they are undoubtedly best fitted to the solid estimates of past time-series of mortality and biomass provided by age-based estimation techniques such as VPA, rather than to the less reliable estimates derived directly from CPUE data.

8.4 CONCLUSIONS

Short-term catch forecasts are required for choosing among the options for managing stocks in the near future, in pursuit of whatever long-term strategy has been adopted. They are reasonably straightforward calculations, which require care and attention to detail, but few large assumptions about aspects which are not well known and reasonably well understood. Moreover, they are not much affected by multispecies biological interactions, although they do depend on the technical interactions caused by several species being caught together in mixed fisheries.

Conversely, the long-term forecasts of catch and biomass, which are needed to choose among possible management strategies, are sensitive to a number of factors that are rarely well known or adequately described. These include systematic variations of growth and maturity rates with stock size and environmental conditions, variations of natural mortality rates as a result of biological interactions, especially predation, and of course the dependence of recruitment on both stock size and environmental factors, which are for all practical purposes unpredictable. For these reasons all such long-term calculations should not be regarded as actual predictions of the future state of the stocks concerned, except in a very general sense. So far as possible they should be presented as comparisons of the effects of following alternative management options, on the assumption that various other uncertain factors remain equal, and suitable Health Warnings should be attached. Even this is not enough, because some factors, such as predation rates, depend on the absolute sizes of future stocks, which themselves also depend on uncertain stock–recruitment relationships. Management decisions can only be based on our best estimates of the future, but because these are inevitably uncertain, they should therefore also be informed by the precautionary principle. It is ironical that in the field of fisheries management, where this principle is highly appropriate because we know from past experience that fish stocks can and do collapse, the default option has usually been to allow continued or increased exploitation until there is incontrovertible evidence of a problem: just the opposite of what is needed. A preference for policies that will be effective in maintaining or increasing spawning stock sizes should therefore be incorporated in the decision-making process.

However, because of the possible imprecision of short-term forecasts, and the major uncertainties associated with long-term forecasts, it is desirable that management targets should also be both progressive, involving moderate changes each year in what has been assessed to be the right direction, and adaptive, so that the long-term objectives can be updated continually in the light of new information, without causing major upheavals, except in crisis situations when stock collapse is considered to be imminent. Management strategies can be designed to promote early action to avoid difficulties, and these should be preferred, because it is extremely difficult to assist stocks by anything other than draconian measures, once they have been severely depleted.

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9 A Bumpy Old Road: Size-based Methods in Fisheries Assessment

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9.1 INTRODUCTION

If we were to take a thousand humans visiting Rome at random and line them up by rows of approximately equal height in St Peter's Square, we could attempt a size–frequency analysis similar to that used in fish populations. The aim is to estimate mortality and growth from the relative frequency in the size classes. But this short-cut human demographic analysis would fail for two reasons. First, humans stop growing in height in their late teens, and subsequently live for another 40 years or so at the same height, except for a slight shrinkage when very old. Secondly, humans breed continuously and are therefore not born in discrete cohorts. In fact, present size–frequency analyses would fail in almost all mammals for one or other of these reasons. But fish are generally born in discrete, often annual, cohorts, following an annual or seasonal breeding season, and individuals grow in size throughout life towards an asymptotic size. The growth of fish is usually well approximated by a von Bertalanffy curve (see Jobling, Chapter 5, Volume 1). Size–frequency analysis looks for peaks of numbers in the size classes to estimate the mean sizes of successive cohorts at integer intervals of age, and at the relative numbers in these cohorts to estimate total mortality rates.

Size-based methods can be used to obtain estimates of growth and mortality when fish are difficult, or too expensive, to age using hard parts. Growth and mortality themselves are employed in assessments of the exploitation status of fisheries, and so, in one sense, it matters little how they are obtained provided they are accurate (Rosenberg and Beddington 1988). When properly used, size-based methods should lead to the same estimates of these parameters as other techniques, although the sources and impacts of uncertainty are different. In some cases, as shown below, size-based methods have advantages over, or can complement, conventional estimates based on direct ageing.

In fish, length is easier to measure accurately than weight (or strictly, mass), so the term 'length-based methods' is in general use. Lengths tend to increase smoothly throughout a fish's lifespan, except in very old fish that are near their asymptotic size (L_∞ or W_∞ – see Jobling, Chapter 5, Volume 1). Huge old cod (*Gadus morhua*) like this greeted Cabot when he discovered 'New Founde Lande' in 1497, but they are hardly ever seen in any fisheries today. In fact, weights are an even better guide to age than lengths, but are rarely used in analyses, mainly because they are harder and slower to measure accurately.

Length–frequency plots are bumpy old things because they reflect actual variance in size with ages as a consequence of individual differences in growth rate, success in food acquisition and assimilation, a range of individual birth dates in one, or sometimes more, cohorts, and inaccuracies in measurement. As we will see, the net result of all these uncertainties makes not only for bumpy old plots, but also means that approximate, 'quick and dirty' or *ad hoc*, length–frequency analyses tend still to be useful checks. Analytical methods for length–frequency data have a long pedigree in fisheries science, but none of them work as well as one would wish, and as a consequence many fisheries researchers have dabbled in the sport of inventing new methods at some stage or another of their careers.

In fact, length-based analysis still presents a bumpy old road for anyone wishing to employ these methods. Hence, this chapter reviews the underlying principles behind the main methods that have stood the test of time, and especially those that are amenable to the revolution that has quietly occurred over the past decade – the simple use of spreadsheets in the analysis of fisheries data. Emphasizing utility over elegance, spreadsheets mean that almost any competent general fisheries scientist can make a rigorous analysis without training in the use of expensive software.

9.2 AGE AND MORTALITY METHODS

9.2.1 A disappearing act: modes and growth models

The sizes of fish of similar age in a cohort vary about a mean. Fish populations usually comprise several such cohorts, which are mixed together in a sample. If we know the shape of the size distributions of the cohorts, we can try to dissect a mixed sample into its constituent cohorts. Size-frequency analysis thus provides a method of ageing fish without the difficulties of preparing and reading hard parts like scales or otoliths, and without having to kill the fish sampled.

Variation in length of fish of a given age generally follows a statistical normal distribution, although other distributions, like the log normal or the gamma may also be employed. Length-frequency plots from a sample of a fish population are therefore mixtures of a series of overlapping length distributions (Everitt and Hand 1981). Length–frequency analysis aims to dissect, to 'decompose' or 'deconvolute', the mixture into its components.

The average sizes and relative abundance of the component cohorts provide measures of growth and mortality. First, if we can follow the mean sizes in a series of samples, we can estimate growth. Secondly, if we can follow the changes in numbers of a cohort with time, provided that the changes accurately mirror changes in the underlying population, we can estimate mortality rates. Variation among individuals in mortality and growth can be thought of as 'smearing' the original cohort structure.

Distributions

It is generally assumed that the variation in length of any one cohort follows a normal distribution. The expected frequency, f, at length L for a normal distribution of mean and standard deviation, is

$$f(L|\mu,\sigma) = \left[Nw/\sqrt{(2\pi\sigma^2)}\right] \times \left[\exp\left\{-0.5[(L-\mu)/\sigma]^2\right\}\right] \qquad (9.1)$$

where N = sample size, μ is the mean length, σ is the standard deviation of the lengths, w is the class width and L is the mid-point of the class. In fisheries work, the assumption of normality should be tested using a subsample of individuals aged by conventional means. A 'quick and dirty' test for normality can be performed using probability paper, or it can be tested more formally using skew and kurtosis coefficients (*or* very rigorously using goodness-of-fit tests between the data and the expecteds for the normal frequencies in each data-length class). Other distributions are sometimes employed. The log normal, in which the lengths, means and standard deviations are transformed to logs, may be appropriate for weight-frequency analysis and sometimes for length frequencies. The gamma distribution is also sometimes used.

Parameters to estimate

For a mixture of normal distributions we set N to total sample size and obtain the expected frequency at length L as:

$$f_L = \sum\left\{\left[Nwp_i/\sqrt{(2\pi\sigma_i^2)}\right] \times\left[\exp\left\{-0.5[(L-\mu_i)/\sigma_i]^2\right\}\right]\right\} \tag{9.2}$$

where N is now total sample size, p_i is the proportion of this total in the ith age group, μ_i is the mean of the ith age group, and σ_i is the standard deviation of the ith age group. For h components, the problem for length–frequency analysis is therefore to estimate the sets of proportions, means and standard deviations. The p_is must sum to one, so we have $(3h-1)$ parameters to estimate:

$p_1;\quad \sigma_1;\quad \mu_1;$
$p_2;\quad \sigma_2;\quad \mu_2;$
$p_3;\quad \sigma_3;\quad \mu_3;$
$\ldots\quad \ldots\quad \ldots$
$p_h;\quad \sigma_h;\quad \mu_h;$

Statisticians have shown that mixtures of normal distributions are 'identifiable' (Yakowitz 1969): that is, we can in principle determine all the parameters in the mixture, provided that the assumption of normality is valid and provided we know the combined probability exactly. In practice, of course, we only have the data histogram to estimate the latter. There is a more detailed discussion of this point in Macdonald and Pitcher (1979).

The appearance of modes

Cohorts of fish which recruit at different times are consequently separated in mean size. The appearance of separate modes in a size–frequency plot of a sample taken from the whole population has long been interpreted by ecologists as revealing age groups (e.g. Petersen 1891). Within any one cohort there will be a spread of sizes resulting from different birth dates and individual growth rates. This spread may obscure the modal sizes of the separate cohorts.

The procedure of estimating growth and mortality from a series of samples by tracking the modes of each cohort has been termed 'modal progression analysis'. There are a number of graphical techniques for achieving this aim, but they work well only when definite modes appear in the length–frequency plot. The problem is that modes may be clear and evident things to the human eye, but with only small changes in the fish population parameters, or to the sampling procedure, they can be surprisingly ephemeral.

The conditions under which modes appear have been formally investigated. For two components in a mixture, Behboodian (1970) showed that separate modes will be seen (bimodality) if:

$$|\mu_1-\mu_2| > 2\min\{\sigma_1,\mu_2\} \tag{9.3}$$

but even then, they will not necessarily be clear to the eye for small sample sizes.

Figure 9.1(a) to (e) illustrates how modes can appear and disappear in length–frequency plots which are the overall sum of underlying normally-distributed cohort components in a mixture. The values were generated from a mixture of four normal components in proportion of abundance 4 : 3 : 2 : 1. The resulting overall length–frequency plot is unimodal in Fig. 9.1(a) but modes begin to appear as the means get further apart in Fig 9.1(b) and (c). Holding the means at 10 units apart, the modes vanish again when the standard deviations are increased in Fig 9.1(d) and (e).

Following these rules, three main factors in the fish population conspire to reduce the separability of modes in length–frequency data.

First, if fish grow according to the von Bertalanffy curve, as they approach L_∞, the cohort means get closer together and are therefore less likely to reveal modes. This is known as the 'pile-up' effect. The 'pile-up' effect is illustrated in Fig. 9.2 and may be investigated using the animated spreadsheet available at <www.fisheries.ubc.ca/projects/lbased.htm>

Secondly, variance in length-at-age increases with length as fish get larger and approach L_∞, and so age groups are more likely to overlap. For randomly-varying L_∞, Rosenberg and Beddington (1987) show that modes will appear in a two-cohort mixture if:

$$\{L_\infty \exp[-k(t-t_0)]\}\times[\exp(-k)-1] > 2s^2L\{1-\exp[-k(t-t_0)]\}^2 \tag{9.4}$$

where s^2L is the variance at length L. This function

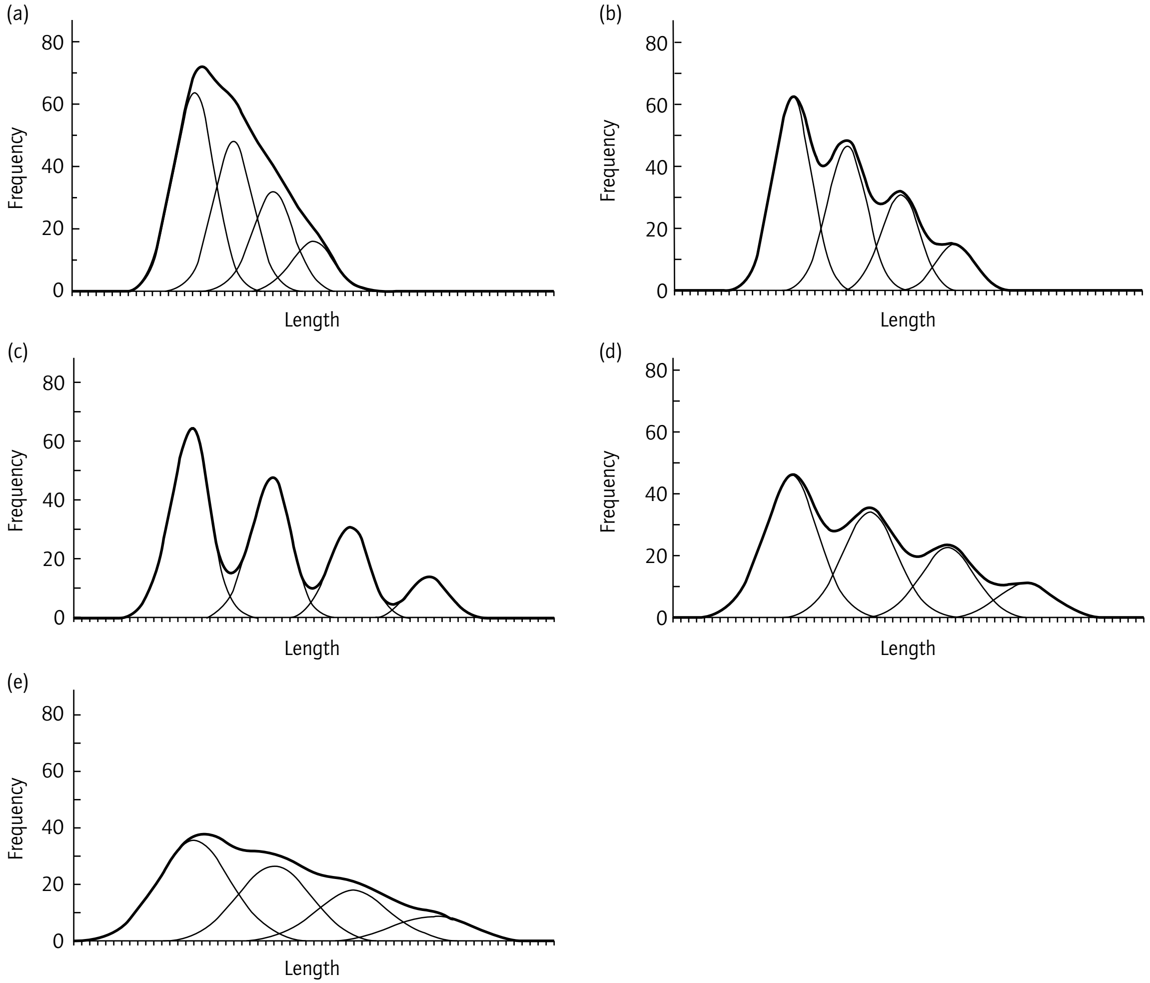

Fig. 9.1 Diagrams show the normally distributed cohort components (thin line) in length–frequency mixtures (thick line) generated from an algorithm (as described in the text). **(a)** The means of the four normally distributed components are 5 units apart and the standard deviations are set to 2.5. The overall envelope, representing the size–frequency plot, is unimodal. The overlap index V = 0.49. **(b)** The means of the four normally distributed components are increased to 7 units apart with the standard deviations remaining at 2.5. Separate modes are beginning to appear in the overall envelope. The overlap index V = 0.29. **(c)** The means of the four normally distributed components are further increased to 10 units apart with the standard deviations remaining at 2.5. Separate modes are clearly evident in the overall envelope. The overlap index V = 0.02. **(d)** The means of the four normally distributed components remain 10 units apart but the standard deviations are increased to 3.5. The modes, especially for the less abundant older age groups, are less evident in the overall envelope. The overlap index V = 0.27. **(e)** The means of the four normally distributed components remain at 10 units apart while the standard deviations are now further increased to 4.5. Separate modes have disappeared the overlap index V = 0.43.

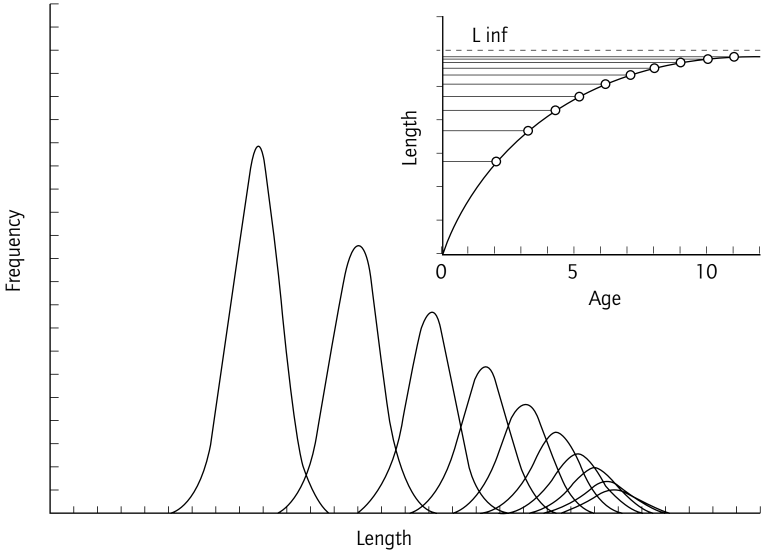

Fig. 9.2 Diagram illustrating the 'pile-up' effect. The larger diagram shows normal distributions of length around the mean lengths of 10 successive annual cohorts. Inset: length-at-age projected (horizontally) from each mean length at integer age (circles) on a von Bertalanffy growth curve. Source: diagram taken from an animated spreadsheet available from *www.fisheries.ubc.ca/projects/lbased.htm.*

will vary with length, so that separate modes are less likely at greater lengths if s^2L increases.

Unfortunately, the way in which s^2L changes with size can be quite complex and there has been no rigorous investigation using actual fish growth. Rosenberg and Beddington (1987) show that if differences in L_∞ are the main source of variation between individual fish, s^2L increases with fish size. On the other hand, if most variation between fish is in the growth parameter k, s^2L peaks at about half L_∞ and then drops as fish approach the asymptotic size. Empirical data usually show variance in length increasing with size, so that for sizes up to 0.7 L_∞ the assumption of a constant coefficient of variation of length (COV-l) seems reasonable. The simulated length–frequency data used in this paper uses a COV-l which falls almost imperceptibly with increasing length at first, but drops rapidly as L_∞ is approached.

The first two problems above affect older age groups more seriously. But the third mechanism which may obscure modes can affect young and old age groups alike. If recruitment of cohorts is continuous, or extended over a large portion of the year, the variance in length by age group will be large and modes may be obscured from young ages on. Unfortunately, recruitment may occur over an extended season in some tropical fisheries for which length-based methods are otherwise ideal.

If modes are present, they probably reveal cohorts, but if modes are absent, there can still be several cohorts present. This means that the older name for these methods, 'polymodal analysis', can be misleading. If modes appear, the simple graphical or approximate computer methods will give good results. If there are no modes, one of the statistical methods will be needed. In their review of length-based methods, Rosenberg and Beddington (1988) recommend the greater use of formal statistical methods, which are not so dependent upon the appearance of modes.

An index of overlap as a guide to the appearance of modes

This section presents an index of overlap which will, in conjunction with a consideration of sample size, indicate whether modes are likely to appear. This in turn will allow the researcher to decide whether simple graphical or *ad hoc* methods are likely to be adequate.

The first step in the calculation of an index, is to decide roughly what the likely means and standard deviations of the proposed age groups are. The overlap index can then be calculated as follows, a quick task using any modern spreadsheet:

$$V = \sum_{i=1}^{i=h-1} \{[(\mu_i + q\sigma_i) - (\mu_{i+1} - q\sigma_{i+1})]/ [(\mu_i + q\sigma_i) - (\mu_i - q\sigma_i)]\}/h \tag{9.5}$$

where $q = 1.96$ to give 95% limits, and h = number of age groups. This is then repeated in order to compare several alternative hypotheses.

The index V reflects the average proportion by which the 95% zone (i.e. 19 out of 20 fish of this age) for the age group is overlapped by the 95% zone for the next age group. When V is negative, there is a very wide separation of the age groups. When V is greater than about 0.25, modes disappear. The V for individual age groups can also be usefully examined where the separation of adjacent ages differs across the length–frequency plot. Example values of V are given in Fig. 9.1(a) to (e).

9.2.2 Assumptions of length–frequency analysis

For length-based methods to work, fish must recruit in discrete cohorts. There is no obvious way that length-based methods could provide both growth and mortality estimates for continuously recruiting populations, like the human example given earlier. For a caveat see the Conclusions section of this chapter. Discrete cohorts usually derive from separate spawning seasons, but there may be more than one of these per year. The cohorts must remain discrete as the fish grow older. This requirement may be relaxed to a certain extent for different methods of analysis, but, generally, the methods work better the more discrete the cohorts and the more separate they remain as they get older. This implies that the growth of individuals in a cohort should be similar, i.e. that variability in growth rates among individuals of the same age is not large.

So there are two sources of variation in size within a cohort of fish:

- different birth dates within the spawning season;
- different growth rates among individuals.

The first of these can be accommodated by most length-based methods, provided that the variance is not too large. But the second is a major problem for all the methods, as it tends to destroy cohort structure.

A further assumption is that the length-frequency data in your sample fully represent the length classes in the fish stock. If they do not, then the sample data will need to be adjusted to compensate for the selectivity of the sample gear. A neat series of tests for this employs the relationship among length at maturity, L_m, age of maximum yield-per-recruit, L_{opt} and temperature in order to evaluate the validity of the length–frequency sample (Froese and Binholan 2000). For example, these authors show how a trawl survey of Nile perch (*Lates nilotica*) taken in Lake Victoria in 1982 missed all fish larger than 100 cm. Since this is far less than L_{opt} = 136 cm, the survey length–frequency data could not be used for assessment of the perch population at that time.

The starting point in all analyses is the length–frequency distribution, adjusted if necessary, with known class width and class boundaries. It is worthwhile taking a lot of care over the class boundaries: lower bound, mid-point and upper bound of the classes are all used in different methods.

9.2.3 Classification of length–frequency analysis methods

Methods may be divided into parametric and non-parametric. Another classification is into simple *ad hoc* methods, which are often essentially graphical or non-parametric, and rigorous statistical estimation methods, which are usually parametric.

Parametric methods depend upon estimating the means, standard deviations and proportions or numbers in each of the cohorts in the mixed sample. These are the parameters of the size-frequency distributions, hence the term parametric. The size distributions are generally taken as normal, but log normal and gamma distributions may also be employed (Macdonald and Pitcher 1979). The methods include both graphical (e.g. probability plots) and computational (e.g. mixture analysis) methods, but all make strong assumptions about distributions. In parametric methods, the number of cohorts generally has to be determined by the user, and several scenarios may have to be compared.

Non-parametric methods do not depend upon estimating the parameters of the cohort distributions directly. So they make only weak assumptions about the distribution of sizes within the cohorts, that they are roughly distributed about some modal or central value, and hence are analogous to non-parametric statistics. The modal lengths of each cohort are fixed to lie upon a curve described by a growth model. Generally the von Bertalanffy model is used, but other models such as a seasonal growth model, can be employed. Hence the non-parametric methods make strong assumptions about growth. In non-parametric methods, the number of cohorts is implicit in the estimates of growth model parameters, and may be revealed when cohorts are sliced into age groups.

The following sections briefly describe graphical methods, most of which are parametric, three non-parametric methods, and two fully statistical parametric distribution mixture methods. Most of them can be carried out using spreadsheets.

9.2.4 Graphical methods

A number of graphical methods aim to estimate the age-group parameters. Graphical methods have the advantage of being quickly performed with a simple spreadsheet, or even pencil and paper, and bypass statistical difficulties. In most methods of this type, successive components are extracted sequentially from the data.

Modal Progression Analysis, the simplest and oldest method, entails the graphical joining of cohorts which appear as clear modes. If this can be done, it may not be worthwhile to go any further with more elaborate methods! Problems arise when deciding which cohorts to join up with which others. For species that actually shrink, such as octopus, lamprey (*Lampetra* spp.), this may be one of the few methods applicable. Modal progression analysis can also be used on the results from a series of formal single-sample estimations: a clear example is discussed by Sparre and Venema (1992).

Gulland and Rosenberg (1990) outlined simple interpretations that may be made from visual inspection of length–frequency plots. Type A, a single mode that stays in the same place through time, can be produced by gear with high selectivity, such as gill-nets, or by fish, for example yellowfin tuna (*Thunnus albacares*), that migrate with age. The authors say that not much can be done with type A although see the conclusion section of this chapter. Type B, a single mode moving steadily upwards, is typical of single-cohort fisheries such as prawns or squid, which are good candidates for any simple analysis. Type C, with many clear modes like Fig. 9.1(b) or (c), may also be a good subject for the classical techniques described below. Type D, with smeared modes like Fig. 9.1(a) or (e), may be hard to analyse.

The use of probability plots was reinvented several times by fishery workers (Harding 1949; Cassie 1954; Harris 1968). Originally they were done on special probability paper, but today it is easy to set them up on a spreadsheet using the built-in normal distribution function. A series of progressively more sophisticated graphical methods were based on the change of slope of a parabolic function of frequency and length (Buchanan-Wollaston and Hodgeson 1929; Hald 1952; Tanaka 1962; Bhattacharya 1967). Some versions of the FiSAT computer package include dissection using a modification of Bhattacharya's method (Pauly and Caddy 1985). Taylor (1965) invented an intricate method. After smoothing the data histogram, components are sequentially extracted from the shape of the left flank of the distribution.

There has been a long search for an improvement upon the subjectivity of the graphical methods, which nonetheless retain their attraction in bypassing the problem of statistically estimating the standard deviations and proportions. In my opinion, none of the later graphical methods offer much improvement on probability plots in deciding among various alternative interpretations in difficult cases, and are hence not worth the considerable extra effort in calculation or computing.

9.2.5 Non-parametric methods

Most non-parametric methods work by scanning a range of L_∞ and k values and working out a goodness-of-fit (GOF) for each combination. The best GOF is searched for by the user or by automatic search, or a combination of both. The best fit gives the estimate of growth. Mortality is estimated from the numbers in the cohorts sliced from the original size distribution using these growth parameters.

Usually, these methods attempt to do this by fitting a growth curve through a whole set of samples taken through time. The von Bertalanffy growth curve, or its seasonal modification, is ordinarily employed, although it is possible to use other growth models, or even empirical growth values, but these options have rarely been used. A goodness-of-fit function based on how well the growth curve passes through the 'peaks and troughs', is maximized for a range of values of L_∞ and k. So growth, and sometimes mortality, is estimated along with the dissection of the length–frequency curves.

Three of these non-parametric methods are outlined in this paper: ELEFAN, originally devised by Daniel Pauly; SLCA, originated by John Shepherd; and the Projection Matrix method, which was developed by Andrew Rosenberg and Marinelle Basson (Rosenberg et al. 1986) from an original method by Shepherd (1987b).

ELEFAN (electronic length–frequency analysis)

Daniel Pauly was the first to realize the potential of this type of method, and working versions of his original ELEFAN first appeared in the late 1970s (Pauly and David 1980). Nowadays, the modern version of this length–frequency method is the ELEFAN 1 module of the widely-used FiSAT package distributed by FAO (Food and Agriculture Organization) (Gayanilo et al. 1996). Pauly (1987) has written a very clear review of the basis of the method.

How ELEFAN works. ELEFAN works by attempting to find a maximum for a goodness-of-fit function based on peaks and troughs: the 'explained sum of peaks'. This is based on how often a von Bertalanffy growth curve hits modes in the data. During fitting, growth curves with different parameters are run and mapped. The maximum of the scoring function is chosen as the best fit. A seasonally modified growth curve can easily be substituted for the standard von Bertalanffy, and, in fact, the same goodness-of-fit technique could be used for any growth curve or pattern.

The number of peaks is identified by those standing out above a 5-point moving average: troughs are the areas below the moving average. The number of peaks gives the maximum 'available sum of peaks' (ASP). A von Bertalanffy curve for the specified L_∞ and k is traced through the data starting at the base of the first peak. A point is scored each time the curve hits one of the peaks: a point is deducted each time it hits a trough. This is repeated for starting times equal to the base of each peak. The maximum value is the 'explained sum of peaks' (ESP). The goodness-of-fit function is the ratio ESP/ASP. This process is repeated for all required combinations of L_∞ and k, the goodness-of-fit mapped and the maximum value chosen as giving the best growth parameters. For each combination of k and L_∞, it is possible to search for the value of t_0, the starting point within a year for the growth curve, relative to the data, which maximizes the ESP/ASP ratio. Note that absolute ages are needed to find the true t_0.

Simulations show that ELEFAN can give clear and correct answers where peaks are well separated in the data, but that it tends to underestimate k (Rosenberg and Beddington 1987). There are two problems with the ELEFAN technique. First, it seems sensitive to the appearance of discrete modes in the data. Second, because it is an *ad hoc* method, it lacks explicit statistical error structure and therefore provides neither standard errors of the estimates nor a guide to performance in any situation. But the latter problem could today be investigated using Monte Carlo simulation methods (Hilborn and Mangel 1997).

Like the other non-parametric methods, ELEFAN does not directly evaluate multiple recruitments during a year, such as occurs in many tropical fisheries, although there is a recruitment pattern routine which helps to detect multiple recruitment pulses. Alternative growth models can be used instead of the von Bertalanffy, and one that has been frequently employed is a seasonal version of this growth curve.

SLCA (Shepherd's length-composition analysis)

Shepherd (1987a) introduced an objective goodness-of-fit function for detecting peaks and troughs, using a damped sine-wave function borrowed from time-series analysis of diffraction patterns. The damped sine-wave function emulates the decreasing spacing of mean lengths-at-age of the von Bertalanffy curve. The SLCA method is conceptually very similar to ELEFAN, the value of a scoring function being mapped against a range of values of L_∞ and k.

How SLCA works. Values of L_∞ and k are chosen for a von Bertalanffy curve. For each, length interval L, $t_{\max}$ and $t_{\min}$ are calculated as the ages corresponding to the start and mid-point of the interval using the growth equation: t is the average of $t_{\max}$ and $t_{\min}$. The test function T_L is estimated as:

$$T_L = [\sin(\pi Q)/(\pi Q)] \times \{\cos[2\pi(t - t_s)]\}, \tag{9.6}$$

where $Q = (t_{\max} - t_{\min})$ and t_s is the proportion of the year since recruitment when the sample was taken. The GOF function is then calculated over all length groups as:

$$S = \sum[(T_L\sqrt{N_L})/\Delta t_L] \tag{9.7}$$

where N_L is the number in each length class, and Δt_L is the time needed to grow through each length class:

$$\Delta t_L = -1/k \cdot \ln[(L_\infty - L_u)/(L_\infty - L_d)] \tag{9.8}$$

where L_u is the upper bound of the length class and L_d is the lower bound. This modification was introduced by Pauly and Arreguin-Sanchez (1995).

To estimate t_0, this is run with t_0 set to zero, to give Sa, then again with t_0 set to 0.25, giving Sb. (Note: this covers the likely range of t_0 values). The maximum score, S_m, for the current combination of growth parameters is then given by:

$$S_m = \sqrt{(Sa^2 + Sb^2)}. \tag{9.9}$$

For any one pair of values of L_∞ and k, t_0 can be easily found as:

$$t_0 = \arctan(Sb/Sa)/2\pi. \tag{9.10}$$

The above is repeated for all the L_∞ and k combinations under consideration, and the values of goodness-of-fit, S_m, are entered into a table of results so that the maximum may be identified. Contours of S_m may be mapped to avoid picking local maxima. As with ELEFAN, the upper limit of length classes needs truncating to avoid bias from the 'pile-up' effect. The 'pile-up' effect can be minimized by the use of the Pauly and Arreguin-Sanchez modification.

Provided ages as defined by the start point in the analysis are known, Shepherd's method can provide a direct estimate of t_0. Published simulations suggest that it is more robust than the ELEFAN algorithm (Basson et al. 1988). Provided that the modes for the younger fish are reasonably clear in the samples, it seems less sensitive to the appearance of modes overall. But Terceiro and Idoine (1990) showed that SLCA suffers from the same general problems as the other methods.

The algorithm of SLCA is firmly linked to the von Bertalanffy model, and it would be hard to modify it for seasonal growth or alternative growth models.

Projection matrix method

The basis of the projection matrix method (Rosenberg et al. 1986) is elegant, simple and different from the previous two methods. The numbers in any size group at time $(t + 1)$ can be predicted from the numbers in that group at time t, using growth, mortality and recruitment from length groups smaller in size:

$$f[g, Z, (f_i)t] \to f\{g, Z, (f_i)t + 1\}. \tag{9.11}$$

Now, if constant mortality is assumed over the time interval, or the pattern with size is known, only the growth model parameters will affect the projected numbers.

How the projection matrix works. First, using the first set of parameters for the growth curve, the expected length frequency is projected forwards from the first sample in the set. Secondly, the goodness-of-fit, G, of this expected data in each class i, proj_i, is compared with the actual length frequencies, obs_i, using least squares:

$$G = \sum \left[(\text{obs}_i - \text{proj}_i)^2 \right]. \tag{9.12}$$

Thirdly, the projection of expected values is repeated using the next set of values for the growth curve parameters. This is repeated for the whole range of parameters and the G goodness-of-fit values tabulated and contoured so that, as with SLCA, the best fit can be chosen. Note that here a minimum value of G is sought. As with SLCA and ELEFAN, the upper-length classes need truncating to avoid bias from the 'pile-up' effect.

The projection matrix method can perform well under a wide range of conditions (Basson et al. 1988). Unlike all the other non-parametric and graphical methods, the Projection Matrix does not rely on the appearance of 'peaks and troughs' (modes) in the data, an advantage it shares with parametric distribution mixture methods. It is also robust against increase of variance in length with age. An advantage is that any growth model could be used for the projection. In its basic form it suffers from the same multiple recruitment problem as ELEFAN and SLCA, but, like ELEFAN, it could be easily modified to deal with this.

In my opinion, of the three non-parametric length–frequency analysis methods, the projection matrix, as the least *ad hoc*, is the one that would stand more statistical development. Unresolved problems in the present version appear to be how to evaluate shifts in the date of origin of the projections, and whether projections from growth year 1 should be applied to samples taken in subsequent calendar years. Seasonality in growth needs to be included, but this should not be difficult as any growth model is easily incorporated in the projection.

Summary: non-parametric methods

All three non-parametric methods can easily give silly answers, and should only to be applied with care and with insight of the ecology of the fish under study. Using Monte Carlo simulations, Isaac (1990) compared how SLCA and ELEFAN perform under a variety of conditions and provides some helpful guidelines. For example, SLCA seems to be better for slow-growing and ELEFAN better for fast-growing fish.

All methods based on the von Bertalanffy curve suffer from multiple optima at harmonic combinations of k and L_∞ (see Kleiber and Pauly 1991), which is not surprising given that a number of alternative fits to length–frequency data will be reasonable statistically. A degree of subjectivity is inevitable in interpreting the GOF response surface: all the methods can generate multiple peaks along ridges of high GOF (see example below) and simulations show that in some cases a high peak is not the correct answer. The recommended non-parametric approach to length–frequency analysis is to try to find solutions which are robust against the particular method used. If all three non-parametric methods indicate similar peak GOFs, then you can have some confidence in the answers. Where they differ, decisions have to be based on additional knowledge of the species in question.

1 The far-horizon ('rubber tuna') problem The far-horizon problem occurs when a good statistical fit is obtained at high L_∞ and k. This fit implies very rapid growth and, by analogy, a k of 2 might correspond to the 'growth rate' of a tuna-shaped rubber balloon inflated rapidly with a tyre pump. This would be an absurdly fast growth rate. A good fit like this would imply that all the bumps and wiggles in the length–frequency data are only noise and there is only one, or a few, cohorts present. Cohort slicing, which assigns fish to ages (see below), and examination of the fitted growth curve against the data histograms will check out whether the suggested far-horizon fit is realistic. SLCA is especially prone to this problem, and, to avoid it, it is recommended to scale the GOF by dividing by ($L_\infty \star k$). The general remedy for all methods is to beware of far-horizon solutions unless (a) you have good evidence that fish actually grow that fast (some do, e.g. *Coryphaena*), and (b) you are satisfied with the implications shown by cohort slicing.

2 The near-horizon ('bumpy road') problem The near-horizon problem occurs when a good statistical fit is obtained at very low or very high L_∞, and low k, where L_∞ is very close to $L_{\max}$. Cohort slicing on these growth values will reveal many age classes. A good fit here implies that every little bump and wiggle in the length–frequency distribution is a cohort, meaning an absurdly slow growth rate. The only remedy is to beware of solutions which are very close to $L_{\max}$ and to examine the implications with cohort slicing. In general k values less than 0.05 are suspect, but of course this can mask growth rates of fish that are long-lived and genuinely slow growing, such as sharks, orange roughy (*Hoplostethus atlanticus*), Pacific rockfish (*Sebastes* spp.) or sturgeon (*Acipenseridae*).

3 General approach to multiple optima It is not always easy to choose one from a set of many GOF peaks, especially if you get them from different methods. In the last resort you may have to retain several peaks right through to the assessment stage and examine the management implications of each one. Additional information can be brought to bear upon the problem. For example, one can look at the implications for age structure of alternative peaks using cohort slicing, or otolith or scale readings of subsamples.

A powerful general approach is to filter the results using data from similar species which have been analysed elsewhere. Pauly and Munro (1984) demonstrated what they termed an 'auximetric' relationship, 'Phi prime', between L_∞ and k that is consistent across species:

$$\Phi' = \log k + 2 \log L_\infty \tag{9.13}$$

Analysis of thousands of such relationships shows that members of a taxon have closely similar auximetric ratios, and so plotting published values of $\log L_\infty$ against $\log k$ can be a good guide to the accuracy of estimates from length–frequency analysis.

Figure 9.3 shows an example of such an analysis of small pelagic zooplanktivores from some African lakes (Pitcher et al. 1996). Values of L_∞ and k that fall outside the boundaries of the regions characteristic of each species are unlikely to be correct and can be avoided. It is recommended to draw up auximetric plots like this one when performing new analyses. Phi prime values can be obtained for many species and locations from the FishBase website, where there is also an online routine for plotting the equivalent of Fig. 9.3 (*www.fishbase.org*).

An example of non-parametric analysis To illustrate the use of the three non-parametric methods, this section compares the fits obtained to some generated test data. Six bi-monthly samples of around 1500 individuals from a hypothetical population are plotted in Fig. 9.4. Fish growth is normally distributed (coefficient of variation = 0.1)

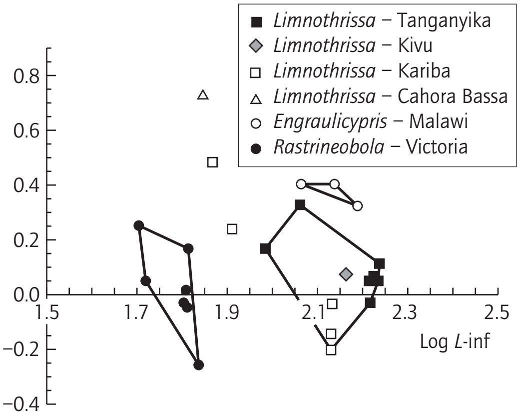

Fig. 9.3 Auximetric plot of published growth parameters of three species of small pelagic cyprinids and clupeids from African lakes. Points within lines indicate values for each species consistent with the Phi prime analysis. Points outside the lines are suspect and should only be used with caution. Circular symbols are cyprinids; square symbols are sardines. (Source: data taken from Pitcher et al. 1996, where full details of sources may be found.)

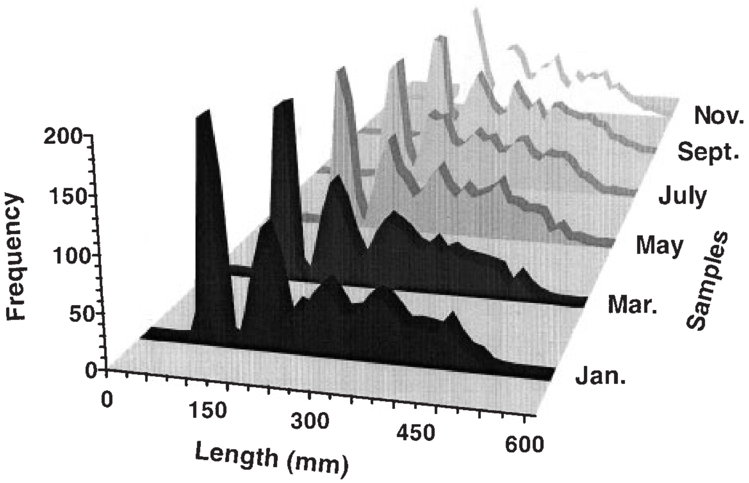

Fig. 9.4 Length–frequency plots of samples taken from a hypothetical fish population with growth and mortality parameters as described in the text.

around a von Bertalanffy curve with $L_\infty = 1000$ mm and $k = 0.1$. The instantaneous mortality rate is set to 0.2 and samples are taken with equal catchability, so that sample sizes reflect abundance.

Goodness-of-fit surfaces for values of L_∞ from 40 to 1500 mm, and k from 0.05 to 0.3 are drawn in Plate 1 for each of the three non-parametric length–frequency analysis methods (see colour plate). Coloured shading runs from red (low) to purple (high). The correct value is indicated by a star on the response surface and cross-wires on the base. All three methods exhibit the banana-shaped area of alternative fits very clearly, and this is intrinsic to any method that attempts to fit a von Bertalanffy curve.

For these data, the projection matrix method is the only one to find the true value. However, the peak GOF is a small bump in the middle of a wide-domed plateau, and it would not have been found without very fine scale intervals in the search procedure. Plate 1 also demonstrates one of the problems with both ELEFAN and SLCA. Both show the highest GOF in banana-shaped peaks that increase at high L_∞ and low k (the 'bumpy road' effect).

SLCA has a smoother GOF surface than ELEFAN. Hence, for SLCA, automated search procedures (such as are embedded in the LFDA package) are less likely to find a spurious local peak. On the other hand, ELEFAN, which has an interesting-looking rough and ridged surface that might confuse a local search procedure, exhibits a huge trough of very unlikely values near to the correct values that might help in focusing attention on the correct area. This example reinforces the recommendation to run all three of the non-parametric methods on any data you may wish to analyse.

9.2.6 Parametric methods

Parametric length–frequency methods work by calculating a GOF between the sample data and a distribution mixture specified by its component parameters. The history of these methods is reviewed by Macdonald and Pitcher (1979). GOF is calculated as the difference between the sample data and the fitted mixture of distributions. The methods usually work by searching automatically for a maximum GOF, but the user can also intervene and guide the fitting process. The number of component cohorts is usually the choice of the user, guided by the GOF values of alternatives. Alternative fits with different numbers of component age groups can be compared:

$$\text{Chi square} = \sum\left\{[(\text{obs}_L) - f_L]^2 / f_L\right\}. \qquad (9.14)$$

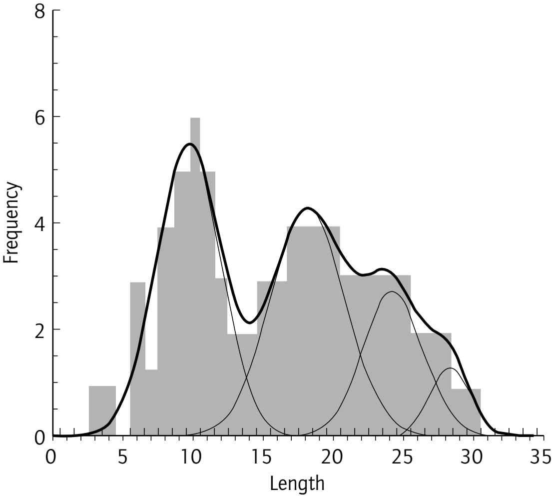

Fig. 9.5 Example of length–frequency analysis as a statistical dissection of a distribution mixture – the MIX technique. Shaded area represents histogram of length frequencies from fish sample data. Thin lines are normal distributions; thick line is overall mixture. Parameters of the component normal distributions are adjusted until difference between overall mixture and histogram is at a minimum (least squares). Source: figures from a spreadsheet that may be obtained from *www.fisheries.ubc.ca/projects/lbased.htm*.

This is the basis of statistical mixture analysis, originally embodied in the MIX technique (Macdonald and Pitcher 1979), although its statistical roots go back to Peterson (1891). The essential calculations, using *f*(*L*) from the first two equations in this chapter, can today be easily performed on spreadsheet (e.g. Fig. 9.5).

The main problem in using the MIX approach is obtaining the number of components in the mixture. The approach recommended by Macdonald and Pitcher (1979) and Macdonald and Green (1988) is to get the best fit for $h-1$, h and $h+1$ components where h is the guessed number of components, the final choice of number of age classes being mainly on the basis of the minimum chi-square. Rosenberg and Beddington (1987) show that MIX growth parameter estimates are quite robust against small mistakes in obtaining the number of components. A more complex but essentially similar statistical method, MULTIFAN (Fournier et al. 1990), gets around the problem by using a von Bertalanffy curve to provide the number of cohorts in a similar fashion to the non-parametric methods. In fact, results from MIX and the more complex multi-sample MULTIFAN are generally very similar (Wise et al. 1994; Kerstan 1995).

Experience suggests that MIX is robust for single-sample analysis, although it tends to underestimate *k* (Rosenberg and Beddington 1987). Where there is a series of samples it has advantages if there is any reason to suspect that growth does not follow a von Bertalanffy curve. This can happen in some fish that switch to piscivory during their lifespan (LeCren 1992). The additional work in the multi-sample MIX technique is to join cohorts in successive samples using an MPA-like method, which can be both an advantage and a disadvantage. Modifications to the MIX approach can easily incorporate information about growth (e.g. Liu et al. 1989) either as starting values for mean cohort sizes and/or as additional constraints on the fitting process. Schnute and Fournier (1980) published an alternative version of this process.

In the tropics, there is often more than one cohort recruiting each year which is a consequence of monsoon-like seasonality in productivity. For example, Koranteng and Pitcher (1987) used MIX to analyse length–frequency data for a West African sparid fishery, where a cohort recruited after each of the two major upwellings each year. The plot of estimated means from MIX was best joined up using a strong assumption that there were two cohorts per year. In fact, similar results can be obtained using ELEFAN if a similar assumption is made (Pauly, personal communication).

An example of the detailed analysis of cohorts of a small freshwater fish is presented in Fig. 9.6 (data from Pitcher 1971). Samples were taken using back-pack electro fishing at approximately every 4 weeks and subjected to mixture analysis using the MIX routines. The progression of mean lengths of each cohort identified from the samples were traced using information from seasonal

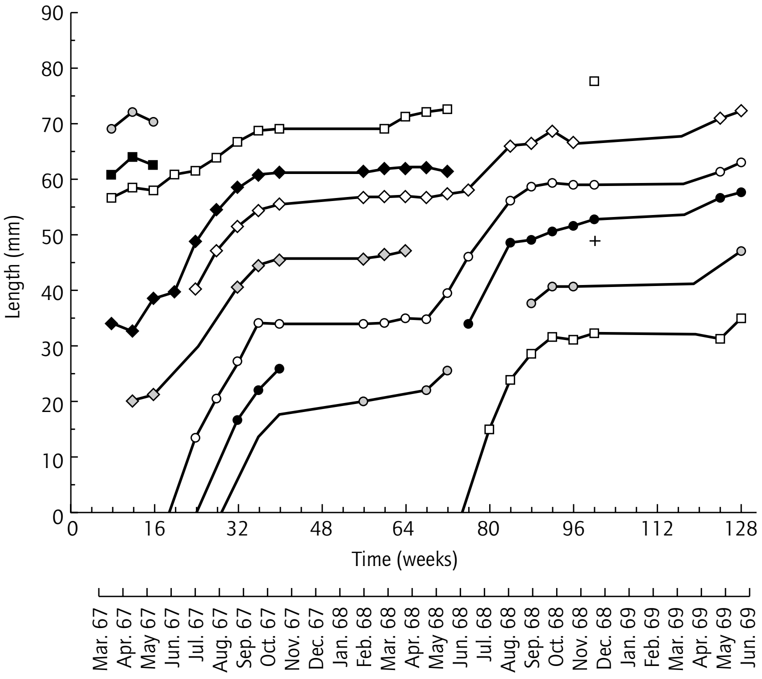

Fig. 9.6 Example of tracing cohort progressions following length–frequency analysis of samples of 90–300 minnows (*Phoxinus phoxinus*) from a 0.5 km reach of the Seacourt Stream, Berkshire (UK) in 1967–9. Mean lengths estimated from each cohort are represented by different symbols: lines join up most likely progressions due to growth. (Source: data redrawn from Pitcher 1971.)

growth (see Pitcher and Macdonald 1973). The picture was complicated by the hatching of several cohorts of eggs from separate groups of spawning fish in summer. Figure 9.6 shows three such young-of-the-year and 1+ age-group cohorts traced from births in 1966 and 1967, but such multiple cohorts were not detected in 1968. This detailed analysis of the growth, and mortality, of sub-cohorts from different hatch-groups would have been difficult with the non-parametric techniques. Overall the best advice is to plot out all means against time and age so that effects like this can be detected.

9.2.7 Cohort slicing and estimation of mortality

Cohort slicing enables attribution of the fish in each length group to an age cohort using the information on mean length-at-age. For parametric methods, this is easy because in overlap zones the proportion of fish in each length class is allocated in proportion to the relative frequency of each age group in the fitted distribution mixture (Rosenberg and Beddington 1988). This is very similar to using an age–length key (Gulland and Rosenberg 1990; Sparre and Hart, Chapter 13, this volume). The relative numbers of fish in the fitted mixture components give the annual mortality rates directly.

But for non-parametric methods, this information will not be available, so the overlap classes may have to be split on an *ad hoc* basis to mimic the changing component proportions. After slicing, the relative numbers in adjacent cohorts may be used to estimate mortality rates. A better method is to track samples through time and examine mortality rates for a cohort though time. Anomalous samples will often show up when these are plotted and can be eliminated from the analysis.

An example from a Hong Kong fish, *Siganus canaliculatus* (white-spotted rabbitfish), is shown in Fig. 9.7 (Pitcher et al. 1998). Combining estimates for the period of the year when both 0+ and 1+ cohorts were present in samples, the total mortality rate is estimated as 7.7 (note this includes offshore migration as discussed below).

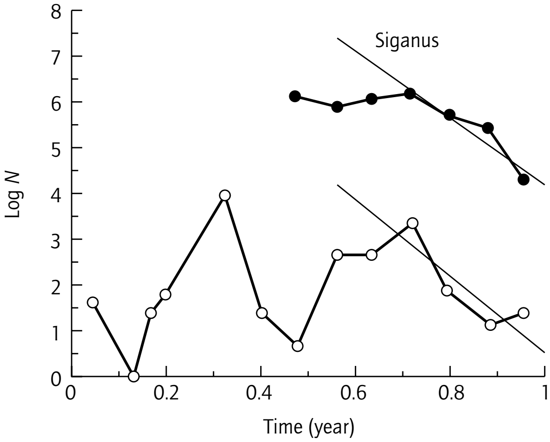

Fig. 9.7 Total mortality rate of Hong Kong white-spotted rabbitfish following cohort slicing of length–frequency samples aged using non-parametric methods with an adjustment for overlap (see text). Plot shows estimated numbers of two cohorts (open circles = 0 + cohort; closed circles = 1 + cohort) over 13 samples. Points at right-hand side of plot are used to estimate mortality rates (solid lines). An example spreadsheet may be downloaded from *www.fisheries.ubc.ca/projects/lbased.htm*.

There are also a range of graphical length-based methods that estimate mortality directly, usually based on scaling the decline in numbers along the right-hand limb of a length frequency plot with the time taken to grow through each length interval. An allied method (Wetherall's) depends on estimating Z/k, and hence, given k, total mortality. These methods have been thoroughly reviewed by Sparre and Venema (1992).

9.2.8 A guide to computer packages

Table 9.1 tabulates available computer packages against features discussed in this chapter, such as the strength of assumptions about distributions and growth. Table 9.1 also shows that nearly all of the published methods may these days be programmed into a spreadsheet such as Excel, with Visual Basic routines written to step across the range of required L_∞ and k values and to call the built-in Excel optimization routines ('Solver'). The routine can record the GOF at each step for later plotting and interpretation. The advantage of this

Table 9.1 Guide to computer packages for length–frequency analysis.

Method	MPA	Efan	SLCA	Proj	PPap	Bhatt	Nmsep	Mix	Mfan
ASSUMPTIONS									
parametric/ non-parametric	NP	NP	NP	NP	P	P	P	P	P
TYPE									
graphical/ computational	G	C	C	C	G	G	C	C	C
DISTRIBUTIONS									
weak/strong	W	W	W	W	S	S	S	S	S
GROWTH									
weak/strong	W/S	S	S	S	W	W	W	W/S	S
SAMPLES									
Single/multiple	M	S/M	S/M	M	S	S	S	S	M
SPREADSHEET?									
Hard/Easy/No	Easy	Easy	Easy	Hard	Easy	Easy	Hard	Easy	No
PACKAGE CODE	–	1,2,5	2,5	2	–	1,5	5	3	4

Notes: *Key to methods*: MPA = Modal Progression Analysis (MPA); Efan = ELEFAN; SLCA = Shepherd's Length-Composition Analysis; Proj = Projection Matrix; PPap = Probability Paper; Bhatt = Bhattacharya's method; Nmsep = Normsep; MIX; Mfan = MULTIFAN. *Key to packages*: (1) Compleat Elefan (ICLARM); (2) LFDA 3.0 (RRAG); (3) MIX (Ichthus); (4) MULTIFAN (Otter); (5) FiSAT (FAO).

approach is that the user retains complete control over the algorithm and the interpretations of alternative maxima. One disadvantage is that some packages contain undocumented improvements and corrections to published methods that spreadsheet programmers may find it hard to obtain information about. Moreover, many existing packages were generally written for DOS and most have not been updated to Windows versions.

A DOS computer package called LFDA (Length Frequency Data Analysis) is available from the Renewable Resources Assessment Group at Imperial College, London, UK (*www.ic.ac.uk*). It includes SLCA, the Projection Matrix and the ELEFAN algorithm, along with various options for estimating mortality, and has some elegant contour plots of the GOF surfaces. Although LFDA, dating from an earlier epoch of computers, only runs a maximum of 10 by 10 values of L_∞ and k, analyses can be repeated over a series of values to create very detailed GOF surfaces, and was used to generate Plate 1. As far as I am aware, LFDA has not been recoded for Windows, but it runs effectively in a DOS window in Windows 98.

Using maximum-likelihood and automatic direct computer search, the MIX programme (Ichthus Software, Hamilton, Ontario, Canada; Macdonald and Green 1988; *http://icarus.math.mcmaster.ca/peter/mix/mix31.html*) finds a mixture of overlapping components which maximizes goodness-of-fit with the length–frequency data. The distributions can be normal, log normal, exponential or gamma. A Windows version is available.

FAO distributes DOS software called FiSAT (FAO-ICLARM Stock Assessment Tools; *http://www.fao.org/fi/statist/fisoft/iclarm.asp*) which implement an updated and improved ELEFAN method, including the seasonal growth model option and a plot of the GOF surface. FiSAT also includes SLCA and the Bhattacharaya method. A Windows version is in development.

The most sophisticated computer package available is MULTIFAN (Otter Software, Victoria, BC, Canada. *http://otter-rsch.com/index.html*), initially published with an impressive example which dissected 12 age groups from Bluefin tuna (*Thunnus thynnus*) samples (Fournier et al. 1990). The software contains some neat graphical short cuts together with powerful optimization routines. MULTIFAN runs in a DOS Window in Windows 95 of NT. A powerful modern version is under development, but its website implies that it will cost over US$10 000. As to costs: LFDA is freeware, FiSAT costs US$40, MIX costs around US$140, while MULTIFAN is very expensive at about US$1500.

9.3 WHEN LENGTH IS KING

Some analyses may only be performed using length-based techniques. This section outlines three of these methods: the first the estimation of yield-per-recruit in multispecies fishery using a single gear such as trawl (see also Shepherd and Pope, Chapter 8, this volume); the second, a way of estimating the offshore migration rate, a common problem in many inshore tropical fisheries; and the third, using a length-based analysis to estimate trophic level.

9.3.1 Ringing the changes on Thomson and Bell: multispecies yield-per-recruit

Fishing gear such as the mesh in a trawl selects fish by size, not age. Converting size to age for one species in the standard way means that yield-per-recruit (YPR) calculations comparing long-term average yield under a range of mesh sizes and fishing rates can be made for this fishing gear. But if more than one species is caught in the trawl, the same size of fish can represent different ages in different species. This means that the yield for each species must be calculated for each length class. Once this is done, the yields can be added to provide multispecies yield-per-recruit estimate for the trawl gear.

The basic length-based yield equation was devised by Thomson and Bell, and is thoroughly described in Sparre and Venema (1992). A version of this multispecies yield-per-recruit analysis is

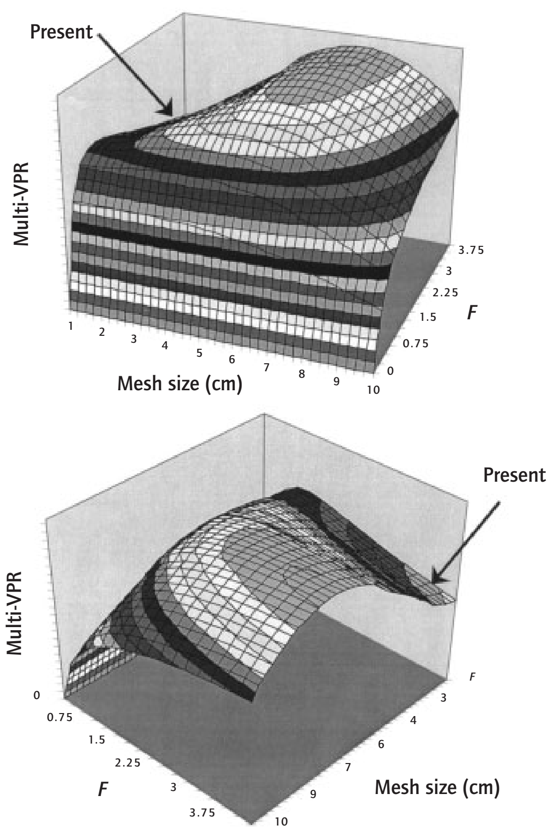

Fig. 9.8 Multi-species value-per-recruit (VPR) surface (front and back views) for the 17 Hong Kong species. VPR is plotted against mesh size in cm, and fishing mortality rate, *F* (vertical axis is value). Approximate present position of fishery indicated by arrow. (Source: from Pitcher et al. 1998.)

available in the FiSAT package, but the equations can fairly easily be programmed into a spreadsheet.

An example of the results from a spreadsheet length-based multispecies analysis applied to Hong Kong trawl fisheries is shown in Fig. 9.8. The work covered 17 species (14 fish and 3 invertebrates) caught in the Hong Kong trawl sector. The overall multispecies YPR was obtained by summing the contributions of each of the species, weighted by their relative recruitment, as advised by Murawski (1984). Relative recruitment can be obtained from time series, or, as in this case, by running a Beverton and Holt biomass-per-recruit (BPR) analysis for each species at the current estimated *F* and age of entry zero. Relative recruitment indices were then obtained by using the estimated biomass of the species, since B/R = BPR and so R = B/BPR. Uncertainty (not shown here) was addressed using Monte Carlo simulations based on random sampling of 74 parameter distributions. In this analysis yield-per-recruit has been converted to value-per-recruit by multiplying each species and size class by its market price.

The location of the present Hong Kong trawl fishery is indicated on the value-per-recruit surface of Fig. 9.8 by an arrow. The analysis suggests that, provided relative recruitment is not altered, the value of the existing fishery could be almost doubled by doubling the mesh size in the trawl (Pitcher et al. 1998).

9.3.2 Estimating the offshore migration rate using length and age

Often, fish migrate offshore into deeper water as they get older and larger, partly as the appropriate refuge from predators changes and partly as a search for larger food. By moving offshore, these may remove themselves from the sampling area, and this offshore migration rate may mask the true total mortality rate and decrease the apparent growth rate. If a sample of fish has been aged using otoliths or other hard parts, the differences between cohorts constructed from the biased growth parameters obtained from this method and those from the samples can be used to estimate the offshore migration rate with age (Pitcher et al. 1998). The method assumes that the probability of fish migrating offshore out of the sampling zone increases linearly with size from a start length ($P = 0.0$) to an end length ($P = 1.0$) at which all fish have left.

First, the von Bertalanffy growth parameter, k, and L_∞ is estimated from length–frequency analysis and an auximetric plot that compares with published values. (For the lizardfish (*Saurida tumbil*) in Fig. 9.9, $L_\infty = 69$ cm and $k = 0.228$.) Keeping the same L_∞, a curve fitted to otolith-derived ages gave

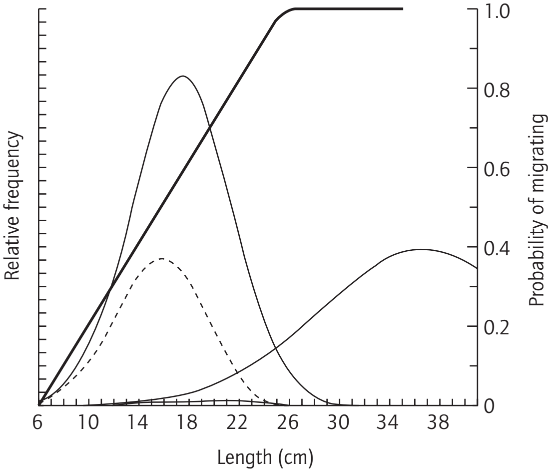

Fig. 9.9 Diagram showing the estimation of offshore migration rate with age for *Saurida tumbil* (lizardfish) in Hong Kong. The analysis is performed on the first two age groups. Start and end lengths for migration probability (thick inclined line) are adjusted until means and standard deviations of two cohorts (solid bell-shaped curves) fit observed truncated distributions (broken curves). True mean lengths are 17.5 and 36 cm, while the mean lengths of fish remaining are 14.1 and 19.1 cm.

Table 9.2 Estimated instantaneous rates of offshore migration for three species of Hong Kong fishes.

Age (year)	*L* infinity	1.5	2.5	3.5
Lizardfish	69	0.90	3.70	–
Croaker	33	4.86	–	6.94
Ponyfish	14	1.85	1.88	–

an apparent k of 0.96 year^{-1}. Mean lengths at age calculated from this apparent growth curve will be biased if fish migrate out of the sampling area. The actual mean lengths at these ages is given by the true growth curve. The next assumption is that the true cohorts have the same COV as the youngest cohort in the otolith samples (in this example, 0.23). If this is true, then 'ideal' cohorts with normally distributed lengths, including both unmigrated and migrated fish, can be set up using the mean lengths from the true growth curve. A distribution of fish remaining is then set up by multiplying the 'ideal' cohort vector by the probability of migrating for each length class. If the correct migration line is chosen, the mean length of this distribution should be equal to the observed mean length for the apparent growth curve. Goodness-of-fit is judged by least squares of the two pairs of mean lengths and standard deviations. The analysis is repeated for all combinations of start and end length, or an automatic search for a minimum performed.

Examples of the goodness-of-fit surface for three Hong Kong fishes are shown in Plate 2 and the calculated instantaneous migration rates with age are shown in Table 9.2. The results show that the small leiognathid ponyfish, which only reaches about 14 cm maximum length, moves offshore at about the same rate once adult at 1+. The croaker moves rapidly out of the inshore area soon after it is a year old, while most lizard fish remain inshore until their second year.

9.3.3 Estimating trophic levels using length and Ecopath

Pauly et al. (2000) have developed a simple method of calculating change in trophic level (ΔTL) where mean body sizes have been reduced by fishing. The estimation depends on an empirical relationship between body size and TL in 180 species of fishes:

$$\begin{aligned}\Delta TL = b\log_{10}\{[L_\infty + \{[Lc\,(M/k)/(1-E)]/\\ [(M/k)/(1-E)+1]\}]/\\ [L_\infty + \{(LcM/k)/(M/k+1)\}],\end{aligned} \qquad (9.15)$$

where Lc = length at first capture; E = exploitation rate, F/Z; M = natural mortality rate; b = slope *pf* relationship between TL and body length in cm which is 0.63 for large carnivores like cod, and 0.24 for small pelagic and demersal fishes; and other parameters are as above.

This method has been used in analysis of decline of TL in Canadian fisheries; the length-based method provided very similar answers to an age-based method.

9.4 CONCLUSIONS

After over 120 years of length–frequency analysis we are justified in asking 'Are we there yet?', and 'Where do we go from here?'

At one time, length-based methods were regarded as being suitable only for the tropics. This has been exposed for the myth that it is (e.g. Pauly 1994). Since that time, the discovery of daily otolith rings has meant that, at least for the young, tropical fish can be aged. And length–frequency analysis has become a cost-effective way of minimizing expensive ageing for many temperate fishes. An unexpected practical use for length–frequency analysis has arisen from Froese and Binholan's (2000) technique, which has led to the printing of posters allowing buyers at markets to reject fishes that are too small.

For conventional length–frequency analysis to determine growth and mortality rates, it seems at first sight that there is nowhere much left to go. Parametric methods are now fully matured, and classic analyses such as mixture analysis may be carried out, complete with uncertainty, on a spreadsheet. Among the non-parametric methods, most of which may also be performed on spreadsheets, the projection matrix stands out as being deserving of further development and rigour. For most normal fisheries work in both the tropics and higher latitudes, in the past decade these analyses have become robust and reliable standard tools. A word of caution is always to map the goodness-of-fit surface rather than rely on optimization routines built into spreadsheets. A further warning is always to perform several different analyses and compare the results.

In one direction, the research frontier of conventional length–frequency analysis is now moving into highly complex integrated catch-at-length models that are far moved from analyses that most fisheries scientists can perform on a spreadsheet. For example, MULTIFAN-CL (Fournier et al. 1998) is described as a length-based, age-structured, likelihood model that circumvents many of the difficulties associated with sequential analyses such as VPA (Shepherd and Pope, Chapter 7, this volume):

> Growth and age structure of the catch are estimated simultaneously with population parameters such as recruitment, selectivity, catchability and natural mortality . . . Spatial structure can be included in the model. . . . Missing data and data of different temporal resolutions are allowable . . . Auxiliary data (such as tagging data) can be incorporated into the model as appropriate. Various structural hypotheses, such as density-dependent growth, trends . . . and seasonal catchability, can be incorporated into the model and tested.

An example of Monte Carlo simulations exploring the sensitivities of such a complex model is given by Fu and Quinn (2000).

In a different direction, length-based short cuts that can be programmed on a spreadsheet can tackle a range of interesting problems – doubtless many of these still remain to be invented and used.

But there may be completely new techniques on the horizon. One recent development may point to an exciting way to deal with our opening example of estimating the growth and mortality of humans massed in St Peter's Square. Smith and Botsford (1998), who bravely say that it is 'analytically more challenging to analyze size frequency distributions that lack multiple age pulses', show how von Bertalanffy parameters estimated from tagging of individuals can be informative about the shapes of length–frequency distributions. Through overlayed Monte Carlo simulations, which can very quickly be graphed on modern computers; they demonstrate how characteristic length–frequency shapes arise even in continuously recruiting animals. The technique has been applied to fish such as lingcod (*Ophiodon elongatus*), and invertebrates such as whelks (*Buccinium undatum*), surf clams (*Macromeris polynyma*), and urchins (*Strongylocentrus franciscanus*).

Long-lived, slow-growing fish that are difficult to age and assess using conventional means currently remain intractable even with complex length-based methods. This problem has not changed. But it is a gap in the fisheries assessment toolbox now that serial depletion by area, depth, species and taxon proceeds apace in the world's overexploited oceans. It seems as though the critical problems for the fisheries of the early 21st century have bypassed single-species analyses such as those presented here. Are length-based ecosystem analyses the hope of the future?

ACKNOWLEDGEMENTS

I am grateful to Peter Macdonald who, a long time ago, initiated me into formal length–frequency analysis using what was then a revolutionary new 4 K computer, the Elliot 803. I also thank Daniel Pauly, who, not so long ago, provided critical comments on a draft of this manuscript.

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10 Ecosystem Models

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10.1 INTRODUCTION: ECOSYSTEM MODELS

Historical sources indicate that the fishers and scholars of centuries past were well aware that the fish and invertebrates then exploited by fisheries were embedded within what we now call 'ecosystems' (see e.g. Thompson 1910; Cotte 1944). As well, this knowledge was used to draw inferences structurally similar to contemporary hypotheses. Thus, for example, Bernard de Palissy (1510–90) interpreted fossil fish as the remnants of populations that had been 'trop pêchées' (i.e. overfished to extinction; Tort 1996, p. 3345), thus admitting to the possibility of humans having such impacts – possibly based on observations at the time. This inference that fishing had ecosystem effects is illustrated by a petition from the year 1376 to Edward III, King of England:

> The commons petition the King, complaining that where in creeks and havens of the sea there used to be plenteous fishing, to the profit of the Kingdom, certain fishermen for several years past have subtly contrived an instrument called 'wondyrechaun' made in the manner of an oyster dredge, but which is considerably longer, upon which instrument is attached a net so close meshed that no fish, be it ever so small, that enters therein can escape, but must stay and be taken. And that the great and long iron of the wondyrechaun runs so heavily and hardly over the ground when fishing that it destroys the flowers of the land below water there, and also spat of oysters, mussels and other fish upon which the great fish are accustomed to be fed and nourished. (Alward 1932)

Incorporating the commonsense knowledge expressed here into a rigorous ecosystem-based understanding of fisheries took, however, an extremely long time, and the path taken was particularly tortuous, with various blind alleys and enticing traps (see also Smith, Chapter 4, this volume). Indeed, many fisheries scientists, accustomed to 'single-species stock assessments', are still uncomfortable with the broad ecological principles required for such understanding, not to speak of regulatory agencies, whose mandate often precludes them from even beginning to address ecosystem-related issues (NRC 1999).

This chapter therefore introduces a number of ecological principles which formalize and render mutually compatible earlier ideas on how the different elements of aquatic ecosystems interact. Moreover, it illustrates how applying these principles can improve one's understanding of a given aquatic ecosystem, and of such systems in general. The link with fisheries is then established by documenting how fish and invertebrate resource species are embedded in ecosystems and how they must (and do) follow the same principles as non-exploited species. Our goal, thus, is to marry key parts of Ecology with the best parts of Fisheries Science. In doing so, we build on the foundations of the two chapters in Volume 1 that examine trophic interactions in freshwater (Persson, Chapter 15) and marine communities (Polunin and Pinnegar, Chapter 14). Our chapter, in turn, provides a theoretical and methodological underpinning for the ecosystem impacts of fishing documented by Kaiser and Jennings (Chapter 16, this volume).

Both ecology and fisheries science share the same ancestry, having been spun off Natural History in the late 1800s. However, their subsequent fates differed. Ecology went to University, theorized, and usually failed to get its hands dirty. Fisheries science, on the other hand, decided to work for the Government, and became very applied, hence a prime suspect every time some fish stock collapses. The union we advocate may be thus likened to a shotgun marriage: the partners do not necessarily match, but strong external constraints force them together. The shotgun itself is the crisis of fisheries, and the ensuing threats to the systems studied by both (aquatic) ecologists and fisheries scientists, and as well, to the funding of these often feuding disciplines. A similar convergence of protected area management and fisheries has been identified in the context of marine protected areas by Polunin (Chapter 14, Volume 1).

Before all, however, we must define the concepts in our title, 'ecosystems' and 'models.' Ecosystems, in this chapter are sites occupied by elements such as individual members of different plant and/or animal species, which interact such that the sum of their mutual interactions is much greater than the sum of their interactions with the elements of adjacent sites. The interactions within the ecosystems thus defined may lead to distinct structures for these ecosystems. However, our definition does not require adjacent ecosystems to be structurally different from each other.

Lakes are excellent examples of ecosystems defined here (Thienemann 1925; Golley 1993). Thus, if consumed at all, the primary production of a lake from phytoplankton and macrophytes is grazed within that lake, as is its secondary production which is composed of zooplankton, and the production by fish and other organisms is supported by feeding on the secondary producers. Indeed, in lakes, it is usually only that part of primary production taken up by the few aquatic insects that make it to the adult stage, and by birds, which is available for transfer to adjacent, terrestrial ecosystems.

This definition, however, also fits more open systems, such as coral reefs, seamounts or estuaries, whose different components have co-evolved such that most of their trophic fluxes are 'internalized', if at the cost of large supporting energy fluxes, in the form of light for coral reefs (Grigg 1982), zooplankton for seamounts (Koslow 1997), or detritus for estuaries (Odum and Heald 1975). On the other hand, this definition of ecosystems may exclude beaches and other shallow-water areas whose inhabitants often consist of the juvenile form of adults living in adjacent, deeper waters. The concept of 'subsystems' is appropriate for such highly connected parts. As will be shown below, stratification by subsystems is crucial when constructing models of ecosystems, our next topic.

Models are coherent representations of systems and/or of the processes therein, and may consist of words ('word models'), graphs or equations. Words alone can often describe complex systems or processes adequately, as in the case of natural selection (Darwin 1859). Graphs can also make compelling cases, as did, for example, the trophic pyramid of Lindeman (1942). However, equations that capture essential aspects of systems or processes always outperform word or graph models, if only because the application of standard algebraic or other mathematical rules to these equations often leads to the discovery of unknown properties of the systems or processes in question. This non-intuitive, and in fact wondrous property of mathematical descriptions (Wigner 1960) has, moreover, the distinct advantage of allowing the testing of hypotheses about future states, or previously unobserved features of ecosystems, besides allowing for testing the adequacy of the initial description.

Our models will thus be mainly equations, though not necessarily complex ones. The criterion for assessing the value of a model is not the extent to which it reproduces the complexity of the real world. Rather, it is the ratio of insight gained versus effort extended. As we shall see, 'simple' models that capture key features of an ecosystem in an obvious fashion are far more useful than complex, but opaque models. Sparre and Hart (Chapter 13, this volume) review both philosophical and practical aspects of using models.

10.2 MULTISPECIES MODELS

The first formal representation of interactions between predator and prey were published by Lotka (1925) and Volterra (1926) and the system of equations they proposed to describe such interactions, now known as Lotka–Volterra equations, are still used – often in strongly modified forms – for exploring mathematically the consequences of certain features of systems of interacting organisms (see Smith, Chapter 4, this volume). The basic form of this system is:

$$\mathrm{d}N_1/\mathrm{d}t = (r - c_1N_2)N_1 \tag{10.1a}$$

$$\mathrm{d}N_2/\mathrm{d}t = (-g + c_2N_1)N_2, \tag{10.1b}$$

where r is the intrinsic rate of population growth of the prey, g is the coefficient of negative growth (decline) of the predators (N_2) in the absence of prey (N_1) and c_1, c_2 are interaction coefficients. Given certain sets of values for these parameters, the predator and the prey will oscillate, sometimes violently: the prey grows, the predator follows and over-consumes the prey which declines, followed by the predator with the prey then picking up again. Volterra, after modifying these equations such as to cover any number of species, teamed up with his son-in-law, the fisheries scientist Umberto D'Ancona, to apply the new formalism to the interpretation of observed cycles in the landings of small prey and large predatory fishes from the Adriatic. The details of this story are in Tort 1996 and the historical setting is given by Smith (Chapter 4, this volume). We note in passing that such cycles, nowadays, would invariably be (if often unjustifiably) attributed to environmental fluctuations.

The exploration of systems of equations such as (10.1a and b) has led to a number of insights about interacting species, notably, that their combined yield to a fishery depends on the character and strength of these interactions (Kirkwood 1982). Thus, the combined yield of a prey and predator is always less than these organisms considered separately. On the other hand, species with mutually beneficial interactions increase the combined yield. These results seem trivial; however, we must realize that single-species fisheries models still largely assume that predation effects can be neglected, with optima being proposed separately for each species, as if they did not interact. On the other hand, the familiarity that marine scientists and ecosystem modellers now have with the Lotka–Volterra approach has had numerous negative impacts. Notably, modellers have uncritically taken over the mass-action assumption implied in the Lotka–Volterra model, i.e. that the consumption of prey by predators is a function of, and only of, their respective numbers or biomass in the ecosystem, just as is the case with reactants in a chemical vat. As we shall see, this assumption ignores the use of spatial structure by potential prey to enable part of their population to hide from, or otherwise render itself invulnerable to, their predator(s) (Krause et al., Chapter 13, Volume 1). This dampens the oscillation otherwise implied by the system. Spatial structure also enables the coexistence of two very similar competing species, whereas the equation systems such as equation (10.1) would predict that one would have to go extinct (Gause 1934).

Another more practical approach to analysis of multispecies situations is to add up yield-per-recruit (i.e. the results of yield-per-recruit analyses, see Shepherd and Pope, Chapter 8, this volume) for a number of species into an overall yield-per-recruit for a given area. Multispecies yield-per-recruit analysis, while tedious to implement, is conceptually straightforward (Beverton and Holt 1957; Munro 1983; Murawski et al. 1991). However, the results suffer from the same defect that plagues single-species yield-per-recruit analyses, that is, strong assumptions must be made as to the level of recruitment for each of the species considered. Usually, this level of recruitment is assumed constant, and the solutions, which then rely on equilibrium assumptions, ignore the violent transient effects often resulting from fishing mortality changes (Shepherd and Pope, Chapter 8, this volume). However, when the signal from the fishery being investigated is very strong, such as in fisheries in which a wide range of species is being growth overfished, this approach can provide estimates of the gain that can be obtained, by, say, reducing fishing mortality on a wide range of species. In such cases, indeed, the method is particularly powerful in that it allows one to distinguish between fisheries with different selection patterns. It also allows one to identify, again under the assumptions of constant recruitment and of no biological interactions, the mix of fishing effort by size or age which optimizes overall yield-per-recruit. Thus, in spite of its clear drawbacks, these techniques are likely to continue being used, specially since they are not very demanding in terms of input parameters. These are growth parameters, estimates of natural mortality, and others, most of which, at least for commercial species, can be obtained online; see *www.fishbase.org*. One software system that can be used to implement this technique is FiSAT (Gayanilo et al. 1996), also available online (*www.fao.org/fi/statist/fisoft/fisat/project.htm)*.

10.3 MODELLING THE NORTH SEA, THE NORTH PACIFIC AND THE GULF OF THAILAND

Simulation models, incorporating basic elements of the Lotka–Volterra approach, but also incorporating components such as those used in yield-per-recruit analyses, may be seen as the next logical step towards dealing with multispecies interactions. Indeed, several attempts have been made to conceptualize and parameterize simulation models of large marine ecosystems, and three of these had a great indirect and direct impact on fisheries research. The North Sea model of Andersen and Ursin (1977) is unique in terms of its extreme complexity and level of details, the consequence of an attempt to track the numbers of fish from the eggs to the adults of dozens of species feeding on each other, each subjected to a different stage-specific mortality, and the vagaries of a varying physical environment. Still, the aggregate behaviour of the model was credible; notably, it generated a particle-size distribution such as observed independently (see Section 10.8 below), and natural mortalities for juvenile fishes well in excess of the values then assumed, for example about $M = 2$ year^{-1} instead of about 0.1 year^{-1} for juvenile herrings. This result was later confirmed by multispecies virtual population analysis, MSVPA (see Pope and Shepherd, Chapter 7, this volume).

However, it is clear that few of Andersen and Ursin's colleagues were convinced of the practicality of this tool for fisheries management. Rather, what it established was that simulating a large marine ecosystem was not an intractable task. Moreover, several of the elements of the Andersen and Ursin model – notably its size-selection submodel (Ursin 1973) – were found to be extremely useful on their own, and have seen use in later modelling approaches, e.g. the length-based MSVPA described by Christensen (1995a) and Shepherd and Pope, Chapter 7, this volume.

The simulation of the Northeastern Pacific ecosystem developed by Laevastu and collaborators, though similarly ambitious, differed from Andersen and Ursin's approach in that no attempts were made to track numbers of individuals. Rather, the model strived to maintain mass balance between the cells of a spatial grid, upon which were overlaid the biomass of commercial fishes, and of their prey called 'forage fishes', and predators which were mostly marine mammals. Here again, the model and its predictions were not adopted as such. Rather, the PROBUB model, as it was later called (Laevastu and Larkins 1981), attracted the attention of researchers in need of a tool for modelling biomass flows in a data-sparse system, the French Frigate Shoals, Northern Hawai'i (Polovina and Tagami 1980). Stripped of its spatial and temporal dynamics, PROBUB led to the first version of Ecopath, a simple mass-balance approach for estimating biomasses in aquatic systems (Polovina 1984). Another indirect effect of work on PROBUB is that it motivated a thorough study of the diet of Bering Sea fishes, and thus enabled the construction of successor models (Trites et al. 1999; also see below).

Another early simulation model relevant to fisheries was that of Larkin and Gazey (1982), describing the Gulf of Thailand. Like Andersen and Ursin for the North Sea and Laevastu and collaborators for the North Pacific, Larkin and Gazey were faced with the need to parameterize a large number of coupled differential equations. However, contrary to the situation for the North Sea and the Pacific, there was, at the time, no hope of obtaining the parameters required for a model of the Gulf of Thailand, then much less studied than the temperate North Sea, or the North Pacific. Thus they pushed as far as they could the process wherein evolutionary first principles are used to derive assumptions about the likely parameter that such values might take. The result, while establishing their ingenuity, confirmed that simulation models structured around coupled differential equations could not be parameterized for most situations such that fisheries scientists and managers would feel comfortable with the results. Clearly, a route had to be found to harness the scattered data on catches, standing stock estimates, and food consumption rates, which marine and fishery biologists have published over the years but which could not be straightforwardly used to parameterize models such as the one of Larkin and Gazey. This, again, leads to the Ecopath model, our next topic.

10.4 ECOPATH AND THE MASS-BALANCE APPROACH

The basic idea behind the mass-balance approach incorporated in Ecopath is both trivial and profound. At any time within the system, and within the elements of that system, the amounts of matter that flow in must balance the amount that goes out plus the change in biomass. This means that if parts of the fluxes in a system and/or biomass in a system are known, the values for the other parts are constrained and therefore can be estimated by subtraction. This principle can be implemented through different sets of equations and we think that the utility criterion, presented in the Introduction, should be that used for determining one's use of one or the other formulation. Polovina (1984), who developed the original Ecopath formulation, emphasized the biomasses as the unknowns in his system, thereby making strong assumptions about the fraction of the fluxes retained within the system. In the reformulation of the Ecopath approach (Christensen and Pauly 1992; Pauly et al. 1993), this emphasis on biomass was replaced by an option to leave other elements of a system of fluxes unknown, notably the ecotrophic efficiency (EE), expressing the fraction of mortality not due to predation or fishing, a parameter far more difficult than biomass to estimate in the field.

The well-known master equation for Ecopath is, for each functional group i:

$$B_\mathrm{i} \cdot (P/B)_\mathrm{i} \cdot EE_\mathrm{i} = Y_\mathrm{i} + \sum B_\mathrm{j} \cdot (Q/B)_\mathrm{j} \cdot DC_\mathrm{ij}, \qquad (10.2)$$

where B_i and B_j are biomasses (the latter pertaining to j, the consumers of i); P/B_i their production/biomass ratio, equivalent to total mortality under most circumstances (Allen 1971); EE_i the fraction of production ($P = B \cdot (P/B)$) that is consumed within, or caught from the system (usually left as the unknown to be estimated when solving the equation above); Y_i is the fisheries catch (i.e. $Y = F \cdot B$); Q/B_j the food consumption per unit biomass of j; and DC_ij the contribution of i to the diet of j.

Herein, solutions for the unknowns, e.g. B_i, are obtained by solving the matrix system in equation (10.2) through a robust inversion routine (MacKay 1981). (The right-hand side of equation (10.2) can also include a biomass accumulation term (B_acc) in cases where the biomass is known to have changed during the period under consideration, thus allowing for non-equilibrium situations (see below), as well as a term for net migration.)

Solving the system of equations (10.2) does not require the Ecopath software per se. Indeed, they can be implemented on spreadsheets (see e.g. Mathisen and Sands 1999). Rather, their key attribute is that it is easy to find estimates of various processes and states in ecosystems which correspond to the parameters of these equations, thus largely solving the parameterization problem that has been besetting earlier modelling approaches.

Moreover, to correct a false impression created by the title of Christensen and Pauly (1992), the Ecopath master equations do not require equilibrium or steady-state. Rather, they require that mass balance occurs during the period under consideration, e.g. that any excess consumption during part of that period is compensated for by reduced consumption during another part. This is particularly important for models of ecosystems that included a strong seasonal component and which either can be represented by parameters averaged over a year, which is the option chosen for many applications so far, or in which monthly change in biomass, diet composition, Q/B and P/B are modelled explicitly.

Constructing an Ecopath model is thus a matter of performing the following steps:

1 *Defining the area in which the ecosystem occurs.* This should preferably be one in which a distinct community of organisms occurs with limited exchange to adjacent ecosystem. This system area may comprise several subsystems, e.g. a gulf may consist of a shallow, mangrove-dominated area, a rocky or coralline intermediate area and deeper mud-covered grounds (Opitz 1993). This spatial articulation of a system in the form of subsystems is important for the spatial considerations discussed further below.

2 *Defining the period represented by an ecosystem*. Typically, this will be a period during which major field surveys have been conducted, providing estimates of biomass, diet composition, and other important elements for many of the most important groups in the system. This period is also one during which major changes in the biomass of the major ecosystem elements can be assumed not to have occurred. Thus, wherever massive changes are known to have occurred, it is better to represent that system by models for each of the periods, before and after the change. Having at least two models also has the advantage that additional inferences on the vulnerability of various species to their predators and to the fisheries can then be made using Ecosim, presented below.

3 *Defining the state variables explicitly included in the system*. Earlier applications of Ecopath tended to be composed of 10 to 20 functional groups representing all species in the ecosystem (see models in Christensen and Pauly 1993). Present applications typically include more groups, from 20 to 50, as required, to represent a wide range of ecological and spatial variability and ontogenic diet changes. Whether one uses few or many state variables, it is important that all taxonomic groups occurring in a system be included, whether or not detailed data on them are available. This can be done by including a group explicitly, with its own state variables. This would be for common, well-documented species. Alternatively it can be done implicitly as part of broadly defined functional groups. A detritus group must also be included, to which all fluxes of ungrazed plants and/or unconsumed dead animals are directed. Bacteria may or may not be added as an explicit group. If they are not an explicit group, it is assumed that they feed from the detritus. In this case, the EE of detritus must be <1; this implies that the detritus produced in a system is not all consumed within that system, i.e. this allows for consumption by bacteria considered to reside 'outside' of that system.

4 *Assembling available estimates of biomass, P/B, Q/B and diet composition*. Contrary to the almost ritually invoked phrase that 'nothing is known of x', over a hundred years of quantitative work by marine biologists, limnologists, fishery scientists and others have generated a vast archive of valuable information on the aquatic ecosystems of the world. Much of it is, admittedly, scattered in a vast and still largely untapped literature, some of it obscure. Constructing Ecopath models requires access to that literature. This task is facilitated in part by FishBase, which can be made to output P/B, Q/B and diet compositions for the thousands of species for which such information has been encoded, and also provides a starting point for the literature search in question (Froese and Pauly 2000). Only after such a literature search has been conducted should field programs be launched aiming at estimating missing parameters. Moreover, to guide both the literature searches and the field work, routines are available in Ecopath which quantify the uncertainty associated with the available input values and thus help identify those components of a model requiring additional field inputs.

Balancing a model then consists of solving the system of linear equations (10.2), under the constraint that the EE values remain equal or less than 1, and that the respiration terms are all positive. This balancing often involves revising initial estimates and is guided by the quantification of the uncertainties as outlined in (4). Formal approaches for explicitly considering these uncertainties involve: (a) the Monte Carlo routine ('EcoRanger'), which uses the uncertainties in (4) in Bayesian mode, as prior distributions, and outputs both distributions of estimates, and posterior distributions for the input values (Pauly et al. 2000, Fig. 3); and (b) a recently developed approach based on simulated annealing, in which fuzzy logic is used to modify qualitative diet compositions within constraints, until the system of equations is balanced.

Once they are balanced and their key features checked for internal consistency and compatibility with similar ecosystems, models can be represented in the form of flow charts, which summarize these key features. Such flow charts (Fig. 10.1) can be extremely information-rich and, in the following, we discuss some aspect of this information in terms of trophic levels that are calculated and not previously assumed. This was also the case with the Lindeman pyramids earlier used to represent ecosystems. We then discuss other aspects of the information contained in ecosystem flow charts.

We stress that the four steps outlined above have now been implemented in hundreds of locations, resulting in over 150 published models. These describe a vast range of ecosystem types from data-rich areas, such as the North Sea and the North Pacific, partly using, for both areas, the same database used for the simulation models discussed above, to the more data-sparse Gulf of Thailand (Christensen 1998) where the straightforward data requirements of the Ecopath model enabled the parameterization based on empirical data that had eluded Larkin and Gazey (1982). This vast range of applications demonstrates the applicability of Ecopath as perceived by users who feel thereby empowered, contrary to the situation prevailing in programmes such as the International Biological Programme (IBP) where many field biologists worked 'for' rather than 'with' the few modellers then working on ecosystems (Golley 1993). This transition has markedly changed the field and made ecosystem-based management a realistic option, as we shall show below, at least as a researchable issue, if not in actual implementation.

10.5 THE TROPHIC LEVEL CONCEPT

Given a Darwinian world, the main limiting factor for most animals is 'safe food'. This is, food that can be consumed without exposing oneself unduly to predation (Jones 1982; Walters and Juanes 1993). Thus, modelling ecosystems is mainly a matter of describing food consumption by prey animal (Mittelbach, Chapter 11, Volume 1; Juanes et al., Chapter 12, Volume 1), and the predation they are exposed to (Krause et al., Chapter 13, Volume 1). This is done either by tracking individuals and their fate, or by tracking the fate of the biomass incorporated in these individuals. The former approach leads to single-species population dynamics, well covered in this volume (see Sparre and Hart, Chapter 13, this volume; Shepherd and Pope, Chapters 7 and 8, this volume); while it is the latter approach, involving biomass, or energy, a close correlate (MacDonald and Green 1983) that is emphasized in this chapter.

Probably the simplest way to describe an ecosystem is to re-express it as a 'food chain', separating its overall biomass into primary producers, herbivores, or first-order consumers, first-order carnivores or second-order consumers, etc., each of these links representing a trophic level (Lindeman 1942, Polunin and Pinnegar, Chapter 14, Volume 1). The International Biological Programme (Golley 1993) was structured around such integer trophic levels, with field workers collecting data on biomass and production at each trophic level, and sending them to 'modellers' tasked with incorporating these data into simulation models. We have mentioned above some of the disadvantages of this separation of data collection and modelling that this arrangement implied. It is, thus, sufficient to add here the radical critique of the trophic

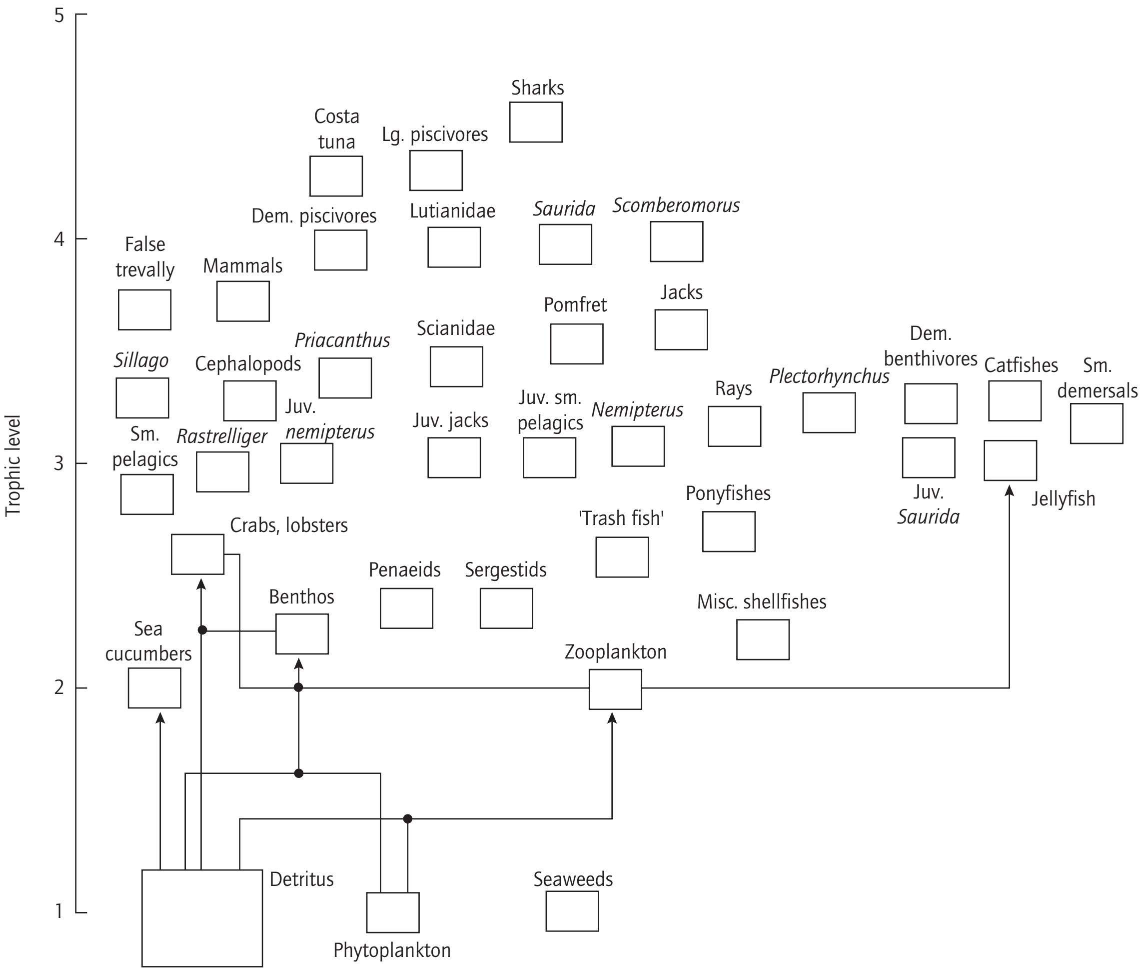

Fig. 10.1 Flow diagram for a trophic model of the Gulf of Thailand. All flows between ecosystem groups are quantified, but only flows exceeding 5 t·km^2·year^{-1} are indicated. The sizes of the boxes are a function of the group biomasses.

level concept which Rigler (1975) presented at a key meeting of the IBP, based on the data collected by the IBP, showing that most aquatic animals, which include all those that are not strict herbivores or detritivores, feed, simultaneously, at different trophic levels. Rigler's critique was extremely influential, and its echoes are still detectable (see Cousins 1985). However, the solution to issues raised by this critique had a simple answer: fractional trophic levels (TL_i; Odum and Heald 1975), computed, for the animals of a given population (i), from the trophic levels of all their prey (j). Thus, we have:

$$TL_i = 1 + \sum_{j=1}^{n} TL_j \cdot DC_{ij}. \qquad (10.3)$$

where DC_{ij} is the fraction of j in the diet of i, and n is the number of prey types. Estimates of trophic levels derived from equation (10.3) and earlier estimates of TL_j exist for marine mammals (Pauly et al. 1998a), and for sharks (Cortés 1999) and other fishes (see Froese and Pauly 2000, and updates in *www.fishbase.org*).

Another widely used method to estimate fractional trophic levels is through the analysis of stable isotopes of nitrogen (reviewed by Polunin and Pinnegar, Chapter 14, Volume 1). This relies on the observation that the ratio of ^{15}N to ^{14}N increases by about 3.4% every time proteins are ingested by a consumer, broken down and resynthesized into its own body tissues (Minagawa and Wada 1984). Kline and Pauly (1998), in the first study of this type, showed that trophic levels estimated from diet compositions, that is, from Ecopath models closely correlated with trophic level estimates from stable nitrogen isotopes.

The variance of trophic level estimates can also be calculated. Given the nature of TL estimates from either stable isotope ratios or diet composition studies, this variance will reflect feeding at different trophic levels, i.e. omnivory by the consumer under study as well as uncertainty concerning the trophic level of its food. Thus, one can define an 'omnivory index' (OI) calculated from:

$$\mathrm{OI} = \sum_{j=1}^{n} (TL_j - (TL_i - 1))^2 \cdot DC_{ij} \qquad (10.4)$$

where n is the number of groups in the system, TL_j is the trophic level of prey j, TL the mean trophic level of the prey (one less than the trophic level of the predator, see above), and DC_{ij} is the fraction of prey j in the diet of predator i, again as defined above. Rigler (1975) argued that trophic levels were only a 'concept', and that mature sciences should deal with concepts only in the absence of measurable, actual entities, which alone allow testing of quantitative hypotheses. The demonstration that trophic levels estimated from diet composition data and equation (10.3) closely correlate with estimates from stable isotopes of nitrogen not only cross-validates these two methods, but also establishes that trophic levels are not just concepts useful for assigning animals to various ecological groups, but actual entities, similar to the size or metabolic rate of organisms, which can be measured by different, independent methods, and whose various features, therefore, can be elements of testable, quantitative hypotheses.

10.6 PRACTICAL USES OF TROPHIC LEVELS: TRACKING FOOD-WEB CHANGES

Ecopath, as shown above, has estimates of trophic level as one of its outputs, along with the standard error of these trophic levels, the square root of the omnivory index. The many estimates of trophic levels that emerge from various Ecopath applications helped confirm various generalizations by Pimm (1982) and others about the structure of food webs. Also, they allowed going beyond these generalizations. Thus, Pauly and Christensen (1995), who had assigned trophic levels to all fish and invertebrates caught and reported in FAO global fisheries statistics, could show, using between-trophic level transfer efficiencies also estimated through Ecopath models, that the primary production required to sustain the present world fisheries was much higher than previously assumed: 8% for the global ocean and between 25% and 35% for the shelves from which 90% of the world catches originates. Also using time series of the same fisheries statistics, and trophic levels for the major species, Pauly et al. (1998c) demonstrated a steady reduction of the mean trophic level of fisheries landings from 1950 to the present, suggesting that the fisheries increasingly concentrate on the more abundant, small, fast-growing prey fishes and invertebrates near the bottom of aquatic food webs. Both of these sets of findings, now validated through more detailed local studies quantifying human impacts on marine ecosystems (e.g. Pauly et al. 2000), relied on trophic-level estimates obtained through Ecopath applications, that is, diet composition studies that were rendered mutually compatible in an ecosystem context. They document the utility of the post-Rigler trophic-level concept.

10.7 ECOSYSTEM STRUCTURE, ODUM'S MATURITY AND ULANOWICZ'S ASCENDANCY

One interesting aspect of food webs is that, once constructed, they can be interpreted using various techniques, and the results interpreted in the light of various hypotheses on the way food webs should be structured. Some of these hypotheses are distinct products, not necessarily connected to other hypotheses. Others are part of broader constructs, such as the theory of Ivlev (1961), or that of Odum (1969).

Odum's theory is interesting in that although it is not strictly quantitative, it makes enough specific qualitative prediction for rigorous tests of its validity to be performed (Christensen 1995b). Thus, food-web models constructed as described above can quantify many of the attributes of ecosystems that are part of Odum's theory (Table 10.1). As might be seen, this theory essentially implies that as systems mature, their biomass will tend to increase, especially the biomass of large animals with high longevities, and detritus will increasingly be recycled through a web whose complexity will tend to increase. Two direct tests of this theory have been performed so far. One consisted of forcing an increase in the biomass of top predators in two marine ecosystems, one coastal and one offshore, and using the Monte Carlo 'EcoRanger' routine to identify parameter values which were randomly selected from within the distribution assumed for each of the models' inputs and where compatible with these increased biomasses. This led to increases in all parameters related to increased maturity in Table 10.1, notably detritus recycling (Christensen and Pauly 1998). The other test consisted of an application of Ecosim, the dynamic version of Ecopath, to be presented below. Therein, a short strong increase in the fishing mortality of the small pelagic species dominant in each system was simulated and the time for the system as a whole to recover was plotted. Here again, detritus recycling was the ecosystem parameter which best correlated with the form of resilience implied here (Vasconcellos et al. 1997). We conclude here that the Ecopath approach can be used to operationalize Odum's theory and to test its basic tenets. The theory survived these tests.

The flow charts generated by Ecopath can also serve to test Ulanowicz's theory of ascendancy as a measure of ecosystem development. This theory combines the information contents embedded in the different flows within the system with the

Table 10.1 Selection from Odum's (1969) list of 24 attributes of ecosystem maturity.

No. in Odum's list	Ecosystem attributes	Development stages	Mature stages
1	Gross production/respiration	>1 or <1	Approaches 1
2	Gross production/biomass	High	Low
3	Biomass supported/energy flow	Low	High
4	Net community production	High	Low
6	Total organic matter	Small	Large
12	Niche specialization	Broad	Narrow
13	Size of organisms	Small	Large
15	Mineral cycles	Open	Closed
16	Nutrient exchange between organisms and environment	Rapid	Slow
17	Role of detritus in nutrient recycling	Unimportant	Important
21	Nutrient conservation	Poor	Good
22	Stability (resistance to perturbations)	Poor	Good

magnitude of these flows to derive a combined measure of information and flow, expressed in 'flow bits'(Ulanowicz 1986). Here, results were not as unequivocal as in the case of Odum's theory. Ascendancy did not correlate positively with maturity as expressed using a combination of parameters derived from Odum's theory (see Christensen 1995b), the implication probably being that Ulanowicz's theory is in need of revision.

Overall, these two examples illustrate that the existing wide availability of quantified food webs constructed using the Ecopath approach can be a boon to theoretical ecology, enabling the testing of hypotheses that have long remained untested and consolidating existing knowledge on the functioning of ecosystems.

10.8 PARTICLE-SIZE SPECTRA IN ECOSYSTEMS

Using data from particle-size counters, Sheldon et al. (1972), proposed that the size spectrum of marine organisms is a conservative feature of marine ecosystems, characterized by a constant slope, for which they provided the rationale, using thermodynamic considerations. The controversy which ensued, still festering among marine biologists, who tend to consider only the small range of organism sizes sampled by automatic plankton particle counters, was largely ignored by fisheries scientists, who quickly established not only that fish abundances also neatly fit (log) linear size spectra, but that the slope of such spectra reflect the exploitation level to which a multispecies fish community is subjected, being steeper where exploitation is high (Pope and Knight 1982; Bianchi et al. 2000).

This provides another constraint for multispecies and/or ecosystem models, which should be expected to generate such spectra as one of their output (as did, the North Sea model of Andersen and Ursin already described).

Individual-based models such as OSMOSE (Shin and Cury 1999) can generate such spectra, as may perhaps be expected (Shin 2000; see also Huse et al., Chapter 11, this volume). Perhaps more surprisingly, it turns out, however, that mass-balance models can also be used to generate size spectra of the ecosystem, and thus build a bridge between the hypotheses advanced by marine ecologists and those of fisheries scientists. We briefly describe the routine of Ecopath which is used to re-express the biomass of fish, invertebrates and marine mammals in various ecosystems in the form of standardized size spectra, whose slope can then be compared. This routine, while assuming steady-state, does the following:

- uses the von Bertalanffy growth curves and the values of P/B (i.e. Z) entered for each group in the model to re-express its biomass in term of a size–age distribution;
- divides the biomass in each (log) weight class by the time, Δt, required for the organisms to grow out of that class (to obtain the average biomass present in each size class);
- adds the $B/\Delta t$ values by (log) class, irrespective of the groups to which they belong.

Figure 10.2 compares size spectra obtained in this fashion for a trophic model of the Gulf of Thailand. The spectra are based on 40 ecosystem groupings ranging in size from phytoplankton to dolphins. The spectra are obtained by running a model describing the 1973 situation, where fishing pressure and resource depletion were moderate, with observed fishing pressure through to 1994, where fishing pressure was high, and the resources severely depleted. Further, a simulation was performed with fishing pressure removed, and the long-term equilibrium used to estimate a spectrum without fishing.

The dots on Fig. 10.2 indicate the actual size spectrum obtained for the 1973 model. It is far from a straight line, but shows a hump in the size range dominated by benthos. This hump is likely to be caused by poor resolution for the benthic groupings, and would probably not appear if these groups were split into finer taxonomic groups than used for the model presented.

The three straight lines on Fig. 10.2 show that the slope of the size spectra, as expected, increases with fishing pressure, here from (–0.17) for the unfished situation, to (–0.18) for the moderately fished, and to (–0.22) for the situation with high

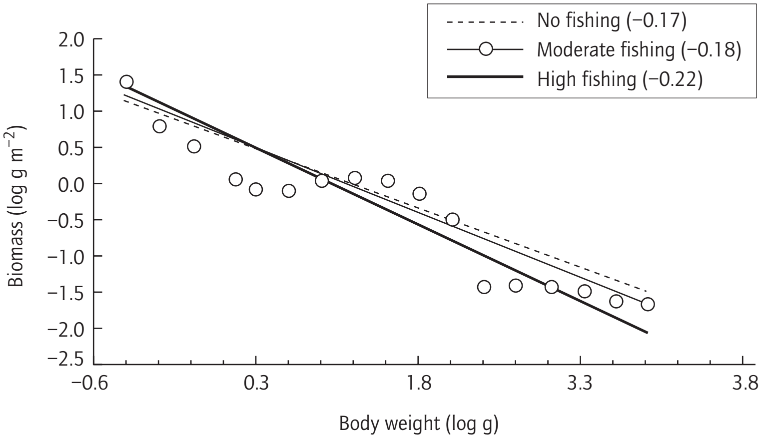

Fig. 10.2 Ecosystem-level size spectra for the Gulf of Thailand. The spectra are derived based on a trophic model with 40 ecosystem groupings (see *www.ecopath.org*). The thin line associated with 'moderate fishing' describes the 1973 situation in the Gulf, while the broken line indicates the slope of the model situation at long-term equilibrium without fishing, and the thick line indicates the 1994 situation, with resources severely depleted by over-fishing. Note that the slopes of the spectra (in brackets) increase with fishing pressure.

fishing pressure. The increased slope is caused by the removal of virtually all higher trophic-level organisms in the Gulf during the time span studied (see Christensen 1998; Pauly et al. 1998b).

The example given here only serves as a taster for how size spectra may be of use as ecosystem indicators of exploitation level, and no generalizations have been drawn so far of how the slopes of the spectra relate to exploitation. We anticipate, however, that the ease with which ecosystem-level size spectra can now be constructed through the Ecopath approach will lead to a blossoming of spectral analysis in the foreseeable future, and that valuable insights will be gained in the process.

10.9 ECOSIM, REFUGIA AND TOP-DOWN VS. BOTTOM-UP CONTROL

The system of coupled linear equations that is behind a balanced Ecopath model (see equation 10.1) above can be re-expressed in terms of the change implied by:

$$\mathrm{d}B_\mathrm{i}/\mathrm{d}t = g_\mathrm{i} \cdot \sum Q_\mathrm{ij} - \sum Q_\mathrm{ji} + I_\mathrm{i} - (M_{0\mathrm{i}} + F_\mathrm{i} + E_\mathrm{i})B_\mathrm{i}, \tag{10.5}$$

where $\mathrm{d}B/\mathrm{d}t$ is the rate of biomass change, g the growth efficiency (i.e. P/Q), F the fishing mortality (i.e. Y/B), M_0 the natural mortality (i.e. excluding predation), I is the immigration rate, E the emigration rate, and Q_ij (Q_ji) the consumption of type j (i) biomass by type i (j) organisms.

This set of coupled differential equations could be easily integrated as they are over time, thus yielding a simulation model with the help of which various scenarios resulting from changes in fishing mortality F, could be explored. This simulation model, however, would be of the Lotka–Volterra type, wherein the amount consumed of a given prey 'i' is proportional to the product of its biomass times the biomass of its predator(s). Such 'top-down controlled' systems, however, are inherently unstable, and usually fluctuate in unrealistic fashion. As animals do not live in reaction vats, modelling predation must reflect the ability of potential prey to hide or camouflage themselves, or generally to evolve strategies that limit their exposure to predators (see Krause et al., Chapter 13, Volume 1). In Ecosim, the dynamic counterpart to Ecopath, the existence of physical or behavioural refugia is represented by prey biomass consisting of two elements: one, vulnerable to predators, the other invulnerable. It is then the rate of transfer between these two partial components of a prey's biomass which determine how much of the prey can be consumed by a predator. When the exchange rate is high, part of the biomass which is vulnerable is quickly replenished and hence we still have top-down control and Lotka–Volterra dynamics. On the other hand, when the replenishment of vulnerable biomass pool is set to be slow, it is essentially that slow rate which determines how much the predators can consume. We speak here of 'bottom-up control', since it is the dynamics of the prey which shape the ecosystem. Issues of top-down versus bottom-up control are addressed further in the food webs chapter by Polunin and Pinnegar (Chapter 14, Volume 1) and Persson (Chapter 15, Volume 1).

These different control types can be represented by replacing Q_{ij} in the above equation by:

$$Q_{ij} = v_{ij}a_{ij}B_iB_j/(v_{ij} + v_{ij}' + a_{ij}B_j), \tag{10.6}$$

where v_{ij} and v_{ij}' represent rates of behavioural exchange between vulnerable and invulnerable state and a_{ij} represents the rate of effective search by predator j for prey i, i.e. the Lotka–Volterra mass-action term.

Thus, Ecosim, which allows users to change the rates of exchange, allows testing the effect of assumptions about bottom-up vs. top-down control. As it turns out, these effects are profound: pure top-down control, which is the Lotka–Volterra assumption, generates, upon the smallest shock, violent oscillations such as do not occur in real ecosystems. Conversely, under bottom-up control, depletion of one species, as, for example through fishing, tends to affect the biomass of only that species and less strongly its key prey and predators; the system as a whole generally remains unaffected even when the species in question is one of its major components (the astute reader will note this to be the unstated assumption behind single-species population dynamics). Thus, at least in terms of the implementation presented here, intermediate control, which is a form of control that is neither fully top-down, nor bottom-up, is required for simulated ecosystems to behave in realistic fashion, this being a major finding obtained through Ecosim (Walters et al. 1997, 1999; Pauly et al. 2000; Christensen et al. 2000; and *www.ecopath.org* may be consulted for further information on this rapidly evolving software).

10.10 SPATIAL CONSIDERATIONS IN ECOSYSTEM MODELLING

As mentioned in the introduction, adding complexity to ecosystem models does not necessarily make them 'better'. Rather, to increase the usefulness of models, what is required is to identify those improvements of existing models for which the gain in new insights outweighs the added complexity and data requirements. As it turned out, the major improvements that can be added to models such as Ecopath and Ecosim are spatial considerations, capable of representing explicitly some of the refugia implied in the above Ecosim formulation.

The formulation developed for this, still based on Ecopath parameterization and its inherent mass-balance assumptions, is one wherein the ecosystem is represented by say, a 20 × 20 grid of cells with different suitability to the different functional groups in the system. Movement rates are assumed symmetrical in all directions around the cell, but are higher in unsuitable habitat. Their exact value is not important. The survival of various groups and their food consumption are assumed higher in suitable habitat, but they otherwise consume prey as they do in Ecopath and Ecosim, as they encounter them within a given cell.

Starting from the Ecopath baseline where functional groups are distributed evenly over suitable habitats, Ecospace simulation iterates towards a solution wherein the biomass of all functional groups is spread over a number of cells, given the predation they experience and the density of prey organisms they encounter in each cell. The distribution maps thus predicted can be compared with existing distribution maps and inferences drawn about one's understanding of the ecosystem in question and the functional group they are in. The rich patterns obtained by the application of this approach to a number of Ecopath files, thus turned into spatial models, suggest that the broad pattern of the distribution of aquatic organisms can be straightforwardly simulated (Walters et al. 1998).

One particularly interesting aspect of Ecospace is that it allows for explicit consideration of ecosystem effects when evaluating the potential impact of Marine Protected Areas (MPA) in a given ecosystem, thus allowing for a transition towards ecosystem-based fisheries management, our last topic.

10.11 TOWARDS A TRANSITION FROM SINGLE-SPECIES TO ECOSYSTEM-BASED MANAGEMENT

The requirement for ecosystem-based management derives its validity from a stark set of alternatives: either the beginning of the 21st century will see a transition towards ecosystem-based management in most areas currently exploited by major fisheries, or it will see the destruction of the ecosystems exploited by these same fisheries. Until recently, the call for ecosystem-based management could be dismissed by regulatory agencies intent on continuing business as usual because ecosystem management tools were not available. The sets of conceptual tools mentioned above, notably Ecopath, Ecosim and Ecospace can, however, be used to identify the key elements of management strategies that would enable fisheries to be sustained by sustaining the ecosystem in which they are embedded. The two major tools available for this are:

1 Ecoseed: a routine for seeding marine protected areas (MPAs), originally covering only one cell within the spatial grid in an Ecopath/Ecospace map, then identifying, by brute-force computations, the sequence of cells which, when added to that initial seed, will contribute most to overall benefits, either in terms of market values calculated as species caught multiplied by their price, minus cost of catching them, and/or in terms of their existence values, for example, as whale abundance to the whale-watching industry. Results of various Ecoseed runs for different systems show, in accordance with theoretical expectation, that MPAs should be large relative to exploited areas. Important here is that MPAs simulated this way consider all trophic interactions between the species included in an ecosystem model and not only the expected biomass increase of a few charismatic species.

2 An optimization approach structured around Ecosim's ability to identify the mix of fleet-specific fishing mortality which optimizes cumulative benefits over a set period, e.g. 30 years, under any of the following constraints:

(a) maximizing net return to the fishery, which generally involves moderate mortality on valuable target species and a small overall level of effort;

(b) maximizing employment, which means identifying the fleet configuration which sustainably exploits the ecosystem, albeit with an effort level as high as possible. This high effort leads to high employment;

(c) maximizing ecosystem maturity, by identifying the fleet configuration which maximizes, for all groups in a system, the sum of product of biomass and B/P. The latter is in accordance with Odum (1969) who predicts the highest product of B and B/P for the long-lived organisms typical of mature systems;

(d) mandated rebuilding, wherein the fleet configuration is sought which enables faster rebuilding towards a set threshold as required. This could result from a consequence of a legal decision;

(e) optimizing a mix of (a)–(d) wherein any of these can be given different weights.

These two approaches combined and used independently allow scientists, for any ecosystem for which a suitably detailed Ecopath model has been previously constructed, to explore the implications of various policies, and to quantify their outcomes in economic and social terms, and in the form of the ecosystem biodiversity they imply. A very important aspect of these simulations is that they invite a discussion of how we want ecosystems to look in the future, and the discussion takes place in a quantifiable manner.

10.12 CONCLUSIONS

The concepts and tools for ecosystem modelling presented above allow for a transition towards ecosystem-based management of fisheries. Obviously, uncertainty remains a major issue in such analyses. For example, the science of how whole ecosystems respond to changes in management remains very weak (Polunin and Pinnegar, Chapter 14, Volume 1). However, not using tools such as described here will not reduce uncertainty. The way to reduce uncertainty about ecosystem function and the impacts of fishing thereon is to construct representations of these ecosystems and to probe their behaviour by posing intelligent questions about the process, and intelligently interpreting the answers. The effect of uncertainties will manifest themselves and they will then have to be confronted using whatever new tools might become available. On the other hand, the effect of fishing on ecosystems is not uncertain. The time has now come for us to generalize from the accumulated experience of a century of marine and fisheries research; the tools presented above provide a context wherein these generalizations can be made.

ACKNOWLEDGEMENTS

We thank Carl Walters for his collaboration, and for crucial contributions towards the development of Ecosim and Ecospace, both of which make Ecopath more useful than it had ever been. We also thank the hundreds of Ecopath users; without them, the generalizations presented here would never have emerged. Finally, thanks to Deng Palomares, without whom this contribution would never have been written.

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11 Individual-based Models

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11.1 INTRODUCTION

Variability in states and traits is pronounced at all life stages of fish populations. This is mainly caused by spatial and temporal fluctuations in the environment, which in turn result in variation in feeding, growth history and adaptation among individuals in a population (Magurran 1986; Salvanes and Hart 2000). This individual variability often has consequences for population abundance, spatial distribution and fecundity. Traditional ecological models, such as the Lotka–Volterra competition models (Pauly and Christensen, Chapter 10, this volume) or the Ricker model for stock recruitment (Myers, Chapter 6, Volume 1), do not take into account variability among individuals. Rather, these models use population abundance as a single characteristic that defines the population dynamics and it is assumed that individuals are identical. Consequently, features such as size structure, known to be important in fish population dynamics, are left out from the model specifications.

The traditional models have been developed into structured population models where the population is divided according to age, stage or some physiological criterion (Metz and Diekman 1986; Sparre and Hart, Chapter 13, this volume). Such structured models have proven successful for many applications in ecology and fisheries science, and the use of differential equations or matrix models allows analytical solutions (Huston et al. 1988; Caswell and John 1992). Even though the structured models do partition a population, it is difficult to incorporate features such as spatial detail into these models, because it is rarely reasonable to assume that all individuals of a certain state occupy the same position in space. Structured models also generally divide the population by one variable, but real individuals may differ with regard to many variables.

These features can be implemented in individual-based models (IBM), which keep track of each individual in a population (DeAngelis et al. 1979; Łomnicki 1988; Huston et al. 1988). In these models individuals can be characterized by state variables such as weight, age and length, and they also allow behavioural strategies to be implemented in a spatial context. This allows the properties of a population to be described by the properties of its constituent individuals. Model validations against data can be done at the individual level, which is an appealing property because observations often are performed on single individuals. Also, models based on individuals benefit from having the same basic unit as natural selection (Darwin 1859; Williams 1966). These issues make individual-based modelling an appealing tool in ecology. The approach is not new per se, but rather it is analogous to the old reductionism that has been very successful in empirical sciences (Łomnicki 1988).

The early work of DeAngelis et al. (1979) and Beyer and Laurence (1980) on modelling growth and survival of largemouth bass (*Micropterus salmoides*) and winter flounder (*Pseudopleuronectes americanus*) respectively, set the scene for extensive later use of IBMs in early life history studies. The major motivation for individual-based modelling of these early life stages has been to explore causes of recruitment variability to commercial fish stocks, an issue that has prevailed and been studied empirically in fishery science since the work of Hjort (1914; see also Myers, Chapter 6, Volume 1 and Smith, Chapter 4, this volume). In order to simulate the survival and spatial distribution of early life stages of fish cohorts, it is important to take account of individual variability, since the eventual survivors tend to differ from average individuals at earlier stages (Crowder et al. 1992). Studies of early life history in fish have consequently been one of the topics where IBMs have been applied most extensively (Grimm 1999). Although the individual-based modelling approach was initiated in the late 1970s, it is only since the influential review of Huston et al. (1988) that it has been applied extensively in ecology. Still it has not been established whether or not IBMs give fundamentally different answers from the classical ecological models because very few paradigmatic studies have challenged the classic models (Grimm 1999). Nevertheless, IBMs provide a flexible tool for simulating individuals and populations.

In contrast to earlier reviews of IBMs (Huston et al. 1988; DeAngelis and Gross 1992; Grimm 1999), this chapter focuses on the use of individual-based modelling in fish ecology and fisheries science. Rather than providing a balanced review of what has been done using IBMs, we will present topics that modellers of fish populations might need to deal with and then provide some relevant examples for the particular fields. As a result of this we will not cover many replicate studies dealing with similar issues, but instead present a wider range of applications taking advantage of the individual-based approach. We start out with a presentation of the IBM concept, including development and evaluation, and provide some recipes for making different kinds of IBMs. Then we move on to a review of existing literature on IBMs.

11.2 SPECIFYING INDIVIDUALS IN IBMs

11.2.1 The attribute vector

Here we refer to IBMs as models that treat individuals as explicit entities, the so-called *i*-state configuration models (Caswell and John 1992). We will focus mostly on these models, but we will also discuss structured models that sometimes have been classified as IBMs (Caswell and John 1992). The *i*-state refers to individual features such as body weight, energy reserves and sex, while corresponding *p*-states represent the whole population such as population abundance and average *i*-states of the population. It can be fruitful to illustrate the concept of IBMs by using an attribute vector $\mathbf{A_i}$ (Chambers 1993), which contains all the states αm_i used to specify an individual i such as age, weight, sex, hormone levels and spatial coordinates (x_i, y_i, z_i) at time t:

$$\mathbf{A_i} = (\alpha 1_i, \alpha 2_i, \alpha 3_i, \ldots \alpha m_i, x_i, y_i, z_i, t). \tag{11.1}$$

The greater the attribute vector, the more differences between individuals can be specified within the model.

In structured models (Metz and Diekman 1986; Tuljapurkar and Caswell 1997), populations are divided into stages based on some key variable, for example age, which is commonly applied in, for example, the virtual population analysis of quantitative fisheries science. Using the attribute vector concept, one may describe structured models as:

$$\mathbf{A_j} = (s_j, n_j), \tag{11.2}$$

where s_j is stage j and n_j is the number of individuals of the population in stage j. The changes in $\mathbf{A_j}$ can then be projected using models such as Leslie matrix models or partial differential equations, which can be called *i*-state distribution models (Caswell and John 1992). In IBMs, each individual is specified independently, which means that the number term n_j of equation (11.2) is 1, and essentially removed from the attribute vector. However, even though the individual-based structure is appealing, it is virtually impossible to simulate even small fish stocks on a truly individual basis because of the great abundances involved. To allow the advantages of the individual-based approach and still be able to simulate large populations such as fish stocks, the super-individual approach was introduced (Scheffer et al. 1995). A super-individual represents many identical individuals and in this case the number of such identical siblings (n_s) thus becomes an attribute of the super-individual:

$$\mathbf{A_s} = (\alpha 1_s, \alpha 2_s, \alpha 3_s, \ldots \alpha m_s, x_s, y_s, z_s, n_s, t). \quad (11.3)$$

where $\mathbf{A_s}$ is the attribute vector of super-individual s. Mortality operates on the super-individual and the number of siblings of each super individual is thus decreased in proportion to the mortality rate (Scheffer et al. 1995). This is an efficient way of maintaining the individual-based structure, and still be able to simulate the large population sizes that occur in natural populations. When the n_s gets below a threshold value, the way the mortality rate operates can be changed to probabilistic mortality using Monte Carlo techniques (see below) for the remaining siblings. Populations with high mortality, such as fish populations, can effectively be simulated by replacing a dead super-individual through random resampling from the live portion of the population (Rose et al. 1993). The internal number n_s of the donor individual is then divided in two and the dead super-individual inherits the attributes of the donor. Thus one may keep the number of super-individuals constant while changing the number of individuals that actually are represented by each super-individual.

The aggregation in super-individuals has some obvious similarities with the structured models (Metz and Diekman 1986; Tuljapurkar and Caswell 1997). However, the structured population models are based on partial differential equations or Leslie matrices, while the super-individual approach still maintains the same structure and representation of processes as in the IBMs discussed above. In structured models all stages are usually assumed to experience the same environment and therefore to respond similarly (Caswell 1996). The super-individual approach is more flexible than the structured models (DeAngelis and Rose 1992), and allows a simple way of scaling IBMs to realistic fish stock abundances. Structured models and configuration models may differ in their applicability depending on the topic in question, but in cases where both approaches can be applied they tend to give similar predictions (DeAngelis et al. 1993).

11.2.2 The strategy vector

In addition to possessing states, real individuals have adaptive traits, such as life history and behavioural strategies that specify how they should live their life. The previous lack of IBM studies involving life-history strategies and behaviour of individuals could be due in part to a lack of appropriate techniques for implementing these features. However, adaptive traits can be modelled by introducing a strategy vector $\mathbf{S_i}$ that specifies the adaptive traits, such as life-history traits or behaviour, of an individual:

$$\mathbf{S_i} = (b1_i, b2_i, b3_i, \ldots, bm_i), \quad (11.4)$$

where bm_i is the adaptive trait m of individual i. The strategy vector may be considered as analogous to a biological chromosome as in the genetic algorithm (Holland 1975), but $\mathbf{S_i}$ may also be updated during the individual's life as a way to simulate learning. For example, this can be done using reinforcement learning (e.g. Ackley and Littman 1992) by allowing rewards for advantageous behaviours and punishments for unprofitable ones. This process allows the individual to produce increasingly more favourable behaviours as it learns about its environment. The combination of attribute vectors and strategy vectors thus enables most relevant characteristics of individuals to be implemented in IBMs.

11.3 FEATURES OF INDIVIDUAL-BASED MODELS

IBMs can be classified by the degree to which different factors such as bookkeeping (i.e. the

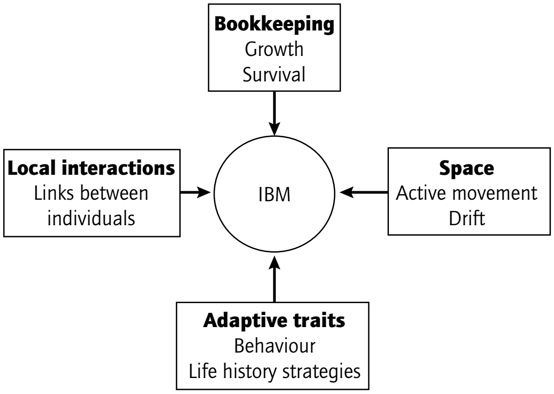

Fig. 11.1 Schematic classification of various types of IBMs. Most IBMs keep track of growth and survival of individuals in a population. Implementation of space allows a wider range of studies to be undertaken. A further increase in the complexity and flexibility of models to incorporate adaptive traits such as behaviour and life history strategies may further promote our understanding of how individuals relate to each other. The simulation of local interactions involves a high resolution both in spatial detail and behavioural actions.

continuous update of the attribute vector), space, adaptive traits and local interactions are specified in the model (Fig. 11.1). Depending on the nature and scale of the problem of interest one may develop a simple bookkeeping model, or complex models taking into account more aspects of individuals. All IBMs contain a bookkeeping procedure, but they need not contain the other features listed in Fig. 11.1. Another common feature of IBMs is to represent ecological processes by mechanistic models.

11.3.1 Mechanistic models

As opposed to empirically fitted models, mechanistic models aim at representing the actual process that is taking place in more detail. Thus instead of simply fitting growth rate as an empirical relationship of, for example, size, a mechanistic model of growth will address the various processes involved. These include encounters with prey (Mittelbach, Chapter 11, Volume 1), the ingestion process (Juanes et al., Chapter 12, Volume 1), and bioenergetics (Jobling, Chapter 5, Volume 1). Mechanistic models are used extensively in IBMs to represent individual processes such as perception, predator and prey encounters, and bioenergetics. These are indicated by bold squares in Fig. 11.2, which shows a flow chart for events related to feeding, growth and predation of fish larvae. In addition to these individual processes, the environment is also often represented through mechanistic models of features such as light and ocean circulation. For a thorough discussion of mechanistic models in fish biology see Giske et al. (1998) and Carlotti et al. (2000).

11.3.2 Bookkeeping

A central aspect of IBMs is the bookkeeping of individuals. As shown above, this is facilitated using the attribute vector. The entire population is tracked using an attribute matrix with dimensions equal to the number of attributes times the number of individuals in the population. All events that may occur in a period of a time step will be addressed sequentially in the IBM, as if they appeared one by one, and it may be important to analyse the processes in a particular sequence. While an organism may be eaten after it has starved to death, it may not starve after having been eaten. The conceptual framework for bookkeeping illustrated in Fig. 11.2 is characteristic of most IBMs, which deal with growth and survival of fish. Monte Carlo simulations are continuously used to decide the outcome of feeding and mortality processes.

11.3.3 Monte Carlo simulations

Monte Carlo simulations are often applied in IBMs, but this approach is rarely well defined. In general, Monte Carlo techniques involve drawing random numbers from some probability distribution, in a way similar to gambling situations from which the name derives. The usual way to apply this concept in IBMs is to assume a probability for some event and then draw a number from a random-number generator to determine

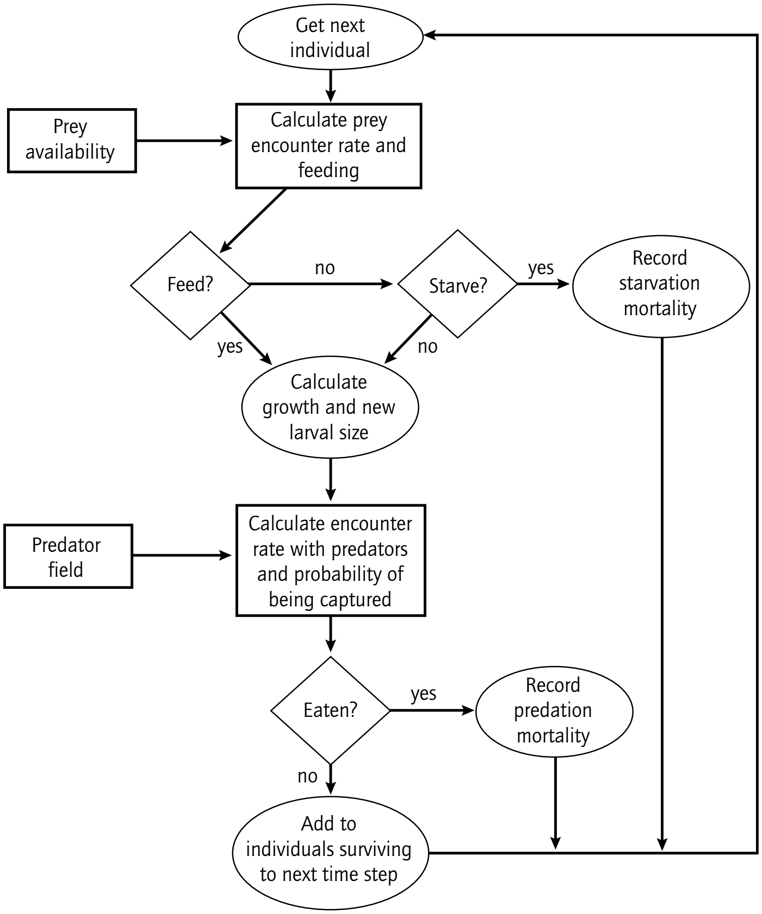

Fig. 11.2 A conceptual model of a sequential representation of events related to growth and survival of fish larvae. The same sequence of events must be repeated for every individual in the population, before starting again with the first individual in the next time step. Bold squares indicate where mechanistic models are applied and ovals indicate where bookkeeping is performed. (Modified from Crowder et al. 1992.)

the outcome (Judson 1994). For example, one might imagine a certain probability that an individual dies during a time step. A random number is then drawn, and if the random number is smaller than the mortality risk, the individual dies. Given that the random numbers are uniformly distributed, the probability of drawing a number within an interval is equal to the size of the interval. If the mortality risk is 0.1, there is a 10% probability that the random number will be between 0 and 0.1, and a similar probability of dying. This can be carried out to determine whether an individual survives, eats food or obtains mating and so forth.

11.3.4 Spatial detail

Traditional ecological models specify space as a homogenous well-mixed compartment (Fig. 11.3). In metapopulation models, space is implemented as habitable patches surrounded by non-habitable areas (Levins 1969). Metapopulation models have been applied to some problems in fisheries science, for example to explain population structuring in herring stocks (McQuinn 1997). A still finer spatial resolution is to arrange space in two- or three-dimensional grids where essentially any spatial scale can be represented (Fig. 11.3). IBMs can be used in all these spatial arrangements.

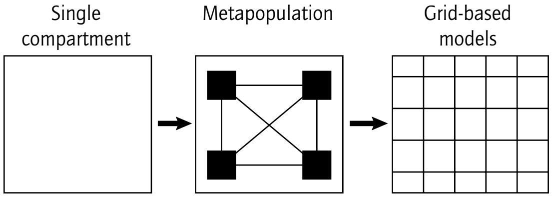

Fig. 11.3 Different ways of representing spatial detail in models. The complexity in spatial representation increases in the direction of the arrows.

Table 11.1 Pseudo-code for implementing spatial detail in studies of larval fish.

```
1 Create current vector from a hydrodynamic model.
2 Add component of active individual movement.
3 Integrate velocity vector over the duration of the time step to
  produce individual trajectories.
4 Find temperature, food concentration, light intensity, predator
  density, etc. along trajectory.
5 Estimate food encounter rate, predation risk, bioenergetics etc.
6 Find state (spatial position, physiological state,
  alive/starved/eaten) of organism at the end of time step.
```

The development of IBMs has made it possible to implement space in ecological models in a more realistic manner than structured models allow. Grid models have been extensively applied in fisheries science for studies of the distribution of eggs and larvae (Bartsch et al. 1989; Werner et al. 1996). An example of how such models are set up is provided below.

Recipe for simulating drift of larval fish

The flow chart in Fig. 11.2 does not contain any decisions made by the organism. This situation may be relevant for the planktonic larval stages. Spatial positioning of fish during this life stage is determined by their buoyancy, the turbulence of the environment and the advective transport of water. In lakes, however, the impact of advective forces is much smaller than in the sea and in rivers, where larval drift is an integrated part of the life cycle of many fishes. Although assuming a spatially homogenous compartment may be a reasonable simplification for some lakes, it is generally not so for ocean systems.

Models for marine fishes have therefore increasingly been developed to incorporate advective fields and temperature data from ocean circulation models (Bartsch et al. 1989; Werner et al. 1996). These models are grid based with a resolution typically of 1–20 km. Physical ocean circulation models provide current velocity vectors for each grid cell at each time step. These vectors are used to move individuals (or 'particles', representing drifting biological organisms) about (e.g. Werner et al. 1996; Lynch et al. 1998; Asplin et al. 1999). The drift path may also be impacted by swimming of the larvae, which is then added to the physical vector (Bartsch et al. 1989; Bartsch and Knust 1994). Once the drift path of a larva is found, the temperature, food, light intensity etc. along this path can also be estimated (Table 11.1). A more thorough description of this coupling is given by Carlotti et al. (2000).

11.3.5 *Adaptive traits*

As mentioned above, the strategy vector $\mathbf{S}_i$ can be used to specify the adaptive traits of an individual. In some studies IBMs are simply tailored to match the life history of target species (e.g. van Winkle et al. 1993), in which case behaviour is not specified explicitly in the model, but the consequences of certain behavioural strategies for growth and mortality may still be simulated. In other cases, finding the best behavioural trait is part of the modelling exercise itself. We mainly discuss behaviour below, but life-history strategies can often be implemented in the same manner. In general three approaches prevail for specifying behaviour in IBMs: rule-based approaches, optimization, and adaptation.

Rule-based approaches

Even though rules may be chosen based on their evolutionary profitability, the essential part of the rule-based approach is that the rules are provided by the modeller and that behaviour results directly from the specified rule. One example of a behavioural rule is random walk, which simply is to move individuals about in a random fashion with equal probability of going in each direction at each time step. Such a simple behavioural procedure resembles a natural situation in many cases of local searching in animals (Berg 1993). Other rule-based concepts specified in models are the use of taxis and kinesis, which specify reactions to stimuli by orientating relative to stimuli position or responding in proportion to stimuli intensity respectively (Tyler and Rose 1994).

Optimization

The second approach to modelling behaviour is generally referred to as the 'optimization approach' (Parker and Maynard Smith 1990). This approach underlies many of the discussions of fish behaviour in Volume 1, as exemplified by Mittelbach's discussions of foraging theory in Chapter 11, Volume 1. The optimization approach in behavioural ecology is ultimate, based directly on the survival value of behavioural traits. Stochastic dynamic programming (SDP) (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000), where the entire solution space is sought and the best solution is chosen, is an example of the optimization approach. SDP relates to states rather than individuals and the optimal strategy is calculated for each state (for example, weight or energy level) at each time step in a backward iteration. This allows state variability and state-specific behaviour to emerge. Once the backward iteration procedure is complete, an IBM can be used to simulate individual trajectories from the start to the horizon of the model. SDP models may use Monte Carlo simulations for determining growth and reproduction, which makes this approach individual-based (Clark and Mangel 2000). Traditionally, population growth rates such as the instantaneous rate of increase r or the lifetime reproductive success R_0 have been applied as fitness measures in optimization models (Roff 1992; Hutchings, Chapter 7, Volume 1). These measures are well suited for situations where the entire lifespan of the animal is considered. However, it is more difficult to assess the profitability of behaviours at an instant. Solutions to this problem can be achieved using 'rules of thumb' that are generated as predictions from evolutionary ecology, such as the ideal free distribution (Fretwell and Lucas 1970), the marginal value theorem (Charnov 1976) and Gilliam's rule (Werner and Gilliam 1984). These concepts are applied to foraging and to habitat choice by Mittelbach (Chapter 11, Volume 1). Given the assumptions, these approaches will provide optimal solutions to the respective behavioural problems.

Adaptation

Adaptive models find 'good' behavioural strategies by using gradual improvements in behaviour through simulated evolution or learning. When simulating evolution, the behavioural strategies are coded numerically on the strategy vector (equation 11.4) and passed on from parents to offspring. This technique is known as the genetic algorithm (GA) (Holland 1975). In the GA a specific measure of fitness such as R_0 can be used to determine which strategy vectors and hence which individuals are the best, and these become parents for the new generation. Variability in the new strategy vectors are provided through recombinations among parents, and mutations (Holland 1975). As mentioned above, reinforcement learning can be used to update behaviours within the lifetime of the individual (Ackley and Littman 1992). This approach can also be used in combination with evolved strategies (Ackley and Littman 1992). When the environment changes markedly on a short time-scale, for example within generations, it can be profitable to allow adaptation through learning. In an artificial neural network (ANN) model this would mean that the weights are changed within the life of individuals, and not only between different generations. Artificial neural networks (ANNs) apply neurobiological principles of synaptic brain activity to perform systematic output by differential weighting of input variables (Rummelhart et al. 1986).

Table 11.2 Recipe for incorporating behaviour and spatial detail in an IBM of a planktivorous fish. The pseudo-code illustrates how the model is executed in a sequential manner, using a programming language such as FORTRAN.

```
1 Initiate attribute and strategy vectors for each individual
2 Year loop
      Create physical environment for the entire year: light,
          temperature, currents
      Initiate food and predator distribution
3 Day loop
      Update distribution and abundance of food, competitors and
          predators
4 Individual loop
      Perform behavioural actions
      Determine growth and mortality
      Update abundance of food items after feeding
      Reproduce if criteria are fulfilled
```

An alternative approach for evolving behaviour in models is to use so-called emergent (endogenous) fitness, which means that individuals with strategy vectors live and reproduce in an evolving population (Strand et al. in press). Thus rather than maximizing a specific fitness measure, those individuals who manage to pass on their own strategies by reproducing with other individuals in the population will be the most fit. However, the degree to which this reflects a natural system depends upon the way the environment is specified in the particular model system. For applications of adaptive models in ecology see below and Huse and Giske (1998), Huse et al. (1999), and Strand et al. (in press).

Recipe for adaptive models with a strategy vector

IBMs containing both spatial detail and behaviour are generally very complex, since they often involve a range of mechanistic models for specifying temperature, drift, feeding and behaviour. The following recipe describes the conceptual flow of a model containing both attribute and strategy vectors and spatial detail. It is based on the model of Huse (1998) and Huse and Giske (1998), where fish behaviour and life history strategies for a planktivorous fish are adapted over many consecutive generations (Table 11.2).

1 The attribute and strategy vectors are initialized for each individual in the population. While the attribute vectors are set to 'common' values, the strategy vectors are initiated randomly within certain intervals. The attribute vector is specified as: $\mathbf{A}_\mathbf{i}$(age, weight, energy level, position), and the corresponding strategy vector is: $\mathbf{S}_\mathbf{i}$(timing of spawning, spawning location, energy allocation rule, size at maturity, movement). Movement behaviour is determined using an ANN and its weights are implemented in the strategy vector.

2 At the start of the year the environment for the coming year is established. As in the previous recipe, temperature and current fields are produced by an ocean circulation model. The predator abundance is assumed to increase linearly with increasing temperature. The food distribution is initiated and is consistently updated below.

3 The day loop runs over each day of the year, and, most importantly, the food distribution is updated according to the production and import from advective transport provided by the physical model.

4 In the individual loop most of the biological features of the IBM are implemented. The first task is to infer mortality. Since the model uses the super-individual approach, a proportion of the number of clones is removed according to the predation risk at the present location. In the same fashion one may include removal of fish caused by fishing mortality. Food intake is determined from local encounters with food, and growth is then calculated using the bioenergetic model of Hewett and Johnson (1992). For adults, surplus energy is divided among growth and reproduction according to the individual allocation strategy. Juveniles, on the other hand, are assumed to put all their energy into growth. At an individually specified spawning time and location, individuals may reproduce given that certain criteria are fulfilled. The new individuals inherit behavioural and life history strategies from their parents by recombination with a probability for mutations, to mimic biological reproduction. These are essential parts of the genetic algorithm. At the end of the individual loop, movement is determined using the ocean drift for the planktonic larvae (see recipe above) or the ANN for fish above a certain size. The ANN calculates movement from information about the local abundance of predators, growth, temperature and position.

These points make up the basic structure of a spatial life-history model of fish. The model is run for a large number of years (300–500) and generates life-history and migration strategies that resemble observed migration patterns (Huse 1998). Although the example is for capelin migrations in the Barents Sea, the model approach is general and can be applied to virtually any fish stock. It has also been applied successfully for simulating vertical migration in mesopelagic fish (Huse et al. 1999; Strand et al. in press).

What is the best modelling approach?

What type of model is 'best' for implementing adaptive traits, or which one of these techniques should one use? The answer is, as often – 'it depends'. For a full discussion of individual-based techniques see Tyler and Rose (1994) and Giske et al. (1998). Some general recommendations emerge from the discussion above. In terms of specification of adaptive traits in IBMs, the strategy vector and the adaptation concept is appealing in many ways. The advantage of this concept is its generality because it can encompass most ecological processes including density dependence, state dependence and stochastic environments (Huse et al. 1999; Strand et al. in press). Furthermore, when using ANNs it is possible to simulate behaviour from stimuli, thereby allowing the use of conventional behavioural terminology and perspective. The downside of the adaptive approach is that it is impossible to know whether the optimal solution is found unless this is calculated by other means. This is, however, ensured using optimality models such as SDP, which is one of the great advantages of that approach. Another advantage of SDP is the ability of this technique to include individual state and time constraints in the optimization criterion. A conclusion can therefore be that if the biological question involves state dependence or making sure that the optimal strategy is found, then SDP should be used. On the other hand, if the study involves problems that have high dimensionality and/or include stochasticity or density dependencies, then the adaptive models will be the best approach. If one is interested in how large-scale patterns and/or complex phenomena emerge from individual behaviour, it can be productive to apply simple behavioural rules.

11.3.6 Local interactions

In some cases, for example in fish schooling (Reynolds 1987; Vabø and Nøttestad 1997; Stöcker 1999), behaviour is dependent mainly upon what conspecifics and predators in the vicinity are doing. A simple modelling approach that takes local interactions into account is cellular automata (for review see Phipps 1992). Under this approach, the modeller defines strict rules that are similar for each individual cell in a lattice. The rules then specify how the automata change state according to the state of their surrounding cells. The emerging pattern of the lattice then results from the local interactions among the automata.

11.4 FORMULATING AND TESTING IBMS

11.4.1 Model formulation

Since IBMs typically are built from an extensive set of submodels, there are many things that can go wrong during model formulation. It is therefore important to develop a common framework for putting together IBMs. Railsback (2001) provides six points that should be considered when formulating an IBM: (1) Emergence: what processes should be imposed by empirical relations and what should emerge from mechanistic representations? (2) Adaptive traits: what kind of adaptive processes should be included in the model? This point has to be related to the spatial scale and the major questions being addressed. (3) Fitness measure: what is the appropriate fitness measure for the adaptive traits of the model? (4) State-based dynamics: how should decision processes depend on individual state? (5) Prediction: what are realistic assumptions about how animals predict the consequences of decisions? (6) Computer implementation: what user interface is necessary for implementing, validating and testing IBMs? In addition to these points it is important to provide results that can be tested against observations. Although testing against real data is not always necessary, since models may provide valuable insight through sensitivity analyses, it is most often an advantage in model development. The points shown above are important to keep in mind when constructing an IBM, and we shall return to some of these as we go along. Other things to keep in mind when formulating a model are that the choice of complexity and model structure should be based on the level of understanding of the environmental and biological processes operating. Lastly a model is at best a highly simplified but biased representation of nature, and uncertainty can be reduced by attacking the problem with several models that differ in assumptions and structure (see also Sparre and Hart, Chapter 13, this volume).

11.4.2 Evaluation of IBMs

Model evaluation is an important part of model development, and for full descriptions of this process see Jørgensen (1988) and Bart (1995). The evaluation process can be divided into verification and validation (Jørgensen 1988). Verification is the process of checking that the internal logic of the computer model is correct and that the model actually does what it is intended to do. This process is performed continuously as a model is developed. Validation, on the other hand, aims at determining the ability of the model in describing observed phenomena. This process can be divided further into checking the validity of: parameter values, and secondary and primary model predictions (Bart 1995). The validity of parameter values is traditionally tested through a sensitivity analysis. Sensitivity analyses involve varying parameter values and studying the effect on model output. For IBMs, which usually have a great number of parameters, it is simply not feasible to test the sensitivity of all these. Rather some 'key' parameters should be chosen for testing. Since IBMs tend to be composed of submodels, many features of an IBM can be tested. This is what is referred to as secondary model predictions. With regard to a fish model this can be, for example, testing the performance of a bioenergetic model used, even though the primary aim of the model is to provide population dynamics of a target species. The primary and secondary model predictions can then be tested independently of each other. A consequence of model evaluation is either to accept the model's performance or, alternatively, to try to revise parts of the model that produce erroneous predictions. One should, however, be careful not to make the model fit observations by changing parameter values or submodels uncritically. This is especially important for IBMs, which typically simulate processes in a mechanistic manner using a large number of parameter values.

When it comes to software implementation, any kind of programming language can be used, but object-orientated languages such as C++ are especially well suited for constructing IBMs (Maley and Caswell 1992). In addition to providing a nice structured programming with individuals as the basic units, these languages generally also provide good visualization opportunities. For example, the object-orientated Swarm package (Langton et al. 1999) is tailored for individual-based simulations and provides a number of features for visualization of results and bookkeeping of individuals and processes. Using Swarm, several aspects of the model may be monitored during development and evaluation. Swarm, which is a shareware product, is currently available for the Objective C and Java languages. Another software package especially developed for individual-based simulations is ECOSIM (Lorek and Sonnenschein 1998). This is not the same as the Ecosim discussed by Pauly and Christensen (Chapter 10, this volume).

11.5 REVIEW OF INDIVIDUAL-BASED MODELS IN FISHERIES BIOLOGY

The ontogenetic development in fishes from eggs to maturity typically involves manyfold increases in body size associated with discrete changes in morphology and increased behavioural repertoires. The way individuals vary therefore changes

Table 11.3 Features characterizing different aspects of the early life history of fish.

What characterizes . . .	Variables	References
the survivors?	egg quality	Kjesbu et al. (1991)
	birth date	Schultz (1993)
	birth position	Berntsen et al. (1994); Slotte and Fiksen (2000)
	egg size	Knutsen and Tilseth (1985)
	development	Blaxter (1986)
	prey encounter	Fiksen and Folkvord (1999)
	bioenergetics	Crowder et al. (1992); Fiksen and Folkvord (1999)
the environment?	food concentration	Cushing (1990); (1996)
	small-scale turbulence	Sundby and Fossum (1990); MacKenzie et al. (1994)
	water	Bartsch et al. (1989); Berntsen et al. *(*1994);
	transportation	Hermann et al. (1996)
	ocean climate	Cushing (1996); Anderson and Piatt (1999)
	light	Miner and Stein (1993); Fiksen et al. (1998)
	turbidity	Chesney (1989); Fortier et al. (1996)
	temperature	Houde (1989); (1997)
	predators	McGurk (1986); Bailey and Houde (1989); Cowan et al. (1996)

through the life cycle. This suggests that modelling should focus on different aspects of life at different times of the life cycle, and that each ontogenetic stage might be specified differently. For example, in the period of change from intrinsic to extrinsic energy uptake, each prey caught by a larval fish is very important, which makes food gathering a vital process to simulate in models. During overwintering or spawning, on the other hand, feeding will be a virtually unimportant activity. In the following we will review studies using IBMs in fish biology by using the structure of Fig. 11.1. Hence we initially discuss relatively simple models, and then add features to the IBMs as we go along. The first paragraph therefore focuses on growth and survival in early life-history studies, whereas the later paragraphs discuss studies of greater relevance to older life stages.

11.5.1 Models of growth and survival

For most, if not all, fish species, mortality at the egg and early larval stages is enormous compared to later in life. Therefore, as early as 1914, Hjort considered recruitment variation as a major research area in fisheries science (Myers, Chapter 6, Volume 1). Recruitment variation may be caused by factors related to the state of the organism, its environment or its parents (Table 11.3; see Myers, Chapter 6, Volume 1). IBMs allow a mechanistic representation of ecological processes, and consequently such models have been applied extensively in studying growth and survival of young-of-the-year fish (see review by van Winkle et al. 1993). Beyer and Laurence (1980) recognized the importance of initial chance events in feeding of larval winter flounder. Since prey ingestion can be described as a Poisson process, some individuals will initially have success and capture prey while others have poor fate. Given that the ability to obtain food is size dependent (Juanes et al., Chapter 12, Volume 1), there will be a positive feedback so that initially successful individuals will grow faster than the others and thus have a higher survival probability. Such scenarios are well represented in IBMs (Beyer and Laurence 1980).

The important survival factors for eggs and larvae are prey and predator encounters, bioener-

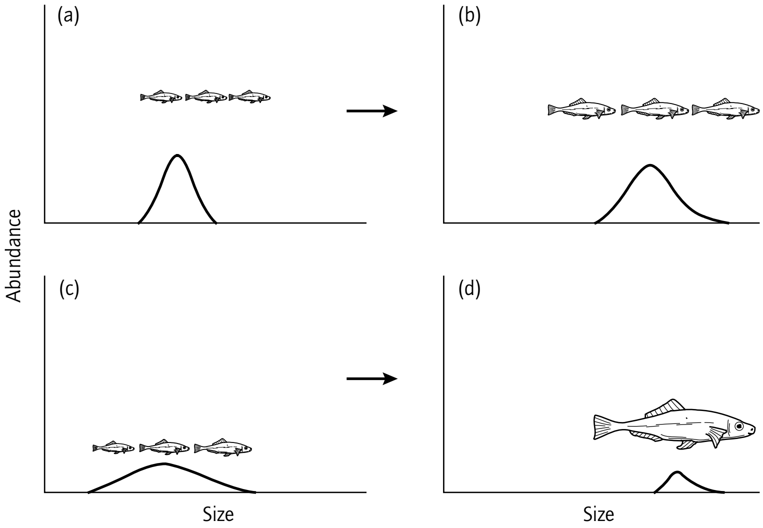

Fig. 11.4 The effect of initial variation in size distribution on the outcome of cannibalistic interactions. Low initial variance **(a)** produces a cohort with homogeneous individuals at a later stage **(b)**, while with a high initial variance **(c)** the biggest individuals get cannibalistic **(d)**. (From Huston et al. 1988; reproduced by permission of BioScience.)

getics and organismal development. With so many factors interacting, modelling is essential in understanding how this affects individuals and populations (Houde 1997). And since egg and larval mortality are high, models of survival should be able to focus on the lucky or clever few. The important decision variables are mainly governed by parent behaviour through choice of spawning site and time, anatomical properties such an egg size and energy density, and by developmental 'programme' displayed through the sequence of organ development (Jobling, Chapter 5, Volume 1). A range of ecological conditions will bring stochasticity to all these variables (Table 11.3). The reliability of predictions from a complex recruitment model will depend on how well these processes are represented mechanistically (Fiksen and Folkvord 1999). In a classic study, DeAngelis et al. (1979) modelled the growth of young-of-the-year largemouth bass. They found that the initial variance in the cohort was important for its development and for whether cannibalism was possible or not. In the case of low initial variance, shown by an even size distribution (Fig. 11.4a), the fish remained homogeneous with none growing big enough to eat the others (Fig. 11.4b). With large initial variance (Fig. 11.4c), however, the individuals that had largest initial size were able to become cannibalistic and eat the smaller fish, which the model run predicted to lead to survival of few but large individuals (Fig. 11.4d). It was demonstrated that the individual variability is clearly important for cohort development even though the initial average weight was the same in the two cases. The model presented by Fiksen and Folkvord (1999) provides a state-of-the-art mechanistic description of the feeding process taking into account environmental features such as small-scale turbulence, light, turbidity, temperature, prey density and size structure. Alongside the model development there has been experimental work used for generating parameter values and testing of model predictions. The great detail of the mechanistic description enables this model to make more realistic predictions than models with simpler environmental description.

11.5.2 Models with adaptive traits

The simplest behavioural models are those without spatial detail. There have been some studies addressing how spawning strategies are affected by seasonal variation in temperature, growth and predation risk. Trebitz (1991) used an IBM to find the best timing and temperature for spawning with and without density dependence. Initially the spawning temperature was given randomly, but subsequent spawning strategies (temperature) were given in proportion to the survival of the strategies (individuals) until age 1. The biomass of each temperature strategy at age 1 was therefore used as a measure of strategy performance. Density-independent and density-dependent model runs predicted different optimal spawning temperatures, with a broad peak at intermediate temperatures for the density-independent situation and an almost temperature-independent profitability for the density-dependent case. This model is in many ways similar to the genetic algorithm discussed above.

11.5.3 Simple spatial systems

Natural systems are very complex. It may therefore be profitable to conduct simulation experiments, which is a computer analogy to laboratory or field experiments, in which focus can be put on a specific research topic without necessarily defining a particular natural system. A simulation experiment is especially fruitful early in theoretical developments or if the problem is general rather than linked to a specific population or environment. Tyler and Rose (1997) studied cohort consequences of different habitat choice rules in a simple spatial system using life-history-based criteria such as Gilliam's rule. Their results suggest that habitat choice rules have strong effects on cohort survivorship and that no single departure rule can be an evolutionarily stable strategy. They therefore concluded that the use of static life-history rules is not an appropriate way to model behaviour in a dynamic environment, as confirmed elsewhere (Railsback et al. 1999). Tyler and Rose (1997) also found that density-dependent effects on juvenile survival can be much greater in spatially explicit models with fitness-based habitat choice than in spatially homogeneous models. SeaLab (LePage and Cury 1997) is a spatial simulator that can be used to test hypotheses about fish reproduction and space use. This model divides space into hexagonal structures, and individuals may choose in which cell to stay and/or reproduce. LePage and Cury (1997) used SeaLab to simulate how reproductive strategies depended on the degree of variation in variable environments. An obstinate strategy, where spawning is performed under the same conditions as the individual is born, and an opportunistic strategy where individuals spawn under novel environmental conditions, were investigated. For extreme environmental variation, only populations with both the opportunistic and obstinate strategies survived. The authors discuss the results with regard to straying in natural populations. A similar artificial environment was applied by Anneville et al. (1998), who explored the effect of density-dependent recruitment relationships using rule-based movement in an hexagonal lattice. Their main conclusion was that local density dependence was often not detectable at large spatial scales, which stresses the importance of being explicit about scale when analysing ecological processes (Levin 1992).

11.5.4 Models of fish distribution

Spatially explicit IBMs incorporate spatial heterogeneity, individual variability and individual movement (Tyler and Rose 1994). Although such models are complicated and necessarily consist of many modules, they provide the potential for highly realistic simulations of fish populations. Many fishes undertake extensive horizontal migrations between feeding, spawning and overwintering areas (Metcalfe et al., Chapter 8, Volume 1). Such migrations involve complex interactions between individuals and the environment that are generally not well understood. Tagging experiments have provided first-hand information about the distribution of migratory fish stocks, and lately telemetric tags have enabled real-time observations of fish movements in the sea (Metcalfe and Arnold 1997; Metcalfe et al., Chapter 8, Volume 1). However, it is difficult to understand the mechanisms controlling the movement of fish just from observations, and model simulations are therefore an important part of exploring the proximate and ultimate processes involved in fish migrations.

Although there is likely to be some common features among fish stocks in how they move horizontally, local adaptation will be important, and it may not be trivial to transfer knowledge about the migration of one stock to other stocks. In the case of vertical migration, however, there may be more common features due to the pronounced vertical gradients and diurnal changes in light that strongly influence visual feeding and predation risk.

Larval drift was among the first topics where spatially explicit IBMs were applied. Werner et al. (1996) considered trophodynamics and ocean circulation in a study of cod larvae on Georges Bank by providing drift and growth trajectories of individuals. They concluded that the region of highest retention coincided with the region of highest growth, illustrating the complementary interaction between trophodynamics and circulation processes. In a similar model of walleye pollock (*Theragra chalcogramma*), Hinckley et al. (1996) found that the inclusion of mechanisms that determine the depth positioning of the drifting larvae are important for determining the direction of horizontal advection.

Through a combination of simple decision rules and a library of surface currents, Walter et al. (1997) modelled sockeye salmon (*Onchorhynchus nerka*) movement in the Northeast Pacific Ocean. Movement was simulated based on random walk, with directed swimming at certain times of the year. Their simple rules for compass bearing predict migration patterns that challenge prevailing complex models of sockeye migration. The most striking result was that inter-annual variation in the surface current led to great changes in the distribution of the salmon given that the same movement rules apply each year. The rule-based approach used by Walter et al. (1997) does not take into account that individual differences in state can cause differences in behaviour. State-dependent habitat choice was considered by Fiksen et al. (1995), who used a stochastic dynamic programming (SDP) to simulate the horizontal distribution of the Barents Sea capelin (*Mallotus villosus*). The model was based on prior simulation results, which specify the physical environment of the Barents Sea, and assumed distributions of predators and prey. By using a time step of one month, the optimal habitat for each state (body weight) was calculated using the SDP equations with lifetime reproductive success as a fitness criterion. The model results compared favourably with the observed distribution of the Barents Sea capelin. In contrast to Walter et al. (1997), Fiksen et al. (1995) assumed that the individual capelin actively made habitat choices to maximize their Darwinian fitness. Huse and Giske (1998) and Huse (1998) used a similar environmental description as Fiksen et al. (1995) to simulate movement of the Barents Sea capelin using an adaptive model with a strategy vector (equation 11.4) containing the weights of an artificial neural network and several life-history traits. Similarly to Fiksen et al. (1995), they assumed that the capelin is adapted to the environment of the Barents Sea. However, rather than assuming optimal habitat choices, an adaptive process over many hundreds of generations was simulated using emergent fitness (see above). The model was applied to study evolution of spawning areas, and it predicted, in accordance with field observations, capelin spawning to occur along the coast of Northern Norway. ANN-based models may rely on proximate sensor information, and at the same time the weights of the ANN are adapted using ultimate forces. In this way ANN models provide a link between proximate and ultimate factors in behavioural ecology. ANNs have also been applied to study tropical tuna (*Katsuwonus pelamis* and *Thunnus albacares*) migrations between the Mozambique Channel and the Seychelles using temperature data gathered by remote sensing (Dagorn et al. 1997). In this case the tuna was assumed to search for areas of low temperature, which are often associated with food-rich frontal zones. The ANN was used to determine which movement action the artificial tuna should make based on information about the temperature map within the daily search radius. The fitness criterion used in the GA for training the ANN was to minimize the distance to the observed arrival point near the Seychelles. As a result of the adaptive process, the simulated tuna eventually managed to get from the starting point in the Mozambique Channel to the Seychelles. In this model the tuna is assumed only to consider foraging potential when making habitat choices and not to consider predation, as in the two studies on capelin mentioned above. Nevertheless, because adult tuna are large they tend to have a low risk of predation compared with smaller fish, and foraging is therefore the key aspect of tuna migrations outside the spawning season.

11.5.5 Local interactions: schooling

Schooling consists of behaviours where coordination between individuals is important. As different from more loosely organized shoals, schools are defined as compact, coordinated and polarized collections of fish (Pitcher and Parrish 1993; Krause et al., Chapter 13, Volume 1). Schooling is a characteristic phenomenon of many fishes, explained mainly as a behavioural feature for predatory defence, but it also acts as a collective mechanism for coordinating migration and reproduction (Pitcher and Parrish 1993). Even though the ultimate causes of schooling are well known, the sensory and behavioural mechanisms involved in coordination and control of schooling remain largely unresolved. Schooling relies on the coordinated movement of individuals, and school models are usually based on the assumption that individuals follow similar behavioural rules, as opposed to most IBMs which allow individual variability. Reynolds (1987) simulated general flocking behaviour, which includes schooling, in a seminal paper on collective behaviour. He showed that by using three simple individual rules, including matching of the movement vector of neighbours, staying close to others, and avoiding contact with other individuals and obstacles, flocking behaviour that resembles observations of birds could be recreated. Vabø and Nøttestad (1997) used a similar rule-based IBM to simulate the behaviour of herring schools (*Clupea harengus*) when attacked by a killer whale (*Orcinus orca*). The model was able to recreate most of the avoidance manoeuvres seen in herring, and the results thus suggest that herring may use simple rules to coordinate their behaviour during predator attacks.

Stöcker (1999) used cellular automata to study energetic aspects of schooling. The results were discussed with regard to tuna, for which saving energy is believed to be an important motivation for school formation. The model predicts school break-ups due to oxygen depletion, and can thus be used to estimate maximum school sizes for tuna. Both Vabø and Nøttestad (1997) and Stöcker (1999) assumed identical rules for each individual. Romey (1996), on the other hand, in another schooling model showed that individuals with biased behaviour compared with the remaining group had a large influence on school behaviour. The degree to which individual differences in behaviour impacts school dynamics may be a function of school size, with a greater impact of individual variability in small schools. The cellular automata technique is well suited for simulating the dynamics of schools with similar individual behaviour, but the IBM models developed by Reynolds (1987) and Vabø and Nøttestad (1997) are more applicable than cellular automata if individual differences in behaviour are believed to be important. For a general discussion of predictions made by cellular automata and a conventional IBM respectively see Lett et al. (1999).

11.5.6 Responsive environments and natural stock sizes

Most of the models above describe individuals in non-responsive environments. This means that individuals are not assumed to impact on their environment, which is unrealistic when density dependence is important. Huse and Giske (1998) applied the super-individual approach to model long-distance migration of the Barents Sea capelin. The number of super-individuals was limited to a maximum of 15 000, and at birth each super-individual represented one million identical siblings. Depletion of zooplankton from feeding and consequent relocation is important for understanding capelin distribution dynamics (Hassel et al. 1991), and by using this approach it was possible to simulate realistic stock sizes of capelin while incorporating trophic feedback. The model predicts that fish should be more dispersed in model runs with trophic feedback compared to those where food was not removed as a result of feeding by the fish, and hence illustrates the importance of including trophic feedback even at large spatial scales.

11.5.7 Applications of IBMs in fisheries assessment

While structured models, such as the virtual population analysis and related approaches, are common in fisheries assessment, IBMs have not been used for this purpose to any degree. Most applications of IBMs have focused on ecological questions of general interest with the aim of exploring how individual variability in state and strategies influence the dynamics at the population level. Improved understanding of the causes of temporal and spatial variation in mortality, growth and recruitment, but also of migration and distribution patterns, has been achieved. Along with the ongoing increase in computing power, new possibilities for individual-based approaches to management problems of fish populations can be possible. In order for IBMs to be used for management purposes it will be essential that the IBMs are robust and reliable with regard to structural assumptions, parameter values, primary and secondary model predictions (Bart 1995). These factors reflect the general recommendations for formulating and evaluating IBMs as discussed above. IBMs have been applied to some degree in combination with bioenergetics models for management purposes (Hansen et al. 1993). IBMs can also be fruitful for management purposes in at least four other areas: (1) in predicting stock recruitment, (2) predicting the response of different exploitation patterns on the stock, (3) by facilitating the abundance estimation process and (4) through estimating stock prognoses in spatially explicit models.

Detailed IBMs (e.g. Fiksen and Folkvord 1999) can be used to elucidate which processes control recruitment to a target stock. For example, it may be profitable to use models that simulate both the dynamics of the parents as well as those of the recruiting larvae. Such models potentially may yield early forecasts of stock recruitment, which is part of the management process.

Since different age and size groups of fish often exhibit different behaviours, spatial dynamics and reproductive capabilities, they impact the stock dynamics in different ways. How fishing effort is distributed over the different size groups and spatial areas may thus affect the population response to harvest (Sparre and Hart, Chapter 13, this volume). IBMs are well suited to simulate the effects that management decisions can have both on population dynamics in the short run and on evolutionary dynamics in the longer run (Martinez-Garmendia 1998).

IBMs can also be used in fisheries assessment to facilitate the abundance estimation process, often performed by acoustics, sampling, or a combination of these. One potential application of IBMs is to predict distribution patterns of fish populations in the ocean given a certain environmental regime, which can allow improved temporal and spatial survey coverage. IBMs can also be applied to take into account the behavioural response of fish to survey vessels and sampling equipment. Diving behaviour and changes in tilt of fish can strongly impact on its echo-reflecting properties from the swim bladder of the fish (Huse and Ona 1996; Brix, Chapter 4, Volume 1), and hence impact on the acoustic estimate obtained. If such behaviours can be predicted and corrected for, the quality of acoustic estimates may be improved. This can be approached using ANNs, where observations of fish behaviour can be used to train the network. By presenting many sets of observed behaviours and relation to the vessel such as angle, depth and distance, the network can be trained using these observations to generalize responses of fish to vessel presence. The response to trawls and other sampling equipment can be simulated in a similar fashion.

IBMs can also be used to predict population dynamics of stocks through spatially explicit models covering the entire target stock. Such models have not made an impact on stock assessment. However, it can be a potential future application area of IBMs, and the modelling approaches of Fiksen et al. (1995) and Huse and Giske (1998) are attempts to move in this direction.

11.6 CONCLUSIONS

Even though IBMs are yet to have made an impact on fisheries management, the modelling technique has become especially popular among fish biologists (Grimm 1999). The reason for this popularity is partly historical, as some of the first applications of IBMs (DeAngelis et al. 1979; Beyer and Laurence 1980), were in fish biology. But as important is the great interest in explaining the observed recruitment variability seen in most fish species (Grimm 1999). IBMs are particularly useful for studying recruitment variability, but in addition the approach allows features such as behaviour and life histories to be studied as discussed above. IBM predictions are generally easy to compare with individual observations, which is another advantage of the approach. The use of super-individuals (Scheffer et al. 1995) allows simulation of realistic fish stock abundances while maintaining an individual-based modelling structure. IBMs are often very complex and composed by many submodels. Model evaluation is therefore very important, and preferably both primary and secondary model predictions should be validated (Bart 1995). Whether or not IBMs really give different answers to ecological problems than do the traditional state-variable models remains to be seen, but nevertheless, IBMs provide modellers with a highly flexible tool for studying individuals and populations.

ACKNOWLEDGEMENTS

We thank Steve Railsback and David Kirby for fruitful comments on an earlier draft of this chapter. Anne Gro Vea Salvanes and Geir Huse were supported by the Research Council of Norway.

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12 The Economics of Fisheries

RÖGNVALDUR HANNESSON

12.1 INTRODUCTION

The subject matter of economics is the use of scarce resources to satisfy practically unlimited demands. This is particularly true of the subdiscipline of fisheries economics. The productivity of wild fish stocks is limited by nature. What makes fisheries economics particularly relevant is that the rules governing the fishing industry often fail to take due account of nature's limited productivity. Economics offers some guidance for what the appropriate rules are.

The subdiscipline of fisheries biology is a good deal older than fisheries economics. Two classic papers on fisheries economics were published in the 1950s by two Canadian economists, Gordon (1954) and Scott (1955) but there were some contributions before that time (see Smith, Chapter 4, this volume). The subject 'took off' in the late 1960s and the 1970s with contributions by Anderson (1973, 1976), Gould (1972), Plourde (1970, 1971), Smith (1968, 1969), and in particular by Clark (1973a, 1976, 1985). Textbooks dealing with fisheries economics are Anderson (1986), Cunningham et al. (1985), Hannesson (1993), and Clark (1976, 1985). Of these, Clark's books are the most mathematically advanced. On the development of the subject, see Scott (1979). Classic biological reference works, useful for the economist, are Beverton and Holt (1957), Ricker (1975) and Hilborn and Walten (1992).

12.2 THE SURPLUS PRODUCTION MODEL

A natural starting point is the surplus production model, where the rate of growth of a fish stock in excess of what is needed to compensate for natural deaths, or surplus growth (G) for short, depends on the size of the stock (S) (Schnute and Richards, Chapter 6, this volume; Sparre and Hart, Chapter 13, this volume, where biomass is called B). This is, needless to say, a great simplification. The usefulness of this model is that it represents the limited productivity of nature in a simple and transparent way and allows one to demonstrate, simply and clearly, some key concepts and processes. In reality the growth of fish stocks depends on a number of factors, most of which vary over time subject to environmental fluctuations. This has important economic implications which will be discussed later. Schaefer (1957) used the surplus production model in applied analyses, and it is sometimes named after him.

Figure 12.1 shows three possible surplus growth curves. One is based on the logistic equation, another on a modified logistic equation with a critical threshold level of viability, and a third is based on yet another modification of the logistic equation, which shows depensatory growth but no threshold of viability. These differences in shape have implications for the shape of the sustainable yield curve, as will be discussed below, and by Schnute and Richards (Chapter 6, this volume).

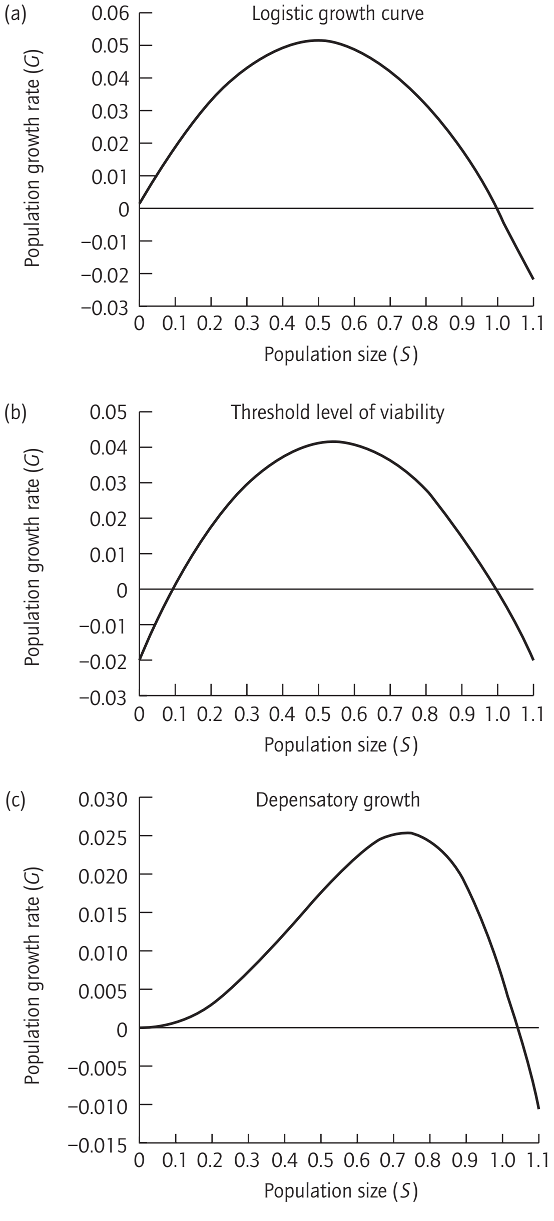

Fig. 12.1 Three examples of a surplus growth function. **(a)** Logistic: $G = aS(1 - S/K)$, with $a = 0.5$ and $K = 1$; **(b)** logistic with a threshold value of viability (A): $G = a(S - A)(1 - S/K)$, where $A = 0.1$ and a and K as before; **(c)** depensatory: $G = aS^{\alpha}(1 - S/K)$, with $\alpha = 2$ and a and K as before. G = rate of growth; S: size of stock; K: maximum stock size (carrying capacity of the environment).

The surplus growth curve shows how much it is possible to fish sustainably. Any quantity between zero and maximum surplus growth is sustainable; if the stock happens to be in equilibrium at some level $S^{\#}$, we can fish the amount $G(S^{\#})$ per unit of time indefinitely, and the stock would remain at $S^{\#}$, because what we are taking away corresponds exactly to the surplus growth. The question is, how much should we take? Should we take the maximum surplus growth or something less? If we take less, we see that we could take that quantity from two different stock levels. Should we take it from a 'small' stock or a 'large' stock?

12.3 FISHING EFFORT AND FISH YIELD

The first step towards answering these questions is to investigate the relationship between the activities of the fishing fleet and the amount of fish it catches. This relationship is in fact highly complex, depending on the technology used and the reaction of a fish stock to continued exploitation and depletion (Misund et al., Chapter 2, this volume).

Fishery biologists early on invented the concept of fishing effort. The purpose was to find an indicator of the abundance of fish stocks, a quantity not easily observed. Fishing effort is a measure of the activity of the fishing fleet directly aimed at catching fish. It can be rigorously defined as the mortality that the fleet causes in a fish stock of a given size and distribution (the importance of these latter two qualifications will become clear presently). Examples of practically measuring effort are hours of trawling (eventually corrected for differences in vessel size), number of hooks lying in the water for a certain number of hours, or days fishing. By definition, fish are caught at a rate equal to the product of instantaneous fishing mortality (F) and stock size:

$$Y = FS \tag{12.1}$$

where Y is the rate at which fish are removed from the stock. If fishing mortality is directly proportional to fishing effort (f), we have

$$F = qf \tag{12.2}$$

where q is a constant (sometimes called availability or the catchability coefficient). Combining (12.1) and (12.2) we get

$$Y/f = qS. \tag{12.3}$$

This means that the catch per unit of effort which is measured over a 'short' period of time, since Y is the rate at which fish are removed, is proportional to the size of the fish stock being exploited and can be used as an index of its size.

The problem with this is that the postulated relationship between fishing effort and fishing mortality depends critically on the assumption that the fish are always evenly distributed over a given area, or that the relative distribution of effort and fish is always the same in a given area. This is not always the case, and perhaps only exceptionally so. If the assumption holds, the density of the fish is directly related to the size of the fish stock; twice as many fish would mean twice as many fish per square kilometre, and twice as many fish would be likely to be dragged up per hour of trawling or to bite the hooks that lie in the water overnight. But consider a different scenario, one where the area over which the fish are distributed shrinks in proportion to the size of the stock. If the size of the stock shrinks by one half, the area where the fish are will also shrink by one half. The density of fish will remain the same as before, in that part of the area where they are located, and if the fishermen know where to find them, as modern technology increasingly allows them to do, the catch per trawl-hour or hook-night would be the same as before, and it would tell us nothing about the size of the stock.

In all probability we have identified two polar cases between which reality is likely to lie. The area over which fish are distributed is likely to shrink somewhat as the stock is depleted, but not in proportion to the depletion. It appears that bottom-dwelling fish like cod (*Gadus morhua* L.) do not contract a great deal as a consequence of depletion, while surface-dwelling stocks that travel in shoals, like herring (*Clupea harengus* L.), do not migrate nearly as widely as the stocks are depleted. But reality departs to a greater or lesser degree from these stylized examples. There are indications that the northern cod stock of Newfoundland became more concentrated as it was depleted (Hutchings and Myers 1994). Hence the catch per unit of effort (CPUE) did not fall as rapidly as the stock abundance, which led Canadian fisheries biologists astray and delayed the necessary cutback in fishing.

We shall in the following stick to these two polar cases, as they are easy to analyse mathematically and to depict graphically. We shall also stick to the definition of effort given previously but note that it is likely to be inadequate for economic purposes. For that we would need a measure of effort that takes into account all activities that give rise to costs. Such a measure would be more comprehensive than 'fishing' effort as defined above. In addition to catching fish, the activities of a fishing fleet involve steaming to and from the fishing ground, searching for concentrations of fish, and handling of the catch and gear. If these activities are always proportional to 'fishing' effort there would not be any problem, but that is not likely; consider, for example, the difference between day-trip boats that always return at night irrespective of whether they have filled up the hold or not and boats that store the catch on board and do not return until the hold has been filled. Because of the obvious problems of generalizing about this we shall leave the matter at that and use the term 'fishing effort' in the sense already defined as a measure of the activity of the fleet and the one that gives rise to costs. In any case it would not be easy to do without the biologist's notion of fishing effort in any applied work, because one would need to relate fish production to the size of the exploited stock and the activity of the fishing fleet.

We thus end up with the following two 'polar' relationships between catch and effort:

$$Y = qfS \tag{12.4a}$$

$$Y = kf. \tag{12.4b}$$

Equation (12.4a) is the case where a stock is always evenly distributed over a given area and where a change in the catch per unit of effort directly reflects a change in the size of the stock. Equation (12.4b) is the case where the area over which the stock is distributed is proportional to the stock size. In that case the density of fish is always constant, and so is the catch per unit of effort, which in equation (12.4b) is equal to k. In order to take into account the intermediate cases, some authors have used the functional form $Y = AfS^{\beta}$, where $0 \le \beta \le 1$. Another way to look at this is to regard the availability coefficient q as being dependent on the stock size; i.e. $q = AS^{\beta-1}$. If the density of the stock is always constant, $\beta = 0$, and the availability would be inversely related to the stock size. For attempts to estimate β for cod and herring, see Hannesson (1983) and Bjørndal (1987, 1988). Empirical evidence of negligible sensitivity of the catch per unit of effort to the stock size can be found in Ulltang (1980) and Butterworth (1981).

12.4 SUSTAINABLE YIELD

We may now combine equation (12.4) with the growth function to derive a relationship between sustainable yield, defined as the catch that is equal to the surplus growth, and fishing effort. Three sustainable yield curves are shown in Fig. 12.2, corresponding to the three growth curves depicted in Fig. 12.1 and the production relationship in equation (12.4a) (equation (12.4b) simply produces a straight line with a slope k, up to a level determined by the maximum surplus growth). The logistic growth equation produces a sustainable yield curve of a similar shape, while the curve with the critical threshold level and the one with depensatory growth give rise to sustainable yield curves that look like loops. Such loop-like curves may also arise if there are 'diminishing returns' to the stock, i.e. if instead of (12.4a) we have the catch equation $Y = AfS^{\beta}$, with $\beta < 1$. (See also Schnute and Richards, Chapter 6, this volume; Sparre and Hart, Chapter 13, this volume.)

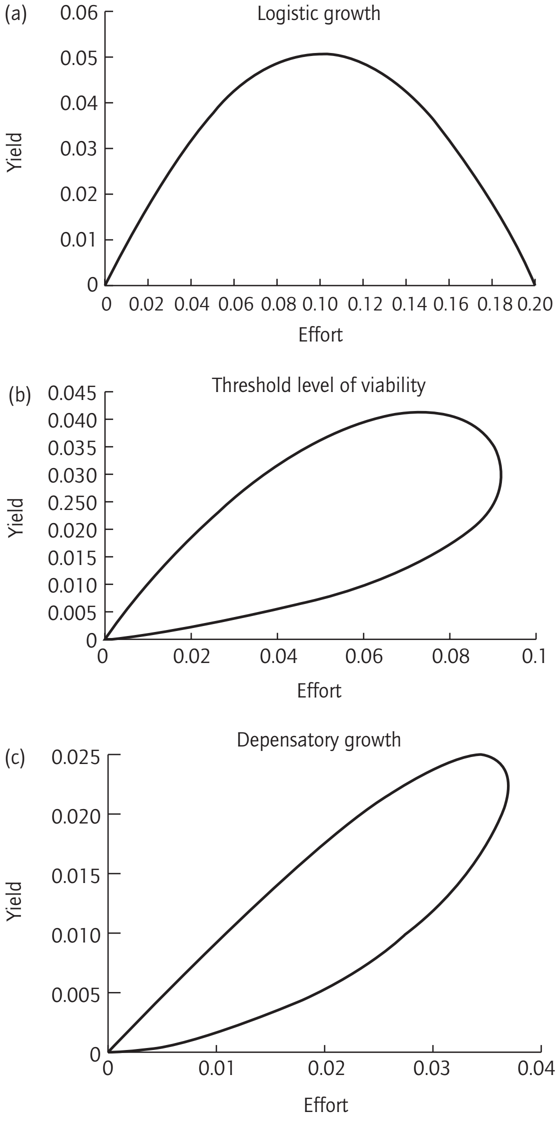

Fig. 12.2 Sustainable yield curves for the growth functions shown in Fig. 12.1 and the catch function $Y = qfS$, with $q = 1$.

Before answering the question what level of sustainable yield we should go for, let us consider what would happen in an unregulated fishery where the access to the fish stock is open to all and free of charge. Assume that the price of fish (P) is constant and independent of the volume of landings, and that the cost per unit of fishing effort (C) is also constant. Assume further that all fishing boats are identical in every respect. The value of sustainable yield per unit of effort will then be PY/f and identical for all boats. Sustainable yield will be obtained when the biological system is in equilibrium, which can only happen when the fishing fleet is also in equilibrium, that is, when there is no investment in new boats. What, then, determines the investment in new boats? Presumably, people will invest in new boats if the value of the catch per unit of effort (or catch per boat) is greater than the cost per unit of effort (the cost of each boat). Hence, the system will not be in equilibrium unless the value of the catch per unit of effort is equal to the cost per unit of effort:

$$PY/f = C. \tag{12.5}$$

Combining this with equation (12.4) we get

$$PqS = C \tag{12.6a}$$

$$Pk > C \text{ or } Pk = C \text{ or } Pk < C. \tag{12.6b}$$

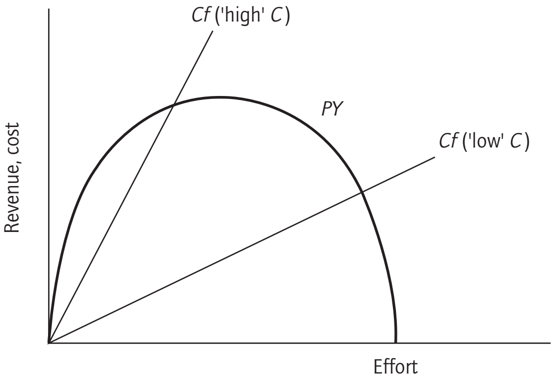

Fig. 12.3 Two bioeconomic equilibria with open access. Equilibrium occurs where the cost line crosses the catch value curve. A lower cost leads to greater effort (f), a smaller stock, and (in this case) a lower sustainable yield. The sustainable catch value is derived using a constant price and the logistic surplus growth function and assuming that the catch per unit of effort is proportional to the stock.

In case (12.6a) there will always be some value of S for which an equilibrium exists, provided there is no threshold value of viability for the stock. Figure 12.3 illustrates two possible equilibria for this case. The equilibrium occurs where the sustainable catch value (left-hand side of (12.6a) after multiplying by f) is equal to the total cost (right-hand side of (12.6a) after multiplying by f). The figure uses the logistic surplus growth equation $G = aS(1 - S/K)$ (see also Schnute and Richards, Chapter 6, this volume). Setting this equal to the catch (qfS) gives $S = K(1 - qf/a)$ and a sustainable catch value of $PqfK(1 - qf/a)$. The two equilibria obtain for a 'low' versus 'high' cost of effort, respectively (high versus low price of fish would give the same kind of comparison). For example, if the cost of effort fell, then effort would increase, 'disturb' the equilibrium and drive the stock down to a new and lower equilibrium level.

Note that the equilibrium may be such that excessive effort is used, in the sense that a given sustainable yield is taken with greater effort than necessary. This happens in our example as a result of technological progress: a lower cost of effort induces the industry to apply greater effort, which in the end results in a smaller sustainable yield. This foreshadows the conclusion that open access may not be the most appropriate 'rule of the game' for the fishing industry.

The existence of an equilibrium value of S is, however, no guarantee that it will in fact be attained. The trajectory towards the equilibrium may have the form of a spiral, and it may spin away from the equilibrium rather than approach it. This is what happens for equilibria in the lower part of the loop-shaped sustainable yield curves in Fig. 12.2. Furthermore, if there is a critical threshold value below which the stock cannot reproduce, the equilibrium will not even exist for a high enough price of fish or a low enough cost of effort. Consider again equation (12.6a), which determines the equilibrium level of the stock. From this we see clearly that a lower cost or a higher price implies a lower equilibrium value of S. Figure 12.4 shows two equilibrium values of S, one for a low cost (or high price) and one for a high cost (or low price). The figure also shows the direction of movement of effort and stock when out of equilibrium, and the spiral

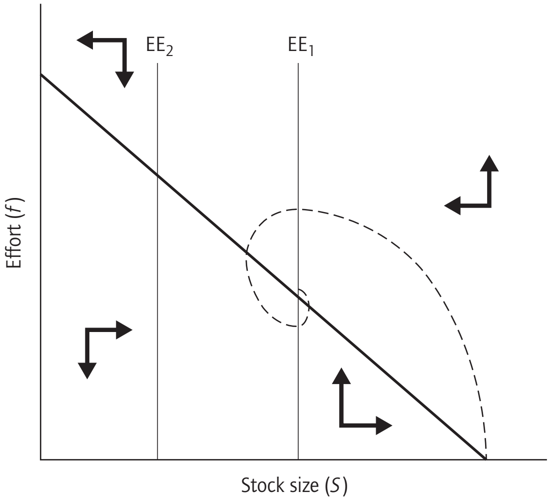

Fig. 12.4 Bioeconomic equilibrium. The downward-sloping line shows all combinations of effort (f) and stock (S) where the yield is sustainable; i.e. where $Y = G$, and $Y = qfS$, and G is given by the logistic equation. The EE-lines show the stock level compatible with economic equilibrium (equation 12.6a), where EE$_1$ implies a low price or a high cost, and EE$_2$ a high price or a low cost. The arrows show movement of variables when out of equilibrium, and the dashed line shows a possible pattern towards equilibrium.

movement towards the equilibrium point (for unstable equilibria we would spiral away). Paths towards equilibrium for real-world fisheries have been analysed by Bjørndal and Conrad (1987) and Conrad (1989).

The risk of extinction as a result of fishing is most dramatic, however, if equation (12.6b) holds. In this case no equilibrium exists except by coincidence; the value of the catch per unit of effort will always be the same, because the density of the fish will always be the same, until the last fish has been taken. This case may come close to describing the situation for the Atlantic herring stocks which nearly collapsed in the late 1960s, due to an increased pressure caused by the introduction of the power block which made it possible to haul purse seines mechanically instead of by hand. This in turn made it possible to use much bigger seines and boats, and led to an enormous increase in fishing capacity over a short time-span. The herring stocks may possibly have been saved by a moratorium that was put in place around 1970. This story alerts us to the fact that nothing except a high cost of catching the last viable animal protects wild animal stocks that are hunted freely from being hunted to extinction, as has in fact happened for certain stocks where the hunting conditions come close to being described by equation (12.6b). A paper by Smith (1975) is a fascinating exposition on why this may explain the extinction of the indigenous American horse (*Equus caballus*) several thousands of years ago. Other examples, such as the Kiwi bird (*Apteryx* spp.) and the American buffalo (*Bison bison*), come to mind. Both these animals were an easy prey to the early settlers in New Zealand and on the North American prairies, respectively.

A special form of open access obtains when the total catch is controlled but everyone is free to participate in the fishery. This typically leads to shorter and shorter fishing seasons, and little or nothing is accomplished from an economic point of view. For a discussion of this, see Homans and Wilen (1997).

12.5 OPTIMAL EXPLOITATION

The stage has now been set for considering economically optimal exploitation of fish stocks. When deriving the optimum sustainable yield of fish stocks it is imperative to keep in mind that fishing is only one of the activities that contribute to our welfare. It need not make sense, for example, to achieve the maximum sustainable yield, as we might be forsaking too much of other goods for that purpose. The fundamental criterion for having achieved optimum sustainable yield is that the last unit of effort expended in the fishery should produce the same value as it would do if used in the best alternative way. If the marginal unit of effort produces a greater value in the fishery than elsewhere, then obviously it makes sense to increase effort in the fishery, and vice versa.

This implies that effort can be used for purposes other than fishing. In the long term this is certainly true; people employed on fishing boats could be employed somewhere else, and capital to be invested in fishing boats could be invested in something else. In the short term, however, reality may look a bit different. Fishing boats are typically not very useful for other purposes and can only be converted to other uses at some cost, and fishermen may need retraining to be employed in other industries. This implies that the short-term opportunity cost of effort (i.e. the value that the effort could produce in other industries) may be lower than indicated by the wage rate or the capital cost on the firms' books. But in the long run the capital cost and the wage rate are likely to reflect the value that labour and capital are able to produce in their best alternative application, and we shall in our analysis below assume that the cost of effort measures the value that effort could produce elsewhere in the economy.

What, then, is the value that effort produces in the fishery? Below we shall take this as being synonymous with the value of the catch. This presupposes that fish are valuable only in so far as they contribute to our material well-being as a source of food or raw materials and that this is correctly measured by the market price. This is likely to be true or nearly true in a great many cases; fish are sought at considerable inconvenience, and even risk of life and limb, for the purpose of selling them in the marketplace. There are, however, other cases where fishing as such has value, such as in recreational fishing (Cowx, Chapter 17, this volume). Clearly, in such cases it would not be enough to measure the value produced by fishing effort by the value of the fish being caught, and the time spent on this activity would not even be a cost. Lastly fish stocks as such may have value, for reasons of maintaining biodiversity or for viewing as wildlife (Reynolds et al., Chapter 15, this volume).

With these caveats we set out to derive the optimum sustainable yield and the associated fishing effort. In doing so we regard the fishery as being managed by a single owner, a social planner trying to maximize the total value of production derived from all resources at disposal in the economy. The condition for optimality is that the value produced by the last unit of fishing effort applied should be equal to the cost of that unit. In the language of differential calculus this can be expressed as

$$P(dY/df) = C. \tag{12.7}$$

Figure 12.5 illustrates the solution and compares it with what obtains under open access, for the case described by equation (12.4a) and the logistic surplus growth equation. Clearly it is not worthwhile to take the maximum sustainable yield. Less effort should be used than needed for that purpose, and the fish stock should be kept at a higher level than corresponds to the maximum sustainable yield. Note also that the optimum effort is less and the equilibrium stock greater than what would result under open access. The yield is not necessarily greater, however, than under open access, unless the effort under open access is sufficiently greater than needed to take the maximum sustainable yield. Loop-shaped yield curves, such as shown in Fig. 12.2, would produce revenue functions of a similar shape. This case is not very interesting, however, as equilibria occurring in the lower part of the curve are unstable.

In the case of equation (12.4b) it would always be optimal to take the maximum sustainable yield. This is so because the value of the catch per unit of effort and the cost per unit of effort are both constant in this case; the value of the catch per unit of effort does not decline as the stock is depleted, due to the constant density of the stock.

Note that the optimum sustainable yield was derived by setting the value of the marginal sustainable yield equal to the unit cost of effort. If the unit cost of effort rises with effort, the marginal sustainable revenue should be equal to the marginal cost of effort (i.e. the cost of the last unit). If the unit cost of effort is constant it is equal to the marginal cost. We would have arrived at the same condition if we had maximized the profit in the fishery: i.e. the difference between revenue and cost $[PY(f) - Cf]$. We did not do so, in order to emphasize that maximization of profit is not an obviously legitimate social goal. It would make perfect sense for somebody who owned the resource, but it

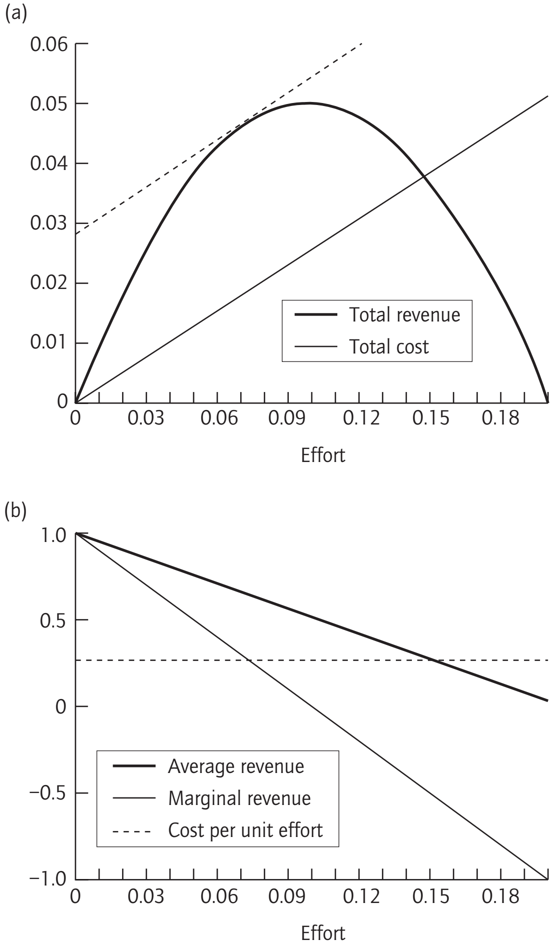

Fig. 12.5 Equilibrium in an open access fishery versus optimum sustainable yield. (a) The curve shows the sustainable revenue (value of the sustainable yield) at a constant price, and the line shows the total cost of effort. Equilibrium with open access occurs where total cost is equal to total revenue, whereas optimum effort occurs where the difference between sustainable revenue and total cost is greatest (i.e., where the dotted line is tangential to the sustainable revenue curve). (b) The downward sloping lines show the sustainable revenue per unit of effort (thin line) and the marginal sustainable revenue ($P(dY/dZ)$, thick line). Equilibrium with open access occurs where the sustainable revenue per unit of effort is equal to the cost per unit of effort (the horizontal dotted line) whereas the optimal effort is where the marginal sustainable revenue is equal to the cost per unit of effort.

would not be a primary goal from a social point of view. What does make sense from a social point of view is to maximize the value produced by the resources at society's disposal. This occurs when the last unit of any productive resource produces the same value irrespective of where it is used. This implies, however, that the profit in the fishery is being maximized. This 'profit' is a bit special, as it is due to the limited productivity of the fish stock and can be seen as a cost of using that productivity. In the economic jargon this goes under the name of resource rent, or fishing rent, due to its analogy with land rent.

Like land rent, the fishery rent is a residual that remains after all factors of production (labour, capital and other inputs) have been paid. The rent reflects the differences in productivity between different 'quality' categories of a resource. Inner city plots yield a higher rent than plots in the suburbs, because of a better location for business. Fertile agricultural land can be rented out or sold at a higher price than poorer land. The profits realized by extracting oil from a well in the sands of Arabia are higher than the profits that can be extracted from underneath the North Sea. And the profit obtainable from fishing cod in the Norwegian Sea is higher than fishing the less coveted saithe in the same area, provided both stocks are properly managed. When fisheries are controlled by some fishing rights scheme, such as individual transferable quotas or transferable boat licences, the resource rent becomes capitalized in the form of a value of a fish quota, or a value of a fishing boat with a licence in excess of what the boat is worth for the purposes of fishing only. If such rights are handed out free of charge they end up as windfall gains for those who got these rights initially and who later sell them in the marketplace. Note, however, that it is possible to reduce or perhaps eliminate these gains by imposing a fee on quotas or licences, or by selling them or renting them out.

Maximization of profit in the fishery would, however, under certain circumstances, lead us astray. Suppose that the price of fish from a particular stock depends on the landings from that stock only because, for example, the fish is sold in a local market and there is no other fish that competes with it. We can write the sustainable profit, alias rent (V), in the fishery as

$$V(f) = P[Y(f)]Y(f) - Cf. \tag{12.8}$$

Maximizing this requires that

$$dV/df = [P + (dP/dY)Y](dY/df) - C = 0. \tag{12.9}$$

This would not be the socially optimal solution. The value produced by the last unit of effort is $P(dY/df)$, as this is what the consumers of fish are willing to pay for the fish caught by the last unit of effort. This should be equal to C, the cost of effort. The term dP/dY is negative, because the price will be lower the more fish is being landed. If the fishery were controlled by a single firm, or an industrial association, it would presumably be aware that it would be eroding its own market by selling more, assuming that all fish must be sold at the same price, and it would take this into account when deciding how much to sell. This would be an example of the exercise of monopoly power, which is not in the social interest. This monopoly power should not be confused with sole ownership of scarce resources like fish stocks; although it makes no sense socially to artificially limit the supply of something just to get a higher price in the market, it makes perfect sense to limit fishing to what the productivity of nature can support, with due account taken of the cost of fishing. This is what sole ownership, or privatized use rights, of scarce resources would attain, in contrast to the overexploitation occurring under open access.

Now that we have relaxed the assumption of a constant price of fish we might as well ask: what would this mean for our previous analysis of open access versus optimum exploitation? The answer is: not a great deal; open access would still result in overexploitation. Similarly, relaxing the assumption that the cost per unit of effort is constant does not cause any fundamental change; what happens is that all the fishing rent would not be absorbed by unnecessary costs; all units, except the last one, would obtain some profit over and above their opportunity cost. In everyday life this would translate into profits being obtained by fishermen who are better skilled than others, or have better equipment than others. Such 'skill rents' or 'equipment rents' are often a conspicuous fact of life in real-world fisheries even under open access. The implications of a volume-dependent price have been analysed by Anderson (1973), and the fishing rents by Copes (1972).

12.6 TIME DISCOUNTING

Up to now we have been concerned with sustainable yield. If we put an equal emphasis on what happens in the short and the long run this is all that matters, but if we value any given benefit we get in the future less than if we get it now, it is not enough just to look at sustainable yields.

The systematic 'devaluation' of effects that occur in the future is called discounting. The implications of time discounting have been analysed by Clark (1973a, 1973b, 1976), Clark et al. (1973), and Clark and Munro (1975). The ethical underpinnings of time discounting are often called into question, as it would seem to amount to a systematic discrimination against future generations. There is, however, another argument in favour of discounting. If it is possible to invest profitably in the economy, we should require that all investment opportunities yield the same return at the margin, or else only invest in such opportunities as yield the highest return. By making profitable investments we do in fact leave a richer world to our descendants. Discounting the future stream of benefits from any investment at the same rate of return as we can get in the best alternative opportunity is a method for ascertaining whether that investment is in fact worth while.

To explain this, suppose we can invest our money in the bank so that it will yield $r \times 100\%$ interest every year. Note that this is not a purely financial phenomenon; the rate of interest in the banks may be expected to reflect rates of return on 'real' investments: that is investment in productive capacity. The reason that the banks can charge a certain rate of interest is that somebody is prepared to borrow the money and pay it back with interest, financed out of profits that he expects to make on the investment.

If we deposit the amount K in the bank we would have $K(1+r)^T$ at the end of T years. Suppose instead that we invest the amount K at time 0 in a project that will provide an income I net of operating cost every year for T years, after which our investment is worthless. At the end of the T years we would have $I[1+(1+r)+\ldots(1+r)^{T-1}] = I[(1+r)^T - 1]/r$, assuming that we continuously invest our income from the project in the bank as it accrues. Hence, if the project is worth while, we must have

$$I\left[1-(1+r)^{-T}\right]/r > K. \tag{12.10}$$

The left-hand side of this is the so-called present value of the income stream I over T years, discounted at the rate r. Hence the criterion for a profitable investment is that the income stream from a project, discounted at a rate of interest equal to the return on the alternative investment, be at least equal to the initial outlay for the project.

The relevance of this is that we can regard any fish that we do not catch immediately as an investment. Why should we leave it in the sea? Because a fish left uncaught contributes to the growth of the stock, through individual growth and through reproduction. If fish did not grow, or did not grow fast enough, it would make no sense to leave them in the sea. Hence, if we exploit a fish stock optimally, the return on a fish we leave in the sea must be equal to the return we can get on catching that fish, selling it in the marketplace and investing the money we get for it at the highest return we can obtain.

What about fish stocks that do not grow fast enough to satisfy the required rate of return? On the basis of the above reasoning such stocks should be fished out and converted to other forms of capital that are more productive. Many people undoubtedly find such a recommendation offensive, but implicit in that attitude is that fish stocks are valuable for other purposes than their surplus production, such as for preserving biodiversity or for tourism.

Consider now a stock that is optimally exploited. For easier exposition we use a continuous time model. The term e^{-rt} is the analogue of the discount factor $(1+r)^{-t}$ in continuous time. If interest accrues n times per year, one unit of money would grow to $(1+r/n)^{nt}$ over t years. Then consider the expression $[1+1/(n/r)]^{(n/r)rt}$. The expression $[1+1/(n/r)]^{(n/r)}$ approaches e as n approaches infinity. Hence the present value of exploiting the stock in perpetuity is

$$PV = \int_0^\infty PG(S)e^{-rt}dt = \frac{PG(S)}{r} \tag{12.11}$$

where r is the discount rate, which equals the rate of return we can earn on an alternative investment project. The immediate gain of increasing fishing by the amount $-\Delta S$ will be equal to $-P\Delta S$ (note that changing the amount fished will cause an opposite change in the stock size). This will change the present value of all future catches by

$$\Delta PV = [P(dG/dS)/r]\Delta S. \tag{12.12}$$

If ΔS represents a departure from an optimal stock level, to be maintained in perpetuity, the sum of these two changes must be zero: i.e. the short-term gain must be cancelled by the long-term loss. Hence, $P\Delta S - [P(dG/dS)/r]\Delta S = 0$, or

$$dG/dS = r. \tag{12.13}$$

The solution is illustrated in Fig. 12.6. We see that the optimum equilibrium stock is in fact smaller than that which corresponds to maximum sustainable yield. In other words, a positive discount rate implies that some biological overexploitation would be optimal. The reason for this is that discounting of the future makes it worth while to incur a permanent loss for the sake of a temporary gain. Even if the absolute value of a permanent loss is infinite, its present value when we discount the future is finite; the positive discount rate turns the infinite series of losses into one that converges to a finite value.

Taking fishing costs into account modifies this conclusion, provided the catch per unit of effort depends on the size of the exploited stock. In

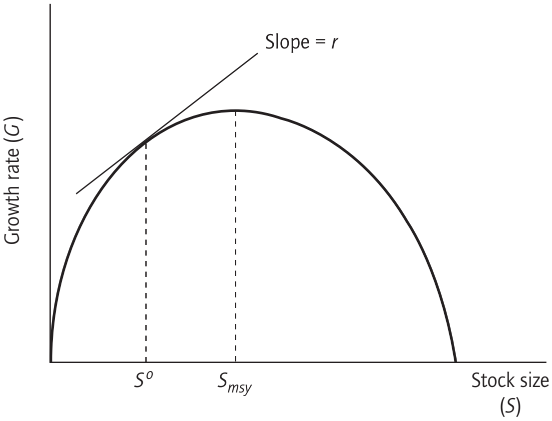

Fig. 12.6 Optimum stock level (S^o) with a positive discount rate when the catch per unit of effort does not depend on the stock level. S_{msy} is the level giving maximum sustainable yield.

that case it is attractive to fish from a large stock rather than a small one, in order to keep down the cost per unit of fish caught. Let the cost per unit of fish caught be denoted by $X(S)$. The immediate gain from increasing the amount fished by $-\Delta S$ is $-(P - X)\Delta S$. The present value of future fishing is now

$$PV = \int_0^\infty [P - X(S)]G(S)e^{-rt}dt = \frac{[P - X(S)]G(S)}{r}. \tag{12.14}$$

The change in the present value resulting from changing the stock by ΔS is now

$$\Delta PV = \{[(P - X)(dG/dS) - (dX/dS)G]/r\}\Delta S. \tag{12.15}$$

Letting immediate gains be cancelled by permanent losses now gives

$$r - (dG/dS) + (dX/dS)G/[P - X(S)] = 0. \tag{12.16}$$

Since $dX/dS < 0$ (fishing from a larger stock reduces the cost per unit of fish landed), it is possible that $dG/dS < 0$ in the optimal solution. This would certainly be true in the absence of discounting ($r = 0$). Thus biological overfishing need not be optimal, even if the future is discounted. But discounting of the future reduces the optimal standing stock; the higher the discount rate (r) is, the greater is dG/dS, and the smaller is the optimal standing stock (see Fig. 12.6).

The implications of discounting could be dramatic. If max $dG/dS < r$ and the unit cost of landed fish is not stock-dependent (X is constant), the implication is that the stock should be fished to extinction; investing in the stock simply would not yield a high enough rate of return to be worth while. The implication is that such stocks should be 'mined', like minerals or oil deposits, which after all are resources with too low a rate of growth (zero or, for oil, negligible) to make exploitation based on surplus growth interesting. There are a number of slow-growing fish and whale stocks that might be in this category. Orange roughy (*Hoplostethus atlanticus*) is a slow-growing fish which matures when it is 30 years old and lives to be 60 to a 100 years old if left unfished. Yields were high in this fishery when it started and the stocks were mined, but the sustainable yields have turned out to be much lower (see, for example, Batstone and Sharp 1999). Given that the stocks of such species are sufficiently valuable as such it would not, of course, be optimal to mine them to extinction, but the point is that if the exploitation of such stocks were a matter to be decided by the industry in its own interest, or by a sole owner, the investment aspect would be likely to prevail. The industry or a sole owner would not attach much value to the stocks as such; these values stem from ethical considerations like preserving species for their own sake, which are not likely to loom large in the profit and loss accounts of private individuals or firms.

Above we have looked at optimal equilibria. Another question is what the adjustment path towards the equilibrium will be like if, say, the fishery starts from a situation with overexploitation. The optimal approach path can be shown to depend on the discount rate and to what extent capital, measured in terms of production equipment, is 'malleable'. The reader is referred to a classic paper by Clark et al. (1979).

12.7 FLUCTUATIONS: SHOULD CATCHES BE STABILIZED?

It was mentioned above that the growth of fish stocks is influenced by fluctuations in the marine environment (Myers, Chapter 6, Volume 1). These fluctuations give rise to variations in the size of fish stocks, even if they are exploited at a rate consistent with long-term sustainability. The fluctuations in stock abundance in turn give rise to fluctuations in catches. Such fluctuations are usually considered an inconvenience by the industry, as fish buyers usually prefer even and secure deliveries. A review of stochastic models in fisheries is provided by Andersen and Sutinen (1984).

One way of responding to the problems caused by fluctuations is to stabilize the catch (Hannesson and Steinshamn 1991). Would this be desirable, from an economic point of view? Consider, first, the revenues from fishing. These are

$$R(Y) = P(Y)Y. \tag{12.17}$$

Now suppose that the fishery is managed by a TAC (total allowable catch) regime where the TAC is set equal to some fraction of the stock available in each period. Suppose, further, that the stock is subject to random fluctuations. Then the TAC will fluctuate as a consequence.

Would a stable catch equal to the expected catch (EY) with a fluctuating TAC provide a larger revenue? It would, if

$$R(\mathrm{E}Y) > \mathrm{E}R(Y) \tag{12.18}$$

where ER is the expected revenue under the fluctuating TACs. This holds if the revenue function is concave, with $dR/dY > 0$, at least for 'low' values of Y, and $d^2R/dY^2 < 0$. This is quite possible. From equation (12.17):

$$dR/dY = P + (dP/dY)Y, \tag{12.19}$$

$$d^2R/dY^2 = 2(dP/dY) + (d^2P/dY^2)Y. \tag{12.20}$$

Because larger landings normally imply a lower price, $dP/dY < 0$. We are not assured that $d^2R/dY^2 < 0$ but it is quite likely.

As an example, consider the demand function

$$P = AY^{-b}. \tag{12.21}$$

The revenue function is

$$R = AY^{1-b}, \tag{12.22}$$

and its derivatives are

$$dR/dY = (1-b)AY^{-b}, \tag{12.23}$$

$$d^2R/dY^2 = -b(1-b)AY^{-b-1}. \tag{12.24}$$

If $0 < b < 1$, $dR/dY > 0$ and $d^2R/dY^2 < 0$ and we have a concave revenue function. The opposite is true if $b > 1$; then we have a convex revenue function, E$R > R($E$Y)$, and fluctuating catches would in fact yield a higher revenue on the average than a stable catch would do. In this latter case the price is highly sensitive to the quantity being sold, and the revenue becomes greater as the quantity becomes smaller, because the price 'goes through the roof'. This case is known as inelastic demand (the elasticity of demand, $-d\log Y/d\log P$, is equal to $1/b$).

It may be noted that stabilizing the catch would imply stabilizing the effort as well if the density of fish is always constant (equation 12.4b). With a constant unit cost of effort the cost would simply be proportional to the catch and irrelevant for whether or not the catch should be stabilized.

Things turn out differently if the cost of landed fish depends on the size of the exploited stock. Let us proceed on the basis of equation (12.4a), where the catch per unit of effort is proportional to the size of the stock. We normalize effort such that $Y = fS$. Setting the TAC equal to a certain fraction of the stock amounts to fixing the effort at the level f^* which, because of the normalization, is equal to the desired fraction to be caught from the stock. Under this catch policy the total cost of fishing will in fact be constant and equal to Cf^*. If, on the other hand, the catch is held stable at a level equal to the expected catch under the said TAC policy ($Y^* = \mathrm{E}Y$), we would have to vary effort according to equation (12.4a):

$$f = Y^*/S. \tag{12.25}$$

The expected effort would be

$$\mathrm{E}f = Y^*\mathrm{E}(1/S). \tag{12.26}$$

Using $Y^* = f^*\mathrm{E}S$, we can write this as

$$\mathrm{E}f = f^*\mathrm{E}S\mathrm{E}(1/S). \tag{12.27}$$

Since $1/S$ is a convex function of S, $\mathrm{E}(1/S) > 1/\mathrm{E}S$, so that $\mathrm{E}S\mathrm{E}(1/S) > 1$. Hence, $\mathrm{E}f > f^*$, which means that stabilizing the catch will be more costly than letting it vary with the stock. What the stabilization policy amounts to is telling the industry to fish with great intensity when the stock is small and the catch per unit of effort is low but to hold back when the stock is plentiful and the catch per unit of effort is high. Hence, even if a stable catch were attractive for marketing and for the processing industry, it would be less attractive, and perhaps decidedly unattractive, for the catching industry, if the catch per unit of effort depends on the abundance of the stock. Hence there is no clear economic argument for stabilizing catches; on the revenue side there are likely to be arguments pulling in that direction but on the cost side the argument is likely to point the other way.

Note, finally, that stabilizing the catch is likely to be a risky option. It amounts to fishing intensively when the stock is low and less intensively when it is plentiful. This may jeopardize the growth of the stock, particularly if there is a threshold level of viability or if low stock levels are somehow inimical to growth as occurs when there is depensation. Some stocks fluctuate so wildly that the TAC is set equal to zero in some years; capelin (*Mallotus villosus*) is an example. Stabilizing the catch at a biologically safe level might in a case like that imply the ridiculously low level of zero. Given that stabilizing the catch is risky or impossible, and in any case not a clearly superior option economically, we turn to the case of fluctuating catches.

12.8 OPTIMUM FLEET CAPACITY FOR FLUCTUATING STOCKS

If fish stocks fluctuate in part for random reasons and the management regime sets a TAC that is somehow related to stock abundance, such as a given fraction of the stock or everything in excess of some target escapement, the optimum fleet capacity will not depend solely on the deterministic stock–growth relationship element that influences the development of the stock; the nature of the random fluctuations will also be a determinant of optimum capacity. In this case optimal management involves determining the capacity of the fishing fleet and its use at any particular time. In 'bad' years the capacity of even an optimal fleet will be too great and its activities must be somehow restricted. These decisions are interrelated: that is, the use of an existing fleet, or the optimum TAC in any particular year, depends on the optimal size of the fleet, provided the stock size is not entirely random but depends as well on a deterministic stock–growth relationship. This latter issue is discussed in Hannesson (1993) but here we shall, for simplicity, ignore the deterministic stock–growth relationship and assume that the growth of the stock is entirely random.

Another simplification we shall make is that the catch per unit of effort is constant and that effort is simply proportional to the number of identical vessels in the fleet. The value of the catch each year will then be

$$R = \min(PQ, PaK) \tag{12.28}$$

where Q is the total allowable catch, K is the size of the fishing fleet, measured as capital investment, and a is the amount one unit of money invested in the fleet can catch if the fleet is used to its full capacity. Here P is the price net of operating costs, which would include fuel, ice, fishing gear, and other expendable equipment.

As explained above, we can find the optimal policy by maximizing the present value of the rent in the fishery. We make the further simplification that we start without any fleet and that the boats we build have no alternative use. The best policy will then be to invest in an optimal fleet at time zero and maintain it forever by setting aside the fraction δK of revenues to cover depreciation of the fleet ($\delta = 1/T$, T being the lifetime of a fishing vessel). The present value of rents is then

$$V = -K + \sum_{t=1}^{\infty} \frac{ER_t - \delta K}{(1+r)^t}. \tag{12.29}$$

If the probability distribution of the stock (and the TAC) is time-invariant, ER will be the same year after year. Then the sum in the above expression will be a convergent geometric series and we get

$$V = -K + (ER - \delta K)/r. \tag{12.30}$$

We get a more intuitive interpretation of this if we multiply on both sides by r (the maximum of V will occur for the same value of K if we multiply V by a scalar). Then we get

$$V^* = ER - (r + \delta)K. \tag{12.31}$$

What we are in fact maximizing is the rent per year, calculated as the revenue net of operating cost less capital cost. The capital cost consists of two elements, the depreciation of capital, δ, and the opportunity cost, r, of tying up capital in a fishing fleet rather than investing in something else giving the return r. The condition for maximum rent is

$$E(dR/dK) = r + \delta. \tag{12.32}$$

What, then, is $E(dR/dK)$? From equation (12.28) we see that $dR/dK > 0$ only when $aK < Q$, i.e. when the total allowable catch is greater than the capacity of the fleet; only then will another vessel make any contribution to the total catch. Define $F(Q)$ as the probability that the total allowable catch is less than or equal to Q. Then we have

$$[1 - F(aK)] = (r + \delta)/Pa. \tag{12.33}$$

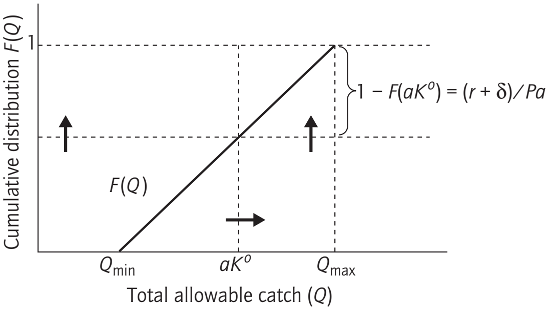

Fig. 12.7 Optimal fleet capacity (K^0) for a total allowable catch (Q) that fluctuates randomly between $Q_{\min}$ and $Q_{\max}$. $F(Q)$ is the cumulative distribution function. The linear form of F implies that the probability density is constant. The arrows show the effect of a higher price, lower capital costs, or technological progress (higher a).

Figure 12.7 shows the optimal solution, with arrows indicating how a lower capital cost ($r + \delta$), a higher price net of operating cost (P), or technological progress (greater a) affects the solution. We see that a lower capital cost, a higher price net of operating cost, or technological progress all increase the optimum fleet capacity, as indeed we would expect. We also see that only exceptionally would it be economically sensible to invest in a fleet that is large enough to take the maximum TAC (the Q-value for which $F(Q) = 1$). This would involve investment in boats that most of the time are not needed, contributing to cost all the time but to revenue only infrequently. Only if the cost of capital is exceptionally low would it make sense to have a fleet that could take even the largest TAC.

Note also how a change in the probability distribution affects the optimal fleet capacity. Suppose it is realized that the minimum total allowable catch could be much lower than $Q_{\min}$ in Fig. 12.7 but that the probability density of Q remains uniform between $Q_{\max}$ and the new $Q_{\min}$. This would rotate the line in Fig. 12.7 clockwise (it is fixed at the point 1, $Q_{\max}$) and thus reduce the optimum fleet capacity.

In this section we have regarded the fleet as being managed by a single owner (the social planner again). Although this approach is useful to derive optimality conditions, from the point of view of the whole economy, this is not how the real-world fishing fleets are run. A pertinent question is: will individual decision makers achieve the optimality? Under open access they certainly will not, but in a market-driven management regime such as individual transferable quotas (ITQs), to be discussed below, they might. There is a presumption, however, that they will in fact overinvest when the crew is remunerated by a share in the catch, but ITQs are likely nevertheless to lead to much less overinvestment than open access. For details of this analysis, see Hannesson (2000).

12.9 MANAGEMENT METHODS

Based on the deterministic, surplus production model it has been concluded that all we need to do to manage fisheries for maximum economic benefit is to tax fishing effort or the landings of fish sufficiently to eliminate all incentives for economic overfishing. The argument is perfectly valid within the framework of the said model, provided that the catch per unit of effort increases with the stock level. For fluctuating stocks there is a case for control by landing fees, provided there is no economic uncertainty and the catch per unit of effort depends on the stock size in a stable and predictable way. Landing fees versus output controls (fish quotas) have been discussed by Weitzman (2002).

We look, first, at the deterministic biomass-growth model. Consider sustainable yield and the production relationship in equation (12.4a), which gives rise to Fig. 12.5. As explained above, the open-access equilibrium occurs where the average sustainable revenue is equal to the cost per unit of effort, while optimal exploitation requires that the cost per unit of effort be equal to the marginal sustainable revenue. We may in fact achieve the optimum solution by moving the line showing cost per unit of effort upwards until it intersects the marginal sustainable revenue line above the optimum level of effort, or by rotating the average sustainable revenue line downwards until it intersects the cost per unit of effort line above the optimum level of effort. These movements would be accomplished by putting a tax equal to t_f on effort, or t_y on the landings of fish, such that

$$P(1-t_y)Y(f^o)/f^o = P(dY/df)\big|_{f^o} \tag{12.34}$$

or

$$C(1+t_f) = P(dY/df)\big|_{f^o} \tag{12.35}$$

where f^o is the optimal level of effort. Either tax would confiscate all rents in the fishery and deter the fishing firms from investing in a bigger fishing fleet than needed to take the optimum sustainable yield.

This solution is neat in theory, but even within the confines of the deterministic model it is not as straightforward to apply as it may seem. Fishing effort is produced by a number of different inputs: manpower, capital, fuel etc. All of these would have to be taxed proportionately in order not to disturb the cost-minimizing combination of inputs. Taxing landings would appear more straightforward, but the optimal tax is determined by the growth characteristics of each stock, so that if many stocks are being fished by the same fleet, the landings from each stock would have to be taxed at a different rate. Finally, there is the case where the density of fish is always constant (equation 12.4b). Here the value of the catch per unit of effort is constant. An optimal tax on landings or on effort would equalize the revenue per unit of effort and the cost per unit of effort for all levels of effort but would fail to identify any particular level of effort.

But the most difficult problems occur when we enter the world of fluctuating stocks and TACs. Note that these fluctuations typically occur on a much shorter time-scale than the lifetime of fishing vessels. We need, therefore, to contract and expand fishing effort over the lifetime of a single boat, perhaps over several cycles. This is not easily accomplished by changing tax rates. Such changes more often than not are time-consuming, unless the management authorities get a mandate to do so swiftly and substantially as the circumstances might require. But even if that mandate existed, the management authority would not know precisely how the industry would react to a change in the tax. It might even react in a direction opposite to what the authority would expect and opposite to what would happen in the long run. A fisherman who has to care for a mortgage or two, a wife, a child, a dog and a car might, in the face of a reduced income due to a higher tax, decide to increase his effort in order to make ends meet in the short run, even if in the long run he could not renew his boat if the high tax were to prevail. Trial and error would presumably teach the authorities how fishermen respond to the tax changes, but that learning process might need a longer time-scale than tolerable to cope with short-term fluctuations in fish stocks.

It is difficult, therefore, to see how one can do without some direct control of the fishing activity, in order to cope with random fluctuations in catches. Two major modes of control are available, a control of fleet capacity and fishing effort, and a control of the catch through catch quotas.

Effort controls

Effort controls only indirectly achieve the short-term objective of keeping the catch of fish within some set limit. These types of control may be very imprecise in this regard; the relationship between effort and catch is seldom precisely known and is likely to depend on the size of the stock and climatic and oceanographic conditions. Fishermen may get around effort controls if all elements of effort are not included: a limited number of fishing days may be made ineffective by using more gear, for example. The only advantage effort controls would seem to have compared to a direct control of the catch is that they may be much easier to monitor; fishing boats can be seen and counted, their trips and even type of activity can be monitored, nowadays by satellite tracking, and the gear and other equipment they use can be inspected. Controlling landings is, on the other hand, often costly or nearly impossible, to say nothing of the throwing away at sea of undersized fish or fish that are not covered by a quota.

Boat licences are related to effort controls. This method can be used for controlling the capacity of the fishing fleet, but it has several limitations. Fishing capacity is a multidimensional variable, and it is difficult to control all of the variables optimally. In order to be effective a boat licence has to specify the size and design of a boat in some detail. Naval architects have been notoriously inventive in circumventing such regulations, packing an impressive amount of fishing capacity into a hull that meets length or tonnage requirements. In some cases such designs have been alleged to reduce the seaworthiness of fishing vessels. Fishing licences therefore are an imprecise method of controlling fleet capacity and one that causes unnecessary costs. Individual transferable catch quotas (ITQs) would appear to do so much more effectively by affecting the incentives to invest, provided they can be effectively implemented.

Individual transferable quotas

Catch quotas have frequently been used for keeping the total catch from a stock within desired limits. As soon as fisheries started to be controlled by TACs it became evident that this caused new problems in fisheries where the capacity of the fishing fleet exceeded that which was necessary to take the permitted catch. Often a fierce competition developed for getting the largest possible share of the TAC. In many cases management responded by dividing the TAC among the boats in the fishery.

From this, ITQs evolved. When the TAC was much less than the catch capacity of the boats, it was clear that cost savings could be achieved by allowing people to trade quotas among themselves rather than having each and every one go out and fish his perhaps very small quota. In that way the owners of active boats could make ends meet, and those who were eligible to participate in the fishery but chose not to got a share of the pie by renting out their quota. Making the quota allocation valid for a long time eliminates the incentives to invest purely for the purpose of getting a share of the rents in the fishery, an activity which in the end is self-defeating; in the long run the rents get absorbed by unnecessary costs, as has already been explained. With a quota allocation that is secure for a period at least as long as the lifetime of a fishing boat the quota holder can predict his future catches, using the best available biological evidence. He would have no incentive to invest in a fishing boat which is larger or better equipped than needed to take the expected future catches, and if a bigger boat is more cost effective he would be able to acquire an additional quota allocation by buying it from somebody else.

ITQs can be determined either as fixed tonnages or shares of the TAC. Using fixed tonnages for stocks where the TAC varies from year to year makes it necessary for the fisheries manager to buy and sell quotas, depending on whether the TAC is above or below the total amount of quotas allocated. If the quota tonnage is set low enough the manager would be selling quota more often than buying and would be making money on these transactions (Hannesson 1989). This would amount to a special tax on the fishing industry. Tonnage quotas transfer the risk associated with fluctuating stocks from the industry to the fisheries manager, usually the government. That risk can indeed be greater than the government is prepared to bear. Fixed tonnage quotas were initially tried in New Zealand, but when it became clear that the yield potential of the orange roughy stocks had been overestimated the government backtracked and redefined the quotas as shares of the TAC (Batstone and Sharp 1999). This is the system in use in most of the ITQ systems in the world today. With share quotas the industry has to bear the risk associated with fluctuating TACs, but quota holders can still make rational predictions of the catches they may expect to get on the basis of their quota, using the best evidence available about fluctuations in the stocks they fish and the criteria on the basis of which the TAC is set. Hence boat owners do not have any obvious incentives to overinvest under a share quota system. The so-called share system, by which labour employed on fishing boats is remunerated with a share in the catch value and not through a fixed wage rate, may, however, to some extent distort the system of incentives and entice boat owners to invest more than is desirable from an overall perspective (Hannesson 2000).

There is a large and still increasing literature on ITQs. The idea may be traced back to Christy (1973, 1975). Arnason (1995) and Batstone and Sharp (1999) contain descriptions of ITQs in Iceland and New Zealand. Boyce (1992, 1996) considers bycatch and other problems under ITQs. A much-quoted critique is Copes (1986). Among other contributions are Grafton (1996), Hannesson (1996, 1997a) and Weninger (1998).

12.10 INTERNATIONAL ISSUES

Management by TACs or other methods affecting catches and fish stocks is meaningful only if the country in question can exercise effective control over the stocks. The establishment of the Exclusive Economic Zone (EEZ) in the 1970s was critical in this respect (for an authoritative text, see United Nations 1983; and Christy and Scott 1965, for a discussion preceding the revolution in the law of the sea in the 1970s). In some cases fish stocks became enclosed by the EEZ of a single sovereign state, while in other cases stocks migrate between the zones of two or more sovereign states, so no single state can exercise effective control over them. Nevertheless, in many cases the states concerned have agreed on effective controls over shared stocks, such as setting an overall TAC and dividing it among themselves. Having accomplished this, each country can apply measures such as ITQs to its own share of the TAC, for the purpose of maximizing its economic benefit from its share of the fishery. Norway has, for example, concluded such agreements with the Soviet Union, subsequently taken over by Russia, and the European Union. The member countries of the European Union have agreed among themselves on the division of the North Sea stocks, but fisheries policy is one of the common policies of the Union.

Still there are many stocks that spend a part of their life history outside any EEZ, and some stocks are mainly or even wholly confined to the high seas. Management of such stocks, and of shared stocks, must be by voluntary consent by the parties concerned, as these are sovereign states. It is particularly difficult to achieve such agreements for stocks on the high seas, not least because the number of interested parties is indeterminate.

Game theory seems an appropriate tool for analysing the question of whether nations will come to agreement on fisheries issues. There already exists a voluminous body of literature on this which it is impossible to review here. Important references are Munro (1979), Levhari and Mirman (1980), Vislie (1987), Kaitala and Munro (1997), and Hannesson (1997b). Here a simple model which at least gives a flavour of the issues will be presented.

Suppose a stock can be fished either at an immature or a mature stage. There is no stock–growth relationship to be taken into account; each period a stock S emerges and can be fully depleted without jeopardizing future recruitment, but if the exploitation is delayed by one period, the stock will grow to $S(1+g)$, where g is the rate of growth. Suppose N identical countries have access to the stock. If they all wait for one period and allow the stock to grow, each would get $S(1+g)/(1+r)N$. The discount rate appears because such waiting is an investment, as already explained. If they fish the stock immediately, each would get S/N, but if all except one decide to wait they would wait in vain; the one who does not play along could take it all.

This gives rise to the following payoff matrix, which shows the return to one player. The lines show the strategy of the player in question, while the columns show the strategy of the other players, all assumed to adopt the same strategy.

	Wait	*Don't wait*
Wait	S/N	0
Don't wait	S	$S(1+g)/(1+r)N$

Provided $g > r$, it would be better for all to wait. The so-called Nash equilibrium in this game does not result in that solution, however. A Nash equilibrium is a situation in which no player can gain by changing his strategy, given the strategy of the other players. If the N-1 players wait, the best the remaining player can do is not to wait, as $S > S/N$. And if the N-1 players do not wait, the best the remaining player can do is to do likewise, because otherwise he would get nothing.

This certainly makes for a pessimistic outlook with respect to the possibility of achieving a mutually advantageous solution. The situation is not, however, well represented by this framework. Fishing is not a one-shot game; fish stocks are renewable, and fishing is an activity that is repeated year after year. What if we look at a strategy which, loosely speaking, means that 'I'll be nice to you as long as you'll be nice to me, but if you're nasty to me I'll be nasty to you for ever after.' In this setting this would mean that a representative player would wait as long as all the rest do likewise, but if one player does not wait for the fish to grow, the others will do the same forever. The present value of the strategy of playing cooperatively forever is

$$\begin{aligned} PV_c &= S(1+g)/(1+r)N + S(1+g)/(1+r)^2 N + \ldots \\ &= S(1+g)/rN, \end{aligned} \tag{12.36}$$

while the present value of not playing cooperatively is

$$PV_n = S + S/(1+r)N + S/(1+r)^2 N + \ldots = S + S/rN. \tag{12.38}$$

Cooperation is profitable if $PV_c > PV_n$, which implies

$$g/N > r, \tag{12.39}$$

which can be interpreted as saying that each player's share in the rate of growth of the stock has to be greater than the rate of interest. Clearly, for reasonable rates of growth and discount rates, the number of participants does not have to be very high to make voluntary agreements unlikely. If the cost per unit of fish landed depends on the stock the likelihood of agreement increases, but decreases again if the costs differ among participants (Hannesson 1995). This game can also be seen as yet another example of how discounting the future makes it worth while to trade off permanent losses against a short-term gain; if r is zero equation (12.39) will always be satisfied, as long as N is finite.

The most recent attempt to come to grips with uncontrolled fishing on the high seas is the UN Agreement on Straddling Stocks and Highly Migratory Stocks, concluded in 1995. One source for the text of this agreement is FAO (1995), and a review of the status of this agreement is provided by Munro (2000). According to this agreement, the authority to manage such stocks rests with regional management organizations. Any country with a 'real interest' (not further defined) has a right to become a member of such an organization, and all countries, even those who are not members, are obliged to abide by the decisions of such organizations. The above analysis indicates that these organizations will not be likely to succeed unless they manage to limit the number of interested parties and the quantity they are allowed to fish. The latter is not possible unless there is an effective system in place to punish violators. At the present time this is up to the state whose flag the offending vessel is flying, with some rights of other interested states to inspect suspected offenders and to take action if the flag state does not do so.

12.11 CONCLUSIONS

It is impossible, within the limited space at our disposal, to cover all issues that arise in fisheries economics. The most important ones have, I hope, been covered but some still remain. Of those remaining the most important ones are management and enforcement costs (see Schrank et al. 2002; Sutinen and Andersen 1985), the recreational use of fisheries (see McConnell and Sutinen 1979; Anderson 1993), and marine protected areas (see Lauck et al. 1998; Hannesson 1998; Sanchirico and Wilen 1999). The last topic has aroused quite a bit of interest over the last few years, but this approach is unlikely to provide a panacea for all fisheries management problems and is certainly no substitute for ITQs or other methods that would get us close to optimal management. On these subjects we refer the interested reader to the bibliographic entries just cited and the further leads that one would find in these references.

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13 Choosing the Best Model for Fisheries Assessment

PER SPARRE AND PAUL J.B. HART

13.1 INTRODUCTION

Fisheries scientists have developed a suite of models for a variety of purposes ranging from fundamental descriptions of fish growth to long-term predictions of population dynamics. While many of the chapters in this volume review the basic concepts, a full description of these could easily have occupied both volumes of this book. For detailed reviews of fisheries models we recommend the excellent books by Hilborn and Walters (1992) and Quinn and Deriso (1999), and for a more general overview, we recommend Jennings et al. (2001). It is also still worth consulting Ricker (1975). Our objective in this chapter is more modest: to outline the basic concepts behind fisheries modelling, and review briefly the major modelling options that confront the fisheries biologist. We hope that this overview will help readers to see how the various methods outlined in Chapters 5–12, Volume 2, fit together, as well as providing links with various chapters in both volumes that review the basics of fish biology.

There is a risk in saying a little about models without saying 'everything' about them, because fisheries managers may become tempted to grab an 'off the shelf' model without paying enough attention to its underlying assumptions, or ensuring that it is applied to an appropriate situation. It is imperative to look at each situation afresh and to choose models that can be tailored to each situation. It is also important to test or 'confront' models with data (Hilborn and Mangel 1997). Our approach here is to provide a suite of examples, which we believe to be representative of contemporary fisheries models. Throughout we have tried to follow three general principles: (1) models should be as simple as possible, (2) the complexity of a model should match the objective and the available data, and (3) models should be judged by their utility rather than by the beauty of the mathematics, because they are tools, not objectives in themselves.

Mathematical models are used to distil a complicated system into a simpler one that we can readily understand and use for predictions. Our ability to model the real world depends on our ability to collect adequate data. Smart models cannot substitute for bad data. It may take hours to develop a mathematical model and months to implement it on computer, but it may take decades to collect an adequate time series of quality fisheries data. The descriptive part of a fisheries research programme, perhaps using the techniques of Geographical Information Systems (GIS), (Meaden and Do Chi 1996), may sometimes be more valuable than a mathematical model, which in the worst case may be a poor reflection of the key mechanisms revealed by the data. Models may not necessarily enhance our understanding of a fisheries system.

13.2 BASIC CONCEPTS

A general expression for a mathematical model is useful for the presentation of guidelines for the choice of model (Schnute 1994). A model is usually framed in the form of a mathematical function, which can be written as

$$F{:}(X_t, P) \rightarrow Y_t, \tag{13.1}$$

where X_t and Y_t are variables at time t and P is a parameter. What equation (13.1) says is that the function F takes values of X_t and P and maps them onto values of Y_t such that there is a unique value of Y_t for each pair of values (X_t, P). In a fisheries context X_t could be some state of the fish stock and Y_t the catch. The dynamics of the state of the stock, say its size, is likely to be a function of not only biological processes such as births and deaths due to natural causes but also deaths due to fishing. As fishing is a variable that can be controlled we need to know the relationship between X_t and the fisheries-related control variable Z_t. So we need a new function G that will describe the way in which X_t changes in response to Z_{t-1}. This is evaluated at $t-1$ because it is assumed that there is a lag between the application of the control and the change in the state of the fish stock. The new function G is then

$$G{:}(Z_{t-1}) \rightarrow X_t. \tag{13.2}$$

Equation (13.1) can now be rewritten as

$$F{:}(G(Z_t), P) \rightarrow Y_t. \tag{13.3}$$

So in general terms we can say that the dynamics of the system is fully accounted for by two functions of X, Z and P,

$$F{:}(X_{t-1}, Z_t, P) \rightarrow X_t \tag{13.4a}$$

$$G{:}(X_t, Z_t, P) \rightarrow Y_t. \tag{13.4b}$$

In most cases of interest F and G and the variables X_t, Y_t, Z_t, and the parameters P, are multivalued and have to be described by vectors. As a result a fish population will be characterized in each year t by a vector of state variables $\mathbf{X}_t = (X_{1t}, X_{2t}, \ldots, X_{mt})$ with dimension m. $\mathbf{Y}_t = (Y_{1t}, Y_{2t}, \ldots, Y_{nt})$ will denote the corresponding vector of n observations obtained annually from this population. Suppose also that a control vector $\mathbf{Z}_t = (Z_{1t}, Z_{2t}, \ldots, Z_{rt})$ represents r quantities known to influence the population dynamics. Then the two vector equations

$$\mathbf{F}(\mathbf{X}_{t-1}, \mathbf{F}_t, \mathbf{P}) = \mathbf{X}_t \tag{13.5a}$$

$$\mathbf{G}(\mathbf{X}_t, \mathbf{Z}_t, \mathbf{P}) = \mathbf{Y}_t \tag{13.5b}$$

encapsulate descriptions of system dynamics and measurement, respectively, where $\mathbf{P} = (P_1, P_2, \ldots, P_k)$ represents a parameter vector of dimension k that remains constant through time. Thus the vector $\mathbf{F}$ governs the evolution from time t to $t+1$ of the m states $\mathbf{X}_t$, and $\mathbf{G}$ relates the n observations $\mathbf{Y}_t$ to the current system state $\mathbf{X}_t$. As outlined by Schnute and Richards (2001 and Chapter 6, this volume), the model (13.5a)–(13.5b) describes the progression of $\mathbf{X}_t$ through the space of all possible states, and is therefore called a state space model.

A concrete realization of (13.5a) and (13.5b) is the discrete form of the logistic equation

$$B_{t+1} = B_t + \alpha B_t\left(1 - \frac{B_t}{B_\infty}\right) - qE_tB_t \tag{13.6a}$$

$$C_t = qE_tB_t \tag{13.6b}$$

where B_t is biomass of fish, E_t is fishing effort and C_t is catch, all at time t. α is the intrinsic rate of natural increase, B_∞ is the carrying capacity and q is the catchability coefficient. In terms of our general form in (13.5a) and (13.5b), $m = n = r = 1$, $k = 3$, $\mathbf{X}_t = B_t$, $\mathbf{Z}_t = E_t$, $\mathbf{Y}_t = C_t$, and $\mathbf{P} = (\alpha, B_\infty, q)$.

A model may be deterministic or stochastic. The deterministic model yields a one-to-one relationship between each X and each Y. With the deterministic model we assume that there is no process error meaning that the equation is perfect, and we can make a precise prediction of $\mathbf{Y}$. This outcome is unlikely in fisheries science. There is always some degree of uncertainty when predicting the development of individual fish, the size of a fish stock, or the capture rate of a fishing fleet. A stochastic model operates with many Y-values for each X-value, as will be discussed later. Deterministic models are easier to handle than are stochastic models. Also the computations and the data demands for stochastic modelling are greater than those for deterministic models. Whether to use deterministic or stochastic modelling is an important choice.

The choice of parameter vector, $\mathbf{P} = (P_1, P_2, \ldots, P_k)$, and the choice of the relationship between **X**, **Z**, **P** and **Y**, here called, **F** and **G**, is essentially the choice of the model. The number of parameters (k) may be small, say 2 or 3, of it may be hundreds or thousands. The number of parameters is an important choice. You may choose to cover many details in your description of the world, or you may choose to apply the minimum number of parameters. There are advantages and disadvantages of both approaches. The model-designer is often not free to choose parameters, but is more or less constrained by the objectives of the model. It may be mandatory to introduce certain parameters into the model to meet certain objectives. Alternatively, some parameters may have to be left out, because the data available cannot be used to estimate them. This is a typical situation for fisheries models, with the number of unknowns greatly exceeding the number of observations (Schnute and Richards 2001).

It may be possible to choose plausible values for parameters that cannot be estimated. The philosophical question faced is whether it is better to ignore a feature of the system description or to use the best possible 'guesstimate' available. Obviously there is no general answer to the question.

Typical examples of fisheries models with few parameters are the surplus production models (equations (13.6a) and (13.6b), and Chapter 6, this volume), which do not account for the size or age composition of stocks. Models accounting for size or age usually have many more parameters. Going from single-stock models to multi-stock models clearly increases the number of parameters. Similarly, going from a one-fleet and one-area model to a multi-fleet and multi-areas model increases the number of parameters yet again. The number of parameters may not be proportional to the number of components, but may be more as there may be a need to model interactions between the various components. If interactions such as that between fish stocks or fishing fleets are not accounted for in the model, one might as well have used the simpler single-species model.

The model may be applied to estimate the parameters, or to predict the value of **Y** for an assumed value of **X**. The latter application is applied to answer 'what-if-then' questions. For example, what will happen to the landings, **Y**, if the fishing effort, **Z**, is a certain number of fishing days per year? In terms of the logistic equation of a fishery (13.6), one might ask what happens when E_t is increased by 10%?

The model may be dynamic or static. A dynamic model predicts output for a time series of years, whereas the static model predicts the average output. A static model may be said to predict what will happen 'on average', say, over the next 10 years, whereas the dynamic model predicts what happens in each individual year. It is usually easier to handle the static than the dynamic models, because there are more details to describe in the dynamic model, and consequently more parameters.

An example from fisheries of a dynamic model is the model of the Pacific halibut (*Hippoglossus stenolepis*) fishery by Thompson and Bell (1934) (Shepherd and Pope, Chapter 8, this volume). This predicted numbers of fish dying over a 13-year period when fishing mortality increased from 40% to 60%. The yield-per-recruit model of Beverton and Holt (1957) is an example of a static model, as is the Ricker stock–recruitment curve (Myers, Chapter 6, Volume 1) which gives the average recruitment for a given spawning stock biomass. Static models in fisheries are most often chosen because data for dynamic models are not available. Often the static models are called 'Long-term prediction models' and the dynamic models are called either 'Short-term prediction models' (that, is 2–3 years) or 'Medium-term prediction models' (10–20 years) (See also Shepherd and Pope, Chapters 7 and 8, this volume).

13.3 STOCHASTIC MODELLING

No model in fisheries can predict the exact value of any variable. To the simple model one should ideally add stochastic vectors, δ and ε, so the stochastic model reads as

$$\mathbf{F}(\mathbf{X}_{t-1},\mathbf{Z}_t,\mathbf{P}) + \delta = \mathbf{X}_t \tag{13.7a}$$

$$\mathbf{G}(\mathbf{X}_t,\mathbf{Z}_t,\mathbf{P}) + \varepsilon = \mathbf{Y}_t. \tag{13.7b}$$

The stochastic vectors δ and ε take unpredictable values from a probability distribution which we may have some knowledge about. Usually, δ and ε are assumed to be normally or log-normally distributed in fisheries models. The stochastic term accounts for all the elements not accounted for by $\mathbf{F}(\mathbf{X}_{t-1}, \mathbf{Z}_t, \mathbf{P})$ and $\mathbf{G}(\mathbf{X}_t, \mathbf{Z}_t, \mathbf{P})$. If the model actually reflects the true relationship between **X** and **Y**, which is rarely the case in any fisheries model, the stochastic term has a known mean value which is usually zero. However, the fisheries models are always incomplete with an unknown bias.

In more detail a stochastic version of (13.6a) and (13.6b) requires three probability distributions to be defined. These are

$$P(\mathbf{X}_t,|\mathbf{X}_{t-1},\mathbf{Z}_t,\mathbf{P}), \quad P(\mathbf{Y}_t,|\mathbf{X}_t,\mathbf{Z}_t,\mathbf{P}), \quad P(\mathbf{Y}_0,|\mathbf{P}). \tag{13.8}$$

The third item determines the initial state of the system. Any distribution can describe the variation in $\mathbf{X}_t$, $\mathbf{Y}_t$ and $\mathbf{X}_0$.

The stochastic terms, δ and ε, can be thought of as containing two components, the measurement error and the process error. Each can be expressed as a linear combination of two terms, $\delta=\delta_m+\delta_p$ and $\varepsilon=\varepsilon_m+\varepsilon_p$. The measurement error $(\delta_m, \varepsilon_m)$ is the deviation expected if the model is correct, and the process error $(\delta_p, \varepsilon_p)$ is the deviation caused by insufficiencies in the model (Schnute 1994). In a dynamic model, the process errors will appear in the entire dynamic system, whereas the measurement errors will occur individually in each time step. As an example of process error and measurement error, we may consider a research survey, which suddenly gives an unexpectedly high density of fish. This may be due to bad survey design, which would lead to measurement error, or to an unexpectedly high stock productivity, which would be the result of process error. A discussion of how to distinguish between the two sources of error is given in Hilborn and Walters (1992).

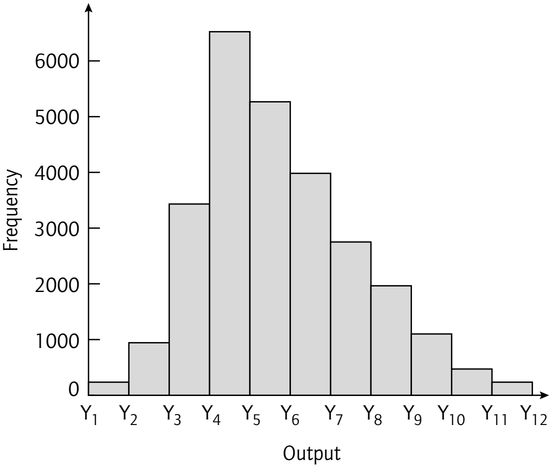

Fig. 13.1 Output from a stochastic simulation in terms of the equation $\mathbf{Y}+\varepsilon=\mathbf{F}(\mathbf{X}, \mathbf{Z}, \mathbf{P})$.

The way in which $\mathbf{Y}_t$ may vary is shown in (Fig. 13.1). Where stochasticity is accounted for in (13.7a) and (13.7b) by the vectors of residuals δ and ε, they may have a probability distribution of an assumed form or a distribution estimated from time series of observations of the pair $(\mathbf{X}_t, \mathbf{Y}_t)$.

When using a stochastic model for prediction, the standard procedure is to let a computer program repeat the same prediction or simulations many times, say 1000 times or 10000 times (the Monte Carlo method; Hilborn and Mangel 1997). In each simulation the computer program draws the values of parameters from a random-number generator. Eventually, the probability distribution is estimated by the frequency distribution of **Y** (see Fig. 13.1). This means that a stochastic model requires as input the characteristics of the probability distribution for the parameter estimates. For a general introduction, see for example Hilborn and Mangel (1997) and Manly (1997). One of the earliest attempts at introducing a stochastic element into a fishery model was by Beddington and May (1977). They attached stochastic process variation to the parameter α of the Schaefer surplus yield equation (equations (13.6a) and (13.6b), and

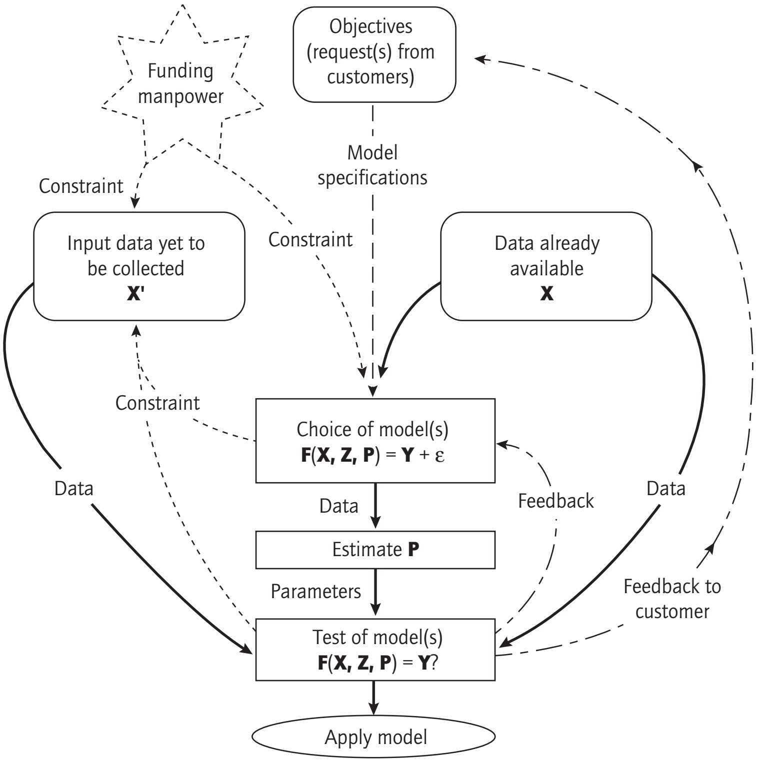

Fig. 13.2 Flowchart for selection of model comprising the steps: Define objectives and identify existing data and data to be collected subject to available funding. Then choose the input, **X**, the control variables, **Z**, the output, **Y**, the parameters, **P**, the relationships between **X**, **Y** and **P**, the stochastic term, ε. Then estimate parameters, **P**, test the model and eventually apply it. For further explanation see text.

Schnute and Richards, Chapter 6, this volume) and showed that the coefficient of variation of yield increased as effort increased, so making the prediction of yield less and less reliable as the fishery took more and more fish.

13.4 MECHANICS OF CHOOSING A MODEL

The choice of a model will depend on what is required as output, and will be constrained by data available to estimate parameters. For a manager the requirement is most likely to be how the fishery will behave under a given measure. Existing models tailored to the particular fishery may meet this objective. For scientists doing pure research, the model may help to explain the workings of nature, and this may often require creation of a new method from first principles. In all cases the task of choosing a model can be broken into five steps:

1 Choosing the states, $\mathbf{X} = (X_1, X_2, \ldots, X_m)$.
2 Choosing the control variables $\mathbf{Z} = (Z_1, Z_2, \ldots, Z_r)$.
3 Choosing the output, $\mathbf{Y} = (Y_1, Y_2, \ldots, Y_n)$.
4 Choosing or estimating the parameters, $\mathbf{P} = (P_1, P_2, \ldots, P_k)$ and the relationships between **X**, **Z**, **Y** and **P**.
5 Choosing the assumption about the stochastic terms, $\delta = (\delta_1, \delta_2, \ldots, \delta_r)$ and $\varepsilon = (\varepsilon_1, \varepsilon_2, \ldots, \varepsilon_r)$.

Figure 13.2 illustrates some key elements in the process of choosing a model. The output, **Y**, is selected to match some objectives defined either by the scientist or perhaps more often by a customer, which is often also the funding body. Also the funding and the manpower available for the creation of the model will place obvious constraints on what can be achieved.

Once the objectives are defined clearly, the next step is to investigate the existing data (**X**) for use as input to the model. Depending on the funding, one may (or may not) consider collection of additional data (**X′**). For example, to apply an age-structured model, age composition data must be available.

The choice of model should aim at utilizing all relevant and available data. Within each family of fisheries model, there are usually a small number of standard relationships, as listed in Table 13.1. The differences between models are due mainly to differences in the degree to which input is aggregated. For example, are data given by geographical areas, by month or by year, and by fishing fleet?

Once the relationships between **X**, **Z**, **P** and **Y** have been determined, and this is usually the easiest part of the task, the next step is to estimate the parameters and then test if the model fits the data. If the model does not fit the data, it should be modified. Ideally, one should work simultaneously with a number of alternative models (Hilborn and Mangel 1997). In many cases, if the aims of modelling are known, and the manager is using standard fisheries data, it is possible to use models already available in the literature.

A typical example of model choice for the management of a fishery would be a situation where the management agency has data on effort exerted by the fleet ($\mathbf{X}_{Fl}$) measured as days at sea and landings in weight of each species ($\mathbf{Y}_{Sp}$). The fishery scientist now needs to choose a model which relates the input variable **X** to the output variable **Y**. An example might be $\mathbf{Y}_{Sp} = q\mathbf{X}_{Fl}\mathbf{B}$ where q is the catchability coefficient and **B** is the biomass vector for each species. Alternatively, the job could be done using a surplus production model (Schnute and Richards, Chapter 6, this volume). In the service of realism, the data on **X** and **Y** could be divided by fleet, area and time in the following way:

$\mathbf{X}_{\mathbf{1},Fl,p,y,Ar,g}$ = Effort of fleet *Fl* in time period p (e.g. month) of year y in area *Ar* using gear g

$\mathbf{Y}_{\mathbf{1},Sp,Sc,Fl,p,y,Ar,g}$ = Landings of species *Sp*, commercial size category *Sc* caught by fleet *Fl* in time p (e.g. month) of year y in area *Ar* using gear g

Very often, fisheries scientists are constrained by managers who want a particular type of output (**Y**) from a model. An example might be where managers want to reduce the amount of discarding, and to that end, they want to introduce technical measures. Suppose further that one of the measures is to close a certain sea area for fishing by certain types of vessels using certain types of gears with certain mesh sizes. An example is the so-called Plaice-box in the North Sea (Pastoors et al. 2000). The output may then be the 'discard ogive' before the introduction and after the introduction of the closed area. The discard ogive can be parameterized by $DL_{50\%}$ and $DL_{75\%}$. To be able to respond to such a request, a number of preconditions must be met. Data must be disaggregated by area, fleet, gear, mesh size, species and body length. A traditional surplus production model cannot be used, as this type of model does not cover many of the features of the problem. Accordingly, a more complex age-structured model is required.

13.5 ESTIMATION OF PARAMETERS

Estimation of the parameters, **P**, from the observations (**X**,**Y**), can be made by, for example, minimization of the so-called modified χ^2 criterion (see for example Sokal and Rohlf 1981):

$$\chi^2 = \sum_{i=1}^{n}\sum_{v=1}^{m}\frac{(F(X_{iv},P)-Y_{iv})^2}{F(X_{iv},P)}, \tag{13.9}$$

when $v = 1, 2, \ldots, m$ sets of observation ($X_{1v}, X_{2v}, \ldots, X_{mv}$) are available. There are other equally well-established techniques for parameter estimation, such as the maximum-likelihood method. Thus, there is a choice of methodology when using the model for parameter estimation, although the results will be almost the same when data fit the model well. The problems emerge when there is a large variation of observations around the values predicted by the model. In this case, the choice of estimation model may have great impact on the estimated values, and sometimes in fisheries the methods are so elastic and the data so bad, that it becomes almost up to the researcher to decide the parameter value, by manipulating the assumptions behind the estimation procedure. It might perhaps be better in these sick cases to admit that the estimation failed, and start the search for either better data or better models.

Together with the estimation of parameter values, the standard methods of parameter estimation will provide estimates of the probability distribution of the parameter estimates themselves. These in turn may be used as input for stochastic modelling.

The most common methodology for parameter estimation in fisheries science is represented by the Statistical Analysis System (SAS) computerized statistical system (e.g. DiIorio 2000). There is no space here for a deeper review of the mathematical features of estimation, but we refer readers to the large literature on mathematical modelling and parameter estimation (see Hilborn and Walters 1992, and Hilborn and Mangel 1997 for an introduction to the literature). It is strongly recommended always to follow the standards of generally accepted textbooks or computerized systems for parameter estimation, such as SAS or the S+ (e.g. Krause and Olson 2000) and to avoid inventing *ad hoc* estimation methods. The SAS procedures entitled 'GLIM' (General Linear Model) and 'MIXED MODELS' (Littell et al. 1999) appear to be able to handle almost any estimation problem encountered in fisheries research. In North America some fisheries scientists are using AD Model Builder (*http://otter-rsch.com/admodel.com*, AD Model Builder 2001) which is an efficient commercial package designed for non-linear estimation. The AD Model Builder is recommended for estimation when models are large, complicated and non-linear. The AD Model Builder makes it easy to code almost any model and to investigate its statistical properties. The Builder is also recommended for estimation when large, non-linear models are based on many observations and have many parameters (see also Pitcher, Chapter 9, this volume).

13.6 THE USE OF MATHEMATICAL MODELS IN FISHERIES

Models of exploited fish populations have developed along several different paths determined by the amount of detail included. Early attempts were constrained by the limited computing power that was available just after the Second World War. There was heavy dependence on integral calculus with equations that could be solved and there was a drive to find simple functions for growth and mortality. These early attempts have left a legacy that has been used to develop some sophisticated models, which use methods that were not available to the pioneers. In this handbook we have acknowledged the legacy by devoting chapters to surplus yield models (Chapter 6, this volume) and dynamic pool models (Chapters 7 and 8, this volume). In addition other chapters deal with traditional models of growth (Chapter 5, Volume 1) and recruitment (Chapter 6, Volume 1). The legacy pervades the practice of fisheries management but fishery scientists have gone beyond the early monolithic models, which tended to ignore differences between fisheries and fish stocks. Most assumed that the Beverton and Holt dynamic pool model could be applied to any species, so long as one could estimate the required parameters. In the remainder of this section we attempt to show how fishery scientists have developed detailed models to cope with the reality not always covered by the original formulations. In many ways, the submodels discussed are really only filling in the cracks that have appeared in the original edifice. There is definitely room for fresh thinking as described in the various chapters which deal with and develop the legacy.

In this section it is helpful to make a distinction between 'full' population models that allow forecasting of yields and stock dynamics under various fishing scenarios, and 'submodels' or 'ingredients' that go into these. For example, many models incorporate body growth rates, and this information is either input directly from data, or represented by an equation, which represents the data. This equation enters as a submodel. In many cases these submodels have been introduced to deal with detail that the earlier models did not account for. There are no hard-and-fast rules here, because, for example, an equation that describes relationships between stock size and recruitment might serve as an end in itself when one wants to predict optimal exploitation rates of semelparous species. Alternatively it might be a component of a full statistical catch-at-age model. But for presentation purposes, we adopt this distinction.

13.6.1 Simple models of fish stock dynamics

Most fisheries models are based on differential or difference equations, here exemplified by the model of the death process which is central to age-structured models of exploited populations:

$$\frac{dN_t}{dt} = -Z_t N_t \text{ or when integrated}$$
$$N_t = N_0 \exp(-Zt), \tag{13.10}$$

where $N(t)$ is the number of survivors from a cohort at time t and Z is the coefficient of total mortality. In fisheries, Z is usually assumed to remain constant during a standard time interval such as a month, a quarter or a year. Using a time step of length Δt, we get a difference equation, where Z is assumed to remain constant from time t to time $t + \Delta t$:

$$\Delta N_t = N_t - N_{t+\Delta t} = N_t[1 - \exp(-Z_t \Delta t)]. \tag{13.11}$$

It is important to notice that Z refers to the entire stock. If the stock is divided into fractions according to geographical areas, there is need for redefining Z when it becomes area-specific. This will be discussed below in connection with 'areas and migration'.

The total mortality, Z, is composed of fishing mortality F, and natural mortality M, which again can be further divided, for example:

$$M = M_0 + \sum_{p=1}^{NP} M_p, \tag{13.12}$$

where p is an index of 'predator type' as is done in multispecies VPA (Andersen and Ursin 1977; Shepherd and Pope Chapter 7, this volume). M_0 is the natural mortality not caused by predation, such as disease, spawning stress and old age and NP is the number of predators. M_p may be modelled as suggested by Andersen and Ursin (1977):

$$M_p = \frac{N_p R_p S_{pr,p}}{\sum_{j=1}^{j=P} N_j w_j S_{j,p}} \tag{13.13}$$

where $S_{j,p}$ is a measure of the suitability of prey j as food for predator p and R_p is the food ration for predator p. The multispecies VPA was an extension of the single-species VPA, which aimed at the estimation of M_p from the investigation of stomach contents of predators (Sparre 1991; Shepherd and Pope, Chapter 8, Volume 2).

13.6.2 Models of fishing

Like natural mortality, fishing mortality may be divided into fleet components:

$$F = \sum_{Fl=1}^{NFs} F_{Fl}, \tag{13.14}$$

where Fl is index of fleet and NF is the number of fleets. A fleet is a group of fairly homogenous vessels with respect to size, fishing operations and fishing grounds.

F_{Fl} may be further modelled, for example by:

$$F_{Fl,St,a} = E_{Fl} Q_{St,Fl} S_{Fl,St,a}, \tag{13.15}$$

where St is an index of a stock and a is an index of age groups. Q is the catchability of fleet Fl catching stock St. Here the F is given the index St to emphasize that almost all fisheries are mixed fisheries catching more than one species, a fact that is often not accounted for in routine stock assessments and certainly not in fisheries where the management system is still relatively primitive.

The gear selection (S) by trawls can be modelled by the logistic curve:

$$S_{Fl,St,a} = \frac{1}{1+\exp(\sigma_1 + \sigma_2 L_{St,a})};\ \sigma_1 = \ln(3)\frac{L_{50\%}}{L_{75\%} - L_{50\%}};\quad \sigma_2 = -\frac{\sigma_1}{L_{50\%}}, \tag{13.16}$$

where $L_{St,a}$ is the mean body length of age group a (see MacLennan 1992 for a review of gear selectivity). $L_{50\%}$ and $L_{75\%}$ are the lengths at which 50% and 75% of the fish entering the gear is retained, respectively. The logistic curve takes values between zero and one, starting with zero and approaching one as L increases (e.g. Hoydal et al. 1982). For some other gears like a gill-net a dome-shaped curve may better reflect the selectivity of the gear (Hovgård and Lassen 2000).

A simple relationship between mesh size (μ) in, for example, the cod-end of a trawl and the retention of fish of a length L is

$$L_{50\%} = S_{Fl,St}\mu_{Fl}. \tag{13.17}$$

The catchability may be modelled by a fleet and stock-specific constant, but it may also be assumed to be a function of stock biomass and the year, accounting for the technical development in fishing techniques:

$$Q_{Fl,year} = Q_0 B^{\beta}(a + by), \tag{13.18}$$

where Q_0, β, a and b are constants and y is year. This is just one among many other mathematical models one can imagine and it assumes that catchability increases with time in a linear fashion.

The catch can be estimated as follows. Assume that the output from the model might be the catch of age group a fish caught by fleet Fl. If we assume F and Z to remain constant in time period Δt (Baranov 1918), and we skip the stock index, then the 'catch equation' gives the catch as:

$$C_{Fl,a} = \frac{F_{Fl,a}}{Z_a} N_a(1 - \exp(-Z_a \Delta t)). \tag{13.19}$$

The yield in weight of the catch accumulated over age groups may also be estimated as

$$Y_{Fl} = \sum_{a=0}^{N} C_{Fl,a} w_a, \tag{13.20}$$

where N is the number of age groups and w_a is the mean body weight at age a. This is the basic form of the dynamic pool model, derived originally in continuous form as an integral equation, by Beverton and Holt (1957) (see Shepherd and Pope, Chapter 8, this volume for further details).

The value of the catch can be estimated by extending the model:

$$V_{Fl} = \sum_{a=0}^{N} C_{Fl,a} w_a Pr_{Fl,a}, \tag{13.21}$$

where Pr is the price per unit weight. Bioeconomic modelling is discussed in detail by Hannesson (Chapter 12, this volume).

The input vector, $\mathbf{Z}_t$, of the general model, $\mathbf{Y}_t = \mathbf{G}(\mathbf{X}_t, \mathbf{Z}_t, \mathbf{P})$ could include the fishing effort, the mesh size and the price, all of which are human inputs to the fisheries system. The yield and the value of the yield may be the output, and the parameters are those listed above which are not variables: $\mathbf{G}$ [$\mathbf{X}_t$, (Effort, Mesh size, Price), $\mathbf{P}$] = (Yield, Value). Fishing mortality may also be considered output, as it is used as a measure for the performance of the fisheries system.

The development of fishery models has made extensive use of the catch equation (13.19). It lies at the heart of Beverton and Holt's (1957) yield-per-recruit model, but since then it has been used extensively in the development of methods to estimate population size and fishing mortality. Equation (13.19) is the basis of VPA, which is described in detail in Chapter 7 (this volume) by Shepherd and Pope. The equation also lies at the root of statistical catch-at-age methods (Hilborn and Walters 1992). These derive an equation, which, in its simplest form, allows the estimation of initial cohort size, fishing mortality and the catchability coefficient from a multiple linear regression of catch on effort. Doubleday (1976) produced a non-linear equation relating catch to effort but a linear, and therefore easier to fit, version was derived by Paloheimo (1980). His equation for a single cohort is

$$\log\left(\frac{C_{a,y}}{E_y}\right)=\log(R_{y-a}q)-q\left(\sum_{k=y-a}^{y-1}E_k+\frac{E_y}{2}\right)$$
$$-M\left(a-\frac{1}{2}\right), \tag{13.22}$$

where $C_{a,y}$ is the catch of age a fish in the yth year, E_y is the fishing effort in the yth year, R_{y-a} is the number of fish recruited at age 0 in year $y-a$, q is catchability and M is natural mortality. The equation is in the form

$$Y=b_0+b_1X_1+b_2X_2, \tag{13.23}$$

which is the equation for a multiple regression. In this case $b_0=\log(R_{y-a}q)$, $b_1=q$, and $b_2=M$. The equation can be fitted using a standard multiple regression package which will give estimates of Rq, q and M, which is unlike VPA and cohort analysis. There is no need to guess F for any ages and normal confidence estimates on the parameters are possible. In this sense these statistical catch-at-age methods are superior to VPA. Even so, the validity of the method is entirely dependent on the assumption that equation (13.10) correctly describes the decay of survivors and that the stock numbers are proportional to the catch per unit of effort (CPUE). Actually, equation (13.22) is equivalent to

$$\frac{C_{a,y}}{E_y}=qR_{y-a}\exp\left[-\sum_{k=y-a}^{y-1}Z_k\right] \tag{13.24}$$

so that the equation essentially says that the CPUE is proportional to stock numbers. The most problematic element in this appealingly simple model is the definition and measurement of effort. Total effort may be composed of effort from many different vessel types and sizes, all of which can be measured in many alternative ways such as sea-days, fishing days, trawling hours and number of hooks. Furthermore, due to technical development, one unit of effort in year y may be different from a unit of effort in, say, year y –5. For this reason equation (13.18) is problematic to apply in practice. For further details of this approach see Fournier and Archibald (1982).

13.6.3 Body growth

When estimating yield it is often useful to have a way of estimating weight at age. This has been reviewed by Jobling (Chapter 5, Volume 1), who presents the von Bertalanffy equation (von Bertalanffy 1934), which expresses the relationship between body weight (or length) and age. Recall that length, L_t, is given as follows:

$$L_t=L_\infty(1-e^{K(t-t_0)}) \tag{13.25}$$

and the length–weight relationship is

$$W_t=aL_t^b, \tag{13.26}$$

where L_t and W_t are length and weight at time t, L_∞ is the asymptotic length at $t=\infty$, K is the rate at which L_t approaches L_∞ and t_0 is the age at which the fish would be zero length. These equations assume a one-to-one relationship between age and length, which may not be the case. When this is true, age–length keys (ALK) can be used (Pitcher, Chapter 9, this volume). For example

$$ALK_{i,a}=\Pr(L_i\le \text{length}<L_{i+1}\,|\,\text{age}=a). \tag{13.27}$$

This gives the probability that an age group of fish has a length belonging to length group i. For the weight at age we get

$$AWK_{i,a}=\Pr(W_i\le \text{weight}<W_{i+1}\,|\,\text{age}=a). \tag{13.28}$$

Keys like the ALK could be applied almost everywhere in the models, and they would always represent a more realistic description of the real world, but the cost would be a very large number of parameters and cumbersome models. A spreadsheet implementation of a fishery model, on Excel for example, can use ALKs easily.

Usually, one needs to keep track of the body weight of all the cohorts, so an extra index is needed, $L_{a,t}$ and $w_{a,t}$, the length and weight at time t of age group a. The body sizes at age may be assumed to remain constant from year to year, but they may also vary. In that case one more index is needed, $w_{y,a,t}$: the weight of age group a at time t in year y.

In ICES, size-based models are assumed to be the same as age-structured models. The entire theory of size-structured models may be reformulated with body length as the basic observation (Chapter 9, this volume, and Sparre and Venema 1992). This approach is particularly useful in the tropics where it is more difficult to read age from otoliths. In addition, in all areas, shellfish do not have otoliths. For these and other species groups, length-based models are more useful (Pitcher, Chapter 9, this volume).

13.6.4 Biomass of stock, catch, discards and landings and value of landings

The von Bertalanffy equation has only three parameters, whereas each age and size class in an age–length key is a parameter. For this reason, careful thought needs to be given before using an age–length key.

The stock biomass at time t in year y may be derived from the one-to-one equation:

$$B_{y,t} = \sum_{a=0}^{a=a_{\max}} N_{y,a,t} w_{a,t}, \tag{13.29}$$

or it may be derived from the age–weight key, which illustrates the extra computations needed when using such a key:

$$B_{y,t} = \sum_{a=0}^{N} \sum_{i=1}^{NW} N_{y,a,t} AWK_{i,a} \frac{W_i + W_{i+1}}{2}, \tag{13.30}$$

where N is the number of age groups and NW is the number of weight groups. To compute the spawning stock biomass (SSB), a relationship is needed between either age or length or weight, and maturity. For that purpose we might go for the easy solution and use a one-to-one relationship between length (or age) and the fraction of mature fish. We may use the logistic curve to estimate the proportion of mature fish, which was also used for trawl gear selection earlier (equation 13.16).

$$Mat_a = \frac{1}{1 + \exp(S_1^M + S_2^M \cdot L_a)};$$
$$S_1^M = \ln(3) \frac{ML_{50\%}}{ML_{75\%} - ML_{50\%}};$$
$$S_2^M = -\frac{S_2^M}{ML_{50\%}}. \tag{13.31}$$

$ML_{50\%}$ and $ML_{75\%}$ is the length at which 50% and 75% of the fish are mature, respectively.

$$SSB_{y,t} = \sum_{a=0}^{N} N_{y,a,t} W_{a,t} Mat_a. \tag{13.32}$$

Where there are large differences between the sexes, we may need to have two models, one for females and one for males. If the maturity ogive is differentiated between sexes, all other equations (for example, stock numbers) must also be separate for females and males.

A more realistic approach would be to use a length–maturity ogive to estimate the proportion of fish aged a that were mature. This empirically based estimate could then be used to calculate spawning stock biomass. This method should only be used if the extra complication yields results which are a significant improvement on the simpler solution shown in equation (13.32).

The catch may be divided into landings and discards, which implies a model for discards. The logistic curve can also be used here to model the fraction of fish caught, and which are discarded (D_a), as a function of body length:

$$D_a = 1 - \frac{1}{1 + \exp(S_1^D + S_2^D L_a)};$$
$$S_1^D = \ln(3) \frac{DL_{50\%}}{DL_{75\%} - DL_{50\%}};$$
$$S_2^D = -\frac{S_2^D}{DL_{50\%}}. \tag{13.33}$$

$DL_{50\%}$ and $DL_{75\%}$ is the length at which 50% and 75% of the fish caught are discarded, respectively. Note that $(1 - D_a)$ is the fraction landed. The total quantity discarded by a fleet D_{Fl} is given by

$$D_{Fl} = \sum_{a=0}^{N} C_{Fl,a} w_a D_a. \tag{13.34}$$

To model the effect of a minimum landing size on discarding we could also use the logistic curve, so illustrating that there are many different applications of this curve in fisheries.

The SSB used as a measure of the performance of the system and the level of discards can be added to the list of outputs. Discarding is a political issue as the rejected fish are considered a waste of potential catches (Kaiser and Jennings, Chapter 16, this volume). Therefore discards can be considered as a part of output. This illustrates that there are no uniqueness rules for nominating certain variables as output, and others as variables.

Fisheries landing statistics are not given by age group but by commercial size category. The commercial size categories may be based on body weight, body length or some other criterion, such as the number of tails per pound for shrimps. These groupings can be transformed into age groups or size groups by keys similar to the *ALK* or they may be modelled under the assumption of a one-to-one relationship using a growth equation and the length–weight relationship.

The real choice to make is not so much the mathematical model, for example the logistic model for gear selection, but rather whether or not to include a submodel for gear selection. The gear selection must be included if the objective of the model is to predict, for example, the effect that mesh-size regulations might have. In other cases one may have a choice of whether to include the submodel.

13.6.5 Models for spatial and seasonal aspects of fisheries

Stock abundance and consequently catch rates may vary from area to area. For this reason fishing effort will also vary between areas, and distribution of resources and fishing areas will vary between seasons. Most management agencies do not account for seasonal and geographical variations but we will introduce here simple models dealing with areas and seasons. These can be implemented when the relevant data are available, for example, through logbook schemes. Some of the problems faced in stock assessment might be reduced by the introduction of models accounting for geographical and seasonal aspects.

Geographical aspects may be dealt with in a simple manner by introducing a finite number of areas, and seasonal aspects by introducing a finite number of seasons. These could be defined in weeks, months or quarters of the year. As an approximation we then assume that within a time period, all parameters remain constant, fish are assumed to be homogeneously distributed within an area, and nothing moves between the areas during a time period. All movements are assumed to occur at the end of the time period, and take no time to happen. Although an approximation to the real world, any precision can be modelled by selecting areas and time periods at a scale that can be supported by the data. For a detailed discussion of the migration of commercial fish species, see Metcalfe et al., Chapter 8, Volume 1.

The Migration Coefficient, *MC*, from area A to area B is defined as the fraction of the animals in area A which moves to area B. In this definition, the 'movements' include the 'move' from area A to area A, which covers the case where the animals do not move. The migration coefficient depends on the starting area (F_{Ar}) and the destination area (T_{Ar}). Note that the sum of migration coefficients over destination areas is always equal to 1.0, as the starting area is also considered a destination area:

$$\sum_{Ar=1}^{N} MC_{a,F_{Ar},T_{Ar},q} = 1.0, \tag{13.35}$$

where a = age group, q = quarter or any time period. For a theoretical discussion of migration in connection with age-based fish stock assessment the reader is referred to Quinn et al. (1990). These authors also discuss the estimation of migration parameters. There are also more sophisticated models, based on differential equations (Olivier and Gascuel, 1999).

The concept of mortality, as it is traditionally applied, refers to the entire stock, not to a fraction of a stock. Consequently, the number of deaths in a

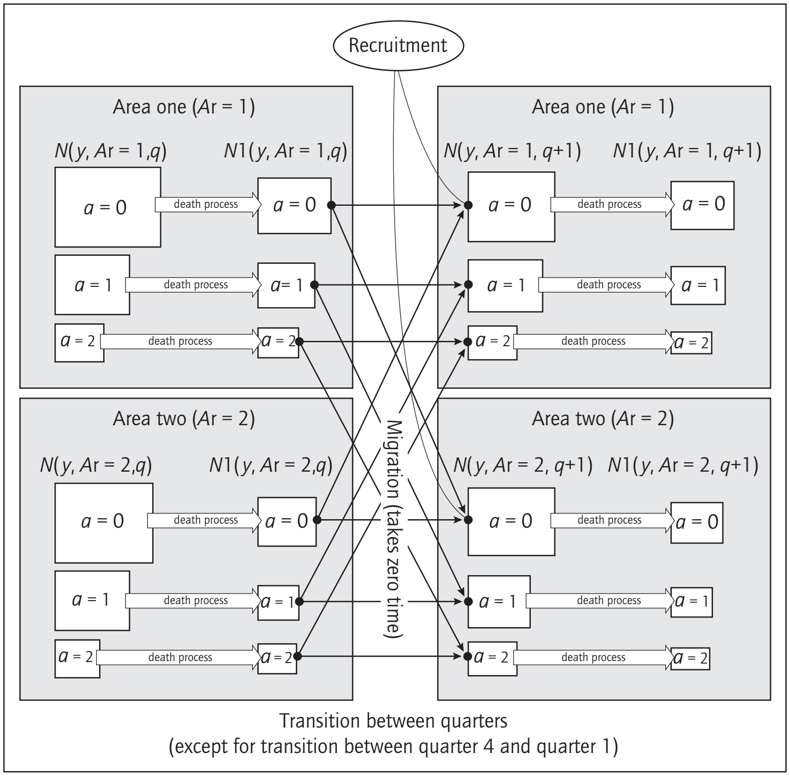

Fig. 13.3 The flow of stock numbers (N(year, area, quarter) $= N(y,Ar,q)$ depicted as small boxes), between model-components from quarter q to quarter $q+1$ (during quarters 1, 2 and 3) and between two areas (depicted as large grey boxes) in a hypothetical example with one stock and three age groups ($a = 0$, 1 and 2). Migrations and recruitments are depicted as thin arrows and the death process by fat arrows. For further explanation see text.

sub-area of the total area occupied by a stock, should not be associated with a mortality, but with some other concept. Here we use the term area-specific mortality, as the concept required to describe the death process within a sub-area. Area-specific mortality is closely related to mortality as normally understood. Let $Z_{\text{stock},y,a,q}$ indicate the traditional total mortality of the stock. The relationship between $Z_{\text{stock},y,a,q}$ and the area-specific total mortalities, $Z_{y,a,Ar,q}$, is

$$Z_{\text{stock},y,a,q} = -\ln\left\{\frac{\sum_{Ar=1}^{NA}\exp(-Z_{y,a,Ar,q}\Delta t)N_{y,a,Ar,q}}{\sum_{Ar=1}^{NA} N_{y,a,Ar,q}}\right\} \tag{13.36}$$

where $N_{y,a,Ar,q}$ = stock number at the beginning of quarter q of year y in area Ar and NA is the number of areas.

To explain the multi-area version of the exponential decay model (see equation 13.10), we use the quarter as the time period. The stock at the end of quarter q of year y in area Ar (before migration) is modelled by:

$$N1_{y,a,Ar,q} = N_{y,a,Ar,q}\exp(-Z_{y,a,Ar,q}\Delta t). \tag{13.37}$$

Note that the indices of N and $N1$ remain unchanged when considering the death process during a quarter of the year. In the model the transition between quarters occurs between just before migration and just after migration. The use of indices in relation to the transition between components is illustrated in Fig. 13.3 for quarters 1, 2 and 3.

The number at the beginning of quarter q in year y in area Ar (just after migration, see Fig. 13.3), if $q = 1,2,3$ is given by

$$N_{y,a,TAr,q+1} = \sum_{FAr=1}^{NA} MC_{a,FAr,TAr,q} N1_{St,y,a,Ar,q} \qquad (13.38)$$

if $q = 4$ (and $a < a_{\max}$) then

$$N_{y+1,a+1,TAr,1} = \sum_{FAr=1}^{NA} MC_{a,FAr,TAr,4} N1_{y,a,Ar,4} \qquad (13.39)$$

where: $a_{\max}$ is the oldest age group.

$MC_{a,Ar1,Ar2,q}$ = the migration coefficient for stock St moving from area $Ar1$ to area $Ar2$ in quarter q of age group a and $N1_{St,y,a,Ar,q}$ = the number of fish in stock St, at the end of quarter q of year y in area Ar (before migration).

Stock number at the end of quarter q of year y in area Ar (before migration) in the oldest age group $a_{\max}$, which is here modelled as a plus group, that is, it contains all the age groups, ($a_{\max}$, $a_{\max} + 1$, $a_{\max} + 2$, . . . $a_{\max} + \infty$). If $q = 1,2,3$ and $a = a_{\max}$ then the equation is the same as for the younger age groups. Only if $q = 4$ and $a = a_{\max}$ is there a difference compared to the younger age groups:

$$N_{y+1,\, a_{\max},TAr,1} = \sum_{FAr=1}^{NA} MC_{a_{\max},FAr,TAr,4} N1_{y,\, a_{\max},Ar,4} + \sum_{FAr=1}^{NA} MC_{a_{\max}-1,FAr,TAr,4} N1_{y,\, a_{\max}-1,FAr,4}. \qquad (13.40)$$

Spatial features in general involve mapping and other means of presentation, as well as spatial analysis, which all falls under the category of GIS (Geographical Information Systems). However, GIS is too big a field to be covered here and the interested reader is referred to the literature on application of GIS in fisheries (Castillo et al. 1996; Fox and Starr 1996; Meaden and Do Chi 1996; Meaden and Kemp 1997; Starr and Fox 1997; Denis and Robin 1998; Foucher et al. 1998).

13.6.6 Some stock–recruitment models

The stock and recruitment problem is the search for a relationship between parental stock size and the subsequent recruitment in numbers of young fish (Myers, Chapter 6, Volume 1). This is a central problem of fish population dynamics, since it represents nature's regulation of population size, whether or not the populations are being exploited. Obviously, there can be no recruits if no adult fish are left to mature, spawn and produce eggs, which hatch and grow to become recruits. Unfortunately, this is about the only thing we know for sure about the stock–recruitment relationship (for a discussion see, for example, Gilbert 1997, Hilborn 1997, Myers 1997 and Myers, Chapter 6, Volume 1).

The problem of recruitment is so important that it has a chapter to itself (Myers, Chapter 6, Volume 1). It is difficult to recommend any of the stock–recruitment models, as very few of them have been shown to provide a convincing fit to observations. Many fisheries scientists use the Beverton and Holt model, when a stock and recruitment model has to be used, but there is no justification for this use other than familiarity. Perhaps the best approach is to use 'no model', meaning that the model is replaced by a stochastic factor multiplied by a constant. Such an approach does not pretend to describe a biological mechanism, which we do not yet understand. Examples of stock–recruitment curves and a discussion of mechanisms of density-dependent mortality are given in detail by Myers (Chapter 6, Volume 1).

13.7 A KEY TO MODELS

In Table 13.1 we present a key to some of the main models used in fisheries. This key is far from exhaustive, and we wish to emphasize that while it lists major techniques, no model can be applied without thinking very carefully about the model's assumptions and applicability to each particular situation. We refer readers to the relevant chapters of this book as well as Quinn and Deriso (1999) for detailed explanations of these assumptions as well as full mathematical derivations. A recent textbook by Jennings et al. (2001) also provides an overview of methods. As noted earlier, some of the models presented here may meet the objectives of giving advice for fishery management by them-

Table 13.1 Key to major groups of fisheries models, including primary chapters of this volume where described (John D. Reynolds assisted with the development of this key).

Goals and data available	Model	Primary chapter
Aim to model individuals?		
Aim to model interactions between fishers?	Game theory, individual-based models	Huse et al.
Aim to model interactions between fishes?	Game theory, individual-based models	Huse et al.
Aim to model a single species?		
Aim to reconstruct past events?		
Historical data on catches and age composition?	VPA, cohort analysis	Shepherd and Pope, 7
Historical data on catches, age composition + auxilliary (e.g. stock and recruitment)?	Statistical catch-at-age models	this chapter
Aim to forecast?		
Data on catches and effort only?		
Stock in equilibrium with fishery? (Be careful!)		
CPUE and effort linked by straight-line regression?	Schaefer production model	Schnute and Richards
CPUE and effort linked by negative exponential curve?	Fox production model	Schnute and Richards
CPUE and effort linked by non-linear curve?	Pella and Tomlinson production model	Schnute and Richards
Stock not assumed to be in equilibrium with fishery?		
All error in model and not in data?	Process-error production model	Schnute and Richards
All error in data and not in model?	Observation-error production model	Schnute and Richards
Data on catches, effort, age and size composition, stock and recruitment?	Yield-per-recruit, dynamic pool, stat. catch-age models	Shepherd and Pope 8, this chapter
Aim to model multispecies?		
Aim to reconstruct past events?	MSVPA	Shepherd and Pope 7
Aim to forecast?		
Data on catches and effort only?		
Data from one location over previous years?	Temporal multispecies production model	Jennings et al. (2001)
Data from many locations?	Spatial multispecies production model	
Data on catches, effort, age and size composition, stock and recruitment?		
Aim to examine multiple species caught in same gears?	Multi-species yield-per-recruit, stat. catch-age models	Shepherd and Pope 8, this chapter
Aim to examine predator–prey interactions among species?	Trophic models	Pauly and Christensen

selves, or they may be submodels of others in the key.

The first triplet presents a choice between models of individuals, single species and several species. Most models in fisheries science have dealt with either population dynamic models of species or, more recently, the population dynamics of many species. Population dynamics treats individual animals as replicates of each other and models accounting for changes in numbers with time only recognize reproduction and death as individual properties. Even then, each individual has the same chance of giving birth and dying. The development of behavioural ecology over the past 25 years has shown the importance of recognizing that two individuals in a population are not the same and within a population there can be more than one strategy for reproduction, feeding and use of space (Krebs and Davies 1997). This conceptual advance, coupled to the power of modern computers, makes it possible to develop models that are based on the actions of individuals. Three powerful methods have emerged that simulate the way in which organisms have adapted themselves to their environment or interact with each other. Genetic algorithms mirror many of the processes that occur during natural selection and neural networks mimic the way in which nervous systems learn about the world. Game theory handles the way in which the reward gained by an individual when interacting with others depends on the strategy used by it and its opponent. The first entry in Table 13.1 recognizes that these new methods are now being applied to problems of interest to fisheries biologists but at present the approach is not used at the stock assessment level. Fisheries scientists who still have to confront the reality of delivering a stock assessment to management authorities may still be reluctant to use the models outlined by Huse et al. (Chapter 11, this volume) but they should certainly look to the area as one from which a totally new set of methods may emerge over the next 20 years.

Multispecies models may account for 'technical interactions', due to more than one species being caught by the same gear (e.g. Misund et al., Chapter 2, this volume), or 'biological interactions', principally through predator–prey relationships. For basic biology of foraging and predation, see the trio of chapters in Volume 1 by Mittelbach (Chapter 11), Juanes et al. (Chapter 12) and Krause et al. (Chapter 13). For ecosystem interactions and impacts see Polunin and Pinnegar (Chapter 14, Volume 1), Persson (Chapter 15, Volume 1), Jones et al. (Chapter 16, Volume 1) and Kaiser and Jennings (Chapter 16, this volume), and for incorporation into fisheries models, see Shepherd and Pope (Chapters 7 and 8, this volume) and Pauly and Christensen (Chapter 10, this volume).

Many models aim to reconstruct past stock sizes and fishing mortality, in order to relate these to fisheries effort and hence predict the future. The simplest method is virtual population analysis, which is often implemented using a computational simplification called cohort analysis (Shepherd and Pope, Chapter 7, this volume). Cohort analysis may be based either on age classes or on length classes if age is not known. VPA/cohort analysis requires initial guesses of fishing mortality and natural mortality, and while these estimates become less important to the reconstruction of stock sizes and fishing mortality in early years, there is considerable uncertainty in estimates for the most recent years (Megrey 1989). Statistical catch-at-age models, discussed in this chapter, are more sophisticated but also more difficult to implement. Single-species VPA has a multispecies analogue (MSVPA) (Shepherd and Pope, Chapter 7, this volume), which has a voracious appetite for data concerning predatory habits of fishes (Sparre 1991; Magnússon 1995; Christensen 1996).

The key in Table 13.1 offers two main routes to forecasting stocks and yields in single-species assessments. One can collapse the effects of age structure and body growth rates, although they are still implicitly incorporated by summing over all age groups, and use production models to assess the behaviour of the entire stock to previous fishing effort (Schnute and Richards, Chapter 6, this volume). Then one can predict how both yields and stock sizes will be affected by fisheries. In the past, researchers were willing to make the assumption that such data were derived from stocks that were in equilibrium with fisheries. However, this is a very dangerous assumption, as fishing effort usually increases steadily during the early years of a fishery, without giving stocks a chance to catch up through density-dependent responses (Hilborn and Walters 1992). More modern methods, reviewed by Schnute and Richards (Chapter 6, this volume) overcome this assumption. Regression-based approaches which assume that the error is in the underlying model rather than in the data (process-error methods) tend to be less precise than methods in which the error is assumed to be in the data (observation-error; Polacheck et al. 1993). For certain purposes, the surplus production models may perform as well as the sophisticated age-based models discussed below. It is not generally the case that complicated models with many parameters have higher predictive power than do simple models. This may not seem fair to the hard-working designers of age-based or size-based models, but if the purpose of the model is to predict CPUE, the surplus production model would work probably as well as the Thompson and Bell (1934) model discussed earlier. But there is an increasing stream of requests from management bodies for an analysis of details. An example would be to assess the effect of technical management measures on catches (see Section 13.6.4). These questions cannot be addressed with a surplus production model. If the key issue is the discarding of young fish, the model must contain some splitting of the stock biomass by size and some description of discard practice. We recommend that it is best to test both the simple surplus production models and the more complicated size-based models and compare and test the performance of each. Whenever the simple model performs as well as the complicated model, it should be used.

Simple forecasting methods that break stocks down into age classes and account for individual body growth are reviewed by Shepherd and Pope (Chapter 8, this volume). Yield-per-recruit and dynamic pool models can be easily calculated and readily understood, and are in widespread use. Statistical catch-at-age models (outlined in this chapter) are more flexible, but they tend to be more difficult for people other than the modeller to evaluate.

There are multispecies counterparts to the single-species forecasting methods (Daan and Sissenwine 1991). Thus, multispecies production models can be used when species are aggregated in catch statistics. Comparisons are then made between an index of fishing effort and catches in either multiple regions (spatial multispecies production models) or over multiple years from a single site (temporal multispecies production models). If numbers and sizes at age are known, then multispecies yield-per-recruit and statistical catch-at-age models can be used. While multispecies models represent a conceptual advance over single-species models, the difficulty of gathering data to parameterize them has prevented their widespread adoption (Evans and Grainger, Chapter 5, this volume; FAO 1999).

A further conceptual advance is provided by trophic models, which attempt to include environmental data and aim to model the whole ecosystem, in principle starting with the sun's radiation, photosynthesis and primary production. One can then model the entire transport of biomass between components of the ecosystem and keep track of the food web, as explained by Pauly and Christensen (Chapter 10, this volume). Software such as Ecopath (Christensen and Pauly 1992; Pauly et al. 2000) makes the bookkeeping fairly straightforward. This approach builds on a groundbreaking model by Andersen and Ursin (1977), which contained all the major components of the ecosystem. The multispecies VPA was developed as a reduced version of this ecosystem. Thus, at some future stage, all the models may be merged into a single mega model.

13.8 THE IMPORTANCE OF TESTING MODELS

Fishery science has a long tradition of modelling the dynamics of exploited stocks. It was probably one of the first areas of ecology where mathematical models were used extensively, and Volterra was stimulated by market data from the Adriatic fisheries to produce his famous equations relating predator and prey abundances (Kingsland 1985, and see Chapter 10, this volume, equation 10.2). The work of Beverton and Holt (1957) was a stunning creation but the models produced were only partly confronted by data. Some of the key models, such as the logistic model of population growth and the yield-per-recruit model of Beverton and Holt (1957), have not been through a proper cycle of prediction and testing against the data.

Some fishery biologists, such as Walters (1986), have proposed ways in which management measures could be designed so as to gain information about the predictive capacities of models. So-called adaptive management recognizes that it is often not possible to decide which is the correct model of an exploited population. Walters (1986) proposed that managers should be prepared to use the fishery to obtain information that would allow differentiation between models. After an initial assessment, a number of models would be proposed, each of which would make different predictions about how the fishery would influence the stock. The area of the fishery should then be split up and different management regimes imposed in each. This differential exploitation pattern could be used to test predictions deriving from the different models. Eventually all but one model would be thrown out as being inadequate. A problem with the approach is that managers are reluctant to manipulate fisheries in a way that could lose fishers money. This discussion points up the fact that advising on which model to use has to be done with extreme caution. A model needs to be chosen because it accounts for the data available, not because it is well known and mathematically tractable. This means that a fishery scientist needs to be intimately knowledgeable about the fishery he or she is working with, know its biology and create new elements of a model to deal with the particular circumstances observed (Mangel and Clark 1988).

In general we do not advocate the use of only one model, but recommend that different models are tested on the same data set (see also Walters 1986; Hilborn and Mangel 1997). A problem often encountered is that several models can give the same answer (Schnute and Richards 2001) and there is insufficient data to determine which model describes the true process. This means that the scientist is not clear about the process that is bringing about the observed events. This could lead to recommendations which would attempt to manipulate the wrong variable. For example, in a typical tropical country one may observe hundreds of stocks of commercial importance, and the concept of fish stock assessment becomes cloudy. It is impossible to collect data for, say, 200 stocks in a developing country. At times, fisheries biologists can be tempted to question the usefulness of fish stock-assessment methodology in general as a tool for fisheries management in tropical countries (Mahon 1997).

When choosing a model that relies on the concept of individual stocks with an age structure, it is obviously important to consider the number of stocks as well as the problems involved in the definition of the stocks. Definition of a stock can be problematic (Begg et al. 1999), and one can question the usefulness of methods such as VPA when faced with a fisheries system with a large number of badly defined stocks. Even in temperate and polar waters, with relatively few stocks, we face severe problems in defining the stocks.

13.9 CONCLUSIONS

This chapter outlines the basic structure of models that have been applied to fisheries and discusses the ways in which models can be selected and applied. A key theme is that each situation will require the fisheries scientist to have a deep knowledge of the biology of the species or ecosystem in question and have the ability to tailor models to suite the particular conditions. Our discussion of the objectives of models has been general but in most cases the output from a model is in the form of some type of reference point that can be used to design management measures. The simplest to grasp might be Maximum Sustainable Yield, a concept that has been through several deaths and reincarnations during its existence (Larkin 1977; Mace 2001; Punt and Smith 2001). Reference points are discussed further in Smith et al. (1993), Caddy and Mahon (1995), Quinn and

Deriso (1999) and Gislason (1999). A particular problem with fishery models is that they are not often tested properly. Models of population growth, such as the logistic, which underlies the surplus production model of Schaefer, are rarely tested to determine if they describe properly the way in which biomass changes over time. It is obvious from what is known about the population dynamics of animal populations that the logistic equation is not a good model, mainly because it is deterministic and does not account for time lags inherent in the life histories of most animal species. Yet despite this, logistic models are still used in fisheries. Future work must focus on producing tested models of population dynamics and fishery scientists must wean themselves away from the so-called traditional models. We need to escape from the legacy of the past.

In this chapter we also try to provide some guidance for choosing a model. The first step is to check whether the minimum requirement of the objective is met by the available data. Then check if there is sufficient funding and manpower as well as time available for the collection of additional data specific to the model. If the objectives are not met or are unachievable then the objectives should be changed. The maximum amount of information should be extracted from the data and the model used must be appropriate for the type and quality of data used. It is always important to make the model as simple as possible with the minimum number of parameters and equations, and one should not invent new equations unless they are really needed. Parameters should be estimated by standard methods, preferably using easy-to-obtain commercial software. When a key parameter cannot be estimated, try to make a plausible guess at it rather than ignoring it. All interacting components of the system should be included. For example, include in the model spatial and temporal factors when these are important for the output. Make the model multispecies and/or multi-fleet whenever these components are important for the output, as they usually are. Wherever possible use bioeconomics to model the behaviour of fishers, such as their discard practice. Try to make a deterministic as well as a stochastic version of the model. The deterministic version is mainly used to understand and check the stochastic version. In general terms, match the model to the needs of the user.

ACKNOWLEDGEMENTS

We would like to thank Jon Schnute for reading a draft of this chapter and suggesting substantial changes, which greatly helped us with our revisions.

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Part 3

Fisheries in a Wider Context

14 Marine Protected Areas, Fish and Fisheries

NICHOLAS V.C. POLUNIN

14.1 INTRODUCTION

Fisheries management and marine protected areas (MPAs), defined as areas of the sea effectively protected from exploitative impact, have traditionally occupied different but overlapping niches within the field of coastal management. A number of differences are evident between them. MPAs have been established for a broad range of scientific, economic, cultural and ethical purposes, orientated for the most part to marine nature conservation (e.g. Jones 1994), but strict evaluation of success is difficult because in most cases, the objectives and criteria of success have been poorly defined (e.g. Polunin 1990; Hockey and Branch 1997). Fisheries management also has multiple potential objectives (e.g. Hilborn and Walters 1992; Hall 1999; Jennings et al. 2001), but these are typically focused on the resources targeted by fishing, and also consider economic and social outcomes of resource use. MPAs are relatively simple area-based regulatory measures, whereas fisheries management spans a whole suite of measures, including restrictions on gears and catches, and seasonal closures. Marine reserves are rather few in number, whether in developed countries such as the United Kingdom (Jones 1999) or tropical developing regions such as in the Caribbean (Stanley 1995), and they are almost all very small in area. Worldwide, the median size of MPAs is approximately 1600 ha (Fig. 14.1). In contrast, the fishing which currently causes most concern is a large-scale activity, and fishery management measures and monitoring activities address human activities over extensive areas (e.g. King 1995).

MPAs and fisheries management have nevertheless increasingly converged in the last few years (e.g. Bohnsack 1993; Botsford et al. 1997). One reason for this is that mobile fishing gears are now recognized to have caused physical damage to fragile marine habitats in many areas (Kaiser and Jennings, Chapter 16, this volume). These impacts are likely to be reversed in areas protected from fishing (e.g. Auster et al. 1996, 1997). It is also expected that through food webs, fishing may have profound indirect effects on marine communities (Kaiser and Jennings, Chapter 16, this volume), some of which might also be reversed in MPAs (e.g. Pinnegar et al. 2000). The contention that conventional fisheries management science is the root cause of the global fisheries crisis has led some to advocate MPAs as a form of precautionary approach to fisheries management (Roberts 1997a), but the practical implications of this proposition are considerable. For example, what science is required to design such areas, and what will they look like? What will be delivered, and what are the uncertainties? If MPAs have to be very much greater in size, such increase in scale would not be inconsistent with holistic approaches to fisheries management, such as 'fisheries ecosystem management' in Australia (Done and Reichelt 1998 and see Pauly and Christensen, Chapter 10, this volume). In a general sense, MPAs may be one of many kinds of zones in a comprehensive coastal management plan (OECD 1993; Bentley et al. 1994).

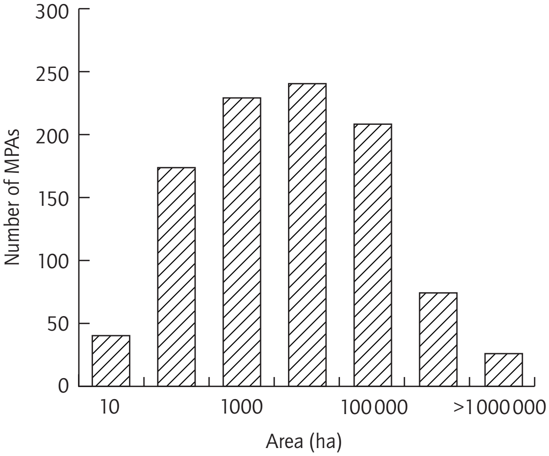

Fig. 14.1 Size distribution of 991 MPAs around the world for which area is known. (Source: after Kelleher et al. 1995, p. 14.)

One of the main objectives of this chapter is to review the known impacts of MPAs with respect to fish conservation and fisheries management objectives, and help to characterize where, and if so how, MPAs may be expected to contribute to the achievement of such objectives. I will also relate MPAs to broader issues of environmental management, including the uses of coastal waters by tourists, participatory conservation and the maintenance of biodiversity.

14.2 WHAT HAPPENS TO TARGET SPECIES IN MPAs?

Fishing is an additional source of mortality, and reduces survivorship of target organisms. Thus the principal direct effects of exploitation are reductions in abundance, age and size. Accordingly, increases in mean numerical abundance, size, age and biomass, of target species depleted by fishing are expected particularly in MPAs. These effects are not assured. They may be mitigated by a number of factors and processes, including mobility and spatial variability of recruitment at large scales relative to the size of MPAs, so that it is necessary to look at the evidence for such effects. This may allow patterns to be discerned in the information.

14.2.1 Abundance and body size of target species

Drawing on data from underwater visual surveys and on fishery catch-per-unit-effort (CPUE) data, and including the case of the North Sea where entire grounds were closed during the First and Second World Wars, evidence for greater abundances in MPAs than in unprotected areas is now available for a range of resource species in more than 40 locations around the world, but there are significant spatial patterns in this evidence (Table 14.1). For example, evidence for fishes derives almost exclusively from underwater visual census work on site-attached species on reefs in the Caribbean, western Mediterranean, Kenya, South Africa, the Philippines, New Zealand and New Caledonia. Jones et al. (Chapter 16, Volume 1) have noted differences in census techniques between temperate and tropical reef areas, and noted that these hamper comparisons of community ecology between these habitats. An exception is the evidence from the North Sea, where information came from catch and market statistics and the area protected spanned complete stocks and the duration of both world wars (Borley et al. 1923; Margetts and Holt 1948). Otherwise, the lack of information on the effects of MPAs or fish abundance from South America, West Africa, South Asia and the Far East is a prominent feature; one of the North America East Coast studies is a fishing-based investigation of reef fishes in Florida, while the other two are equivocal and are complex assessments of large-scale closures (Table 14.1).

In a meta-analysis of 12 MPAs, selected on the basis of full reporting of relevant data, Mosquera et al. (2000) showed that an overall positive effect of protection is discernible in the abundance of fishery target species but not in that of non-target species. Where many species have been investigated, increase in abundance of target species in MPAs has not been detected in all cases (Table 14.1). Species other than fishes which have been

Table 14.1 Changes (increase, or * = no increase, _ = increase in some species, not others, – = no information) in abundance of various marine fishery target species in areas closed to fishing, or otherwise very lightly fished, in different parts of the world.

	W. South America	E. South America	Caribbean	W. North America	E. North America	Western Europe	Southern Europe	West Africa	East Africa	South Asia	Southeast Asia	East Asia	Australasia	South Pacific
Fish	–	–	3.21.25.32.34.	–	35.	31.	4.24.28.29	–	2.6.7.30.	–	1.	–	5.42.	22.33.
Decapods	15*	–	8.	39*	11.	–	–	–	–	–	–	12.	9.10.40.	–
Molluscs	15.	–	13.27.	19.23.	17.18*.38	–	29.	–	16.36*	–	–	–	20.40*	14*
Urchins	15.	–	37.	–	–	–	–	–	–	–	–	–	–	–
Other	26.	–	–	–	–	–	–	–	–	–	–	–	–	–

1. Russ 1985, Alcala 1988, White 1988, Alcala and Russ 1990, Russ and Alcala 1996.
2. McClanahan and Shafir 1990, Samoilys 1988.
3. Clark et al. 1989.
4. Bell 1983.
5. McCormick and Choat 1987, Cole et al. 1990, Babcock et al. 1999.
6. Buxton and Smale 1989.
7. Bennett and Attwood 1991.
8. Davis 1977, Davis and Dodrill 1980, 1989.
9. Cole et al. 1990.
10. Bowen and Hancock 1985.
11. Leary 1985, Klima et al. 1986, Roberts 1986.
12. Yamasaki and Kuwahara 1990.
13. Weil and Laughlin 1984.
14. Heslinga et al. 1984.
15. Castilla and Durán 1985, Moreno et al. 1984, Castilla and Fernandez 1998.
16. Lasiak and Dye 1989.
17. Rice et al. 1989.
18. McCay 1988.
19. Tegner 1989, 1992.
20. Shepherd 1990.
21. Munro 1999.
22. Wantiez et al. 1997.
23. Wallace 1998.
24. García-Rubies and Zabala 1990.
25. Polunin and Roberts 1993.
26. Algae: Castilla & Bustamante 1989.
27. Stoner and Ray 1996.
28. Francour 1991.
29. Pipitone et al. 2000.
30. Roberts and Polunin 1992.
31. Borley et al. 1923, Margetts and Holt 1948.
32. Rakitin and Kramer 1996, Chapman and Kramer 1999.
33. Polunin 1999.
34. Polunin and Williams 1999.
35. Funicelli et al. 1988.
36. Hockey and Bosman 1986.
37. Smith and Berkes 1991.
38. Fogarty and Murawski 1998.
39. Armstrong et al. 1993.
40. Edgar and Barrett 1999.

found to be more abundant in MPAs than unprotected areas include muricid gastropods, abalone, limpets, lobsters, sea urchins and kelp, where these are exploited; these are from reef habitats. The overwhelming evidence is that greater abundances develop in MPAs when site-attached species in the area have been substantially depleted by fishing.

Evidence for greater average sizes of target species in MPAs than in unprotected areas comes almost entirely from the study of site-attached reef fishes investigated by underwater visual census; many of the studies are the same as those which have demonstrated abundance effects (Table 14.2). For reef fishes, the evidence is from work in the Caribbean, Florida, the Mediterranean, Kenya, South Africa, the Philippines, New Zealand and Australia. Several target invertebrate species have also been found to be larger in size within MPAs (Table 14.2), and these are again associated with reef habitat.

14.2.2 Fecundity, recruitment and movement of target species

Increase in fecundity with body size is expected to occur in fish and other fishery organisms (Duarte and Alcaraz 1989; Elgar 1990). Given the variability of fecundity data and the lesser increase in fecundity with size in some species (Wootton 1990; Sadovy 1996), population fecundity will not increase appreciably in all species within MPAs, but greater total fecundities of site-attached fishes should occur in MPAs than in unprotected areas. There will, of course, be exceptions.

The rate at which population fecundity can be expected to increase will depend upon the rate of growth and mortality and the relationship between fecundity and body size (Sadovy 1996). Because greatly increased survivorship within MPAs is likely, species so protected should attain maximal population fecundities within five years or so. Slower-growing species may take 10–20 years to do this (Polunin 1997).

If maximal population fecundities are to produce a greater egg output rate by the stocks of females within MPAs then spawning must be frequent enough in the larger individuals for the egg production to be raised. In tropical snappers (Lutjanidae), spawning may be more frequent and occur over a longer period in larger than in smaller animals (Grimes 1987), but more data are needed to underpin the supposition that greater fecundities give rise to a greater total egg production in MPAs than in unprotected areas. It is reasonable to expect that in site-attached species which do not become more vulnerable to fishing through movement out of protected areas, depleted local populations in MPAs will support substantial increases in egg production.

In both reef fish population ecology and fisheries population dynamics, the relationship between any increased egg output and actual recruitment is uncertain (e.g. Sale 1991; Myers and Barrowman 1996; Myers, Chapter 6, Volume 1; Jones et al., Chapter 16, Volume 1). The scientific basis for such uncertainty varies between the two fields; to workers on reef fishes, recruitment refers to the supply of settlers from the plankton (though see Hixon 1996) and is measured at very small spatial scales, while to fisheries scientists it is the abundance of fish of a size large enough to be fished and measured from large-scale fisheries data (e.g. Hilborn and Walters 1992; Myers, Chapter 6, Volume 1). Much of the evidence has supported the origin of recruitment variability lying in the egg and larval stages, which in fishes are rarely of less than two weeks' duration (e.g. Brothers et al. 1983; Houde 1987; Thresher and Brothers 1989). It has been inferred that in reef fishes, and most probably all marine fishes, recruits travel distances from spawning sites that are commonly 25–50 times greater than the small spatial scales of most MPAs (Fig. 14.1). These distances may be modulated by current patterns that will vary greatly over time. For particular localities, species and seasons there may be a high likelihood of small-scale local retention of larvae, settlers and recruits (Jones et al. 1999; Swearer et al. 1999). The extent to which increased egg output rates from MPAs will lead to greater abundances of late juvenile and adult reef fishes within particular MPAs remains an open question. A major reason for this is that the dynamics of larvae and new settlers are little known. In marine animals that do not possess larvae, or

Table 14.2 Changes in average size (increase, * = no change, _ = increase in some cases, not others, – = no information) of various marine fishery target species in areas closed to fishing in different parts of the world.

	W. South America	E. South America	Caribbean	W. North America	E. North America	Western Europe	Southern Europe	West Africa	East Africa	South Asia	Southeast Asia	East Asia	Australasia	South Pacific
Fish	–	–	$\underline{21}$.$\underline{27}$.$\underline{28}$.$\underline{31}$.	–	29.	26.	2.22.	–	$\underline{4}$.5.17.$\underline{25}$.	–	1.	–	3.16.18.23*.$\underline{32}$	$\underline{19}$.
Decapods	11*	–	6.$\underline{7}$.	–	–	–	–	–	–	–	–	8.	32.	–
Molluscs	11.	–	9.	$\underline{20}$.	13.14*.32.	–	–	–	12.30.	–	–	–	15.$\underline{32}$.	10*.
Urchins	11.	–	–	–	–	–	–	–	–	–	–	–	–	–
Other	24.	–	–	–	–	–	–	–	–	–	–	–	–	–

1. Russ 1985, Alcala 1988, Alcala and Russ 1990.
2. Bell 1983, Francour 1991.
3. McCormick and Choat 1987, Cole et al. 1990, Babcock et al. 1999.
4. Buxton and Smale 1989.
5. Bennett and Attwood 1991.
6. Davis 1977.
7. Klima et al. 1986, Roberts 1986.
8. Yamasaki and Kuwahara 1990.
9. Weil and Laughlin 1984.
10. Heslinga et al. 1984.
11. Castilla and Durán 1985, Moreno et al. 1984, Castilla and Fernandez 1998.
12. Lasiak and Dye 1989.
13. Rice et al. 1989.
14. McCay 1988.
15. Shepherd 1990.
16. Ayling and Ayling 1986.
17. McClanahan and Muthiga 1988.
18. Beinssen 1989a.
19. Wantiez et al. 1997.
20. Wallace 1998.
21. Polunin and Roberts 1993.
22. García-Rubies and Zabala 1990.
23. Ferreira and Russ 1995.
24. Algae: Castilla and Bustamante 1989.
25. Roberts and Polunin 1992.
26. Borley et al. 1923, Margetts and Holt 1948.
27. Rakitin and Kramer 1996.
28. Polunin and Williams 1999.
29. Funicelli et al. 1988.
30. Hockey and Bosman 1986.
31. Chapman and Kramer 1999.
32. Fogarty and Murawski 1998.
33. Edgar and Barrett 1999.

have very short egg and larval stages, build-up of spawning stock biomass in an MPA may well lead to greater recruitment in the MPA, but in fisheries such cases are rare (e.g. Carr and Reed 1993; Allison et al. 1998). In the Discovery Bay Fishery Reserve, Jamaica, where target species have been severely fished down, nearly all the larval settlement was by species with extended pelagic phases (Munro and Watson 1999). In areas lacking such stock depletion, local recruitment which is less reliant on the vagaries of larval and early post-settlement life is a possibility. It is possible to say, that in areas with extensive and severe depletion, the scope for local recruitment will have been substantially lost. It must be said that, larval supply is not the only process governing the abundance of animals of exploitable size; for example, abundance of juvenile *gruntfish* (Haemulidae) has been found to be lower within the Barbados Marine Reserve than outside it and this is attributable to the greater density of piscivorous fishes as a result of protection (Tupper and Juanes 1999).

The spatial scale of the movement of species that are targeted by a fishery will clearly influence the likelihood that abundance will increase in MPAs (Kramer and Chapman 1999). In the reef-associated species which thus far have best exhibited abundance and size increases in MPAs, home-ranging and territorial behaviour appear to be very common. The spatial scale of routine movement is indicated by home range and territory size, and this is expected to increase exponentially with increase in body length. An indication of the positive relationship between mean home range area and mean fork length for 15 reef fish species is given by Kramer and Chapman (1999). There seem to be no data on how home range area might vary with size within important target species, such as the snappers (Lutjanidae) and groupers (Serranidae) of tropical reefs. It is reasonable to suppose on energetic grounds that as body size increases in MPAs, so fish will tend to range over greater distances. Among species in temperate waters, the plaice *Pleuronectes platessa* exhibits a linear relationship between migration distance and body length in Dutch waters (Rijnsdorp and Pastoors 1995). This means that the probability of movement can be expected to increase as body size of depleted target species increases in MPAs. For territorial species in MPAs of given sizes, it will be possible for individuals to move across boundaries into similar habitat where there is fishing. Movement may, however, be curtailed by habitat discontinuities; in the case of reef fishes, reef edges and open sand constitute such barriers to movement. Such discontinuities should therefore help promote biomass accumulation in MPAs (Kramer and Chapman 1999).

14.3 WHAT ARE THE POTENTIAL BENEFITS TO FISHERS?

Even in the case of sedentary species in reef habitats, fishers may be disadvantaged by MPA creation because they lose part of their ground and thus access to part of the stock, and total catches may therefore decline when MPAs are put in place unless total fishing effort is reduced (Beverton and Holt 1957, p. 393; Horwood et al. 1998). A short-term decline may ultimately be made good through recruitment and/or movement effects, the latter being referred to as 'spillover' (Rowley 1994). It is therefore appropriate to assess the evidence for recruitment and spillover before reviewing the evidence for impacts of MPAs on actual catches.

14.3.1 Spillover and recruitment effects

In contrast to the number of studies on abundance and size effects, few studies have addressed the movement of target species across the boundaries of MPAs (Table 14.3). Spatial differences in size and abundance have been used to infer movement, but tagging and tracking can alone indicate, the extent and direction of movements. Holland et al. (1993, 1996) used both to infer the extent of movement by the trevally (*Caranx melampygus*) and goatfish (*Mulloides flavolineatus*) in and out of the MPA around Coconut Island, Hawaii. Funicelli

Table 14.3 Movement of target species in and out of MPAs (* = no movement across MPA boundary recorded, _ = movement in some species not others) and changes in overall fishery catch (increase, * = no change, _ = increase under some conditions, not others) of various marine fishery target species in areas closed to fishing (^{a} = seasonal only) either in practice or inferred from simulation (^{b} = data from modelling only) in different parts of the world.

	W. South America	E. South America	Caribbean	W. North America	E. North America	Western Europe	Southern Europe	West Africa	East Africa	South Asia	Southeast Asia	East Asia	Australasia	South Pacific
Spillover														
Fish	–	–	14.18*.25	–	1.15.	–	–	–	16*.19.27*	–	–	–	17.20.	2.
Decapods	–	–	3.13.	–	–	–	–	–	–	–	–	11.	26.	–
Yield														
Fish	–	–	9^b	–	10^b	4.21.22.23* .24^b.28^b	5^a	–	8*	–	7.	–	–	6^b
Decapods	–	–	–	–	12*	–	–	–	–	–	–	–	26*	–
Urchins	–	–	–	29	–	–	–	–	–	–	–	–	–	–

1. Funicelli et al. 1988.
2. Holland et al. 1993, 1996.
3. Klima et al. 1986, Gitschlag 1986.
4. Borley et al. 1923, Margetts and Holt. 1948.
5. Garcia and Demetropoulos 1986.
6. DeMartini 1993.
7. Alcala and Russ 1990.
8. McClanahan and Kaunda-Arara 1996, T.R. McClanahan and S. Mangi, unpublished data 1999.
9. Sladek Nowlis and Roberts 1999.
10. Polacheck 1990, Guénette and Pitcher 1999.
11. Yamasaki and Kuwahara 1990.
12. Klima et al. 1986.
13. Davis 1977, Davis and Dodrill 1980, 1989.
14. Chapman and Kramer 2000.
15. Bryant et al. 1989, Rutherford et al. 1989.
16. Buxton and Allen 1989.
17. Beinssen 1989b, 1990.
18. M. Corless, B. Hatcher, W. Hunte and S. Scott, unpublished data.
19. Attwood and Bennet 1994.
20. Davies 1996.
21. ICES 1990.
22. Bailey 1991.
23. ICES 1999, Pastoors et al. 2000.
24. Beverton and Holt 1957, Horwood et al. 1998.
25. Munro 1999.
26. Kelly 1999.
27. Watson 1996.
28. Daan 1993.
29. Quinn et al. 1993.

et al. (1988) tagged mullet (*Mugil cephalus*), drums (*Sciaenops* spp.) and spotted seatrout (*Cynoscion nebulosus*), while Rutherford et al. (1989) tagged grey snapper (*Lutjanus griseus*), to infer movements within and out of MPAs on the east coast of Florida. Other studies have demonstrated movements of decapods, including crabs in Japan (Yamasaki and Kuwahara 1990), and lobsters in Florida and New Zealand (Davis 1977; Davis and Dodrill 1980, 1989; Kelly 1999), and shrimp (Klima et al. 1986; Gitschlag 1986) in Florida. The evidence from such studies is that movement does occur across MPA boundaries, but that the distance over which it occurs routinely in reef-associated species tends to be small; most information indicates spatial scales of less than one kilometre. In other species, such as mullet (Funicelli et al. 1988), or most commercial species in the North Sea, it is evident that the spatial scale of movement can be much greater, although it should be noted that in reef species the scale of movement may be greater than indicated by the short-term studies above. This movement can occur in a variety of contexts, including home-ranging and foraging behaviour (Holland et al. 1996), spawning migration (Holland et al. 1993), and changes in habitat as animals get older (Parrish 1987). The distance range of movement in reef-associated species is similar to that of their home ranges, but such data probably do not include seasonal movements. These movements include those for spawning which occur over greater distances and may be important as the susceptibility of species to fishing is likely to be greater in some species during spawning (Fulton et al. 1999).

The build-up in spawning biomass which occurs in site-attached species in MPAs may lead to greater egg output, but the consequences of this for recruitment are uncertain and there appear to be no data indicating greater availability of fish to any fishery as a result of the greater supply of larvae. Assuming a metapopulation structure such as may occur in some arrays of patch reefs over distances of tens of kilometres, it is likely that MPAs will enhance yield especially when the fishing mortality is high (Man et al. 1995). In some cases, such as in the southeastern USA, the spawning stock biomass may be so depleted that recruitment is stock dependent (Plan Development Team 1990; Ault et al. 1998) and will therefore tend to increase as biomass accumulates within MPAs, but clearly this will depend upon the species being relatively sedentary (e.g. DeMartini 1993). The actual range over which such recruitment can be expected to occur is a matter for debate. In a small number of marine fishes (e.g. the scorpaenid *Sebastes* and eelpout *Zoarces*) and invertebrates with direct development, or very limited planktonic lives, the range should be small, but in most cases the fish recruitment supported by MPAs maybe distributed over tens to hundreds of kilometres. The shape and orientation of the dispersal envelope will depend on species, season and other factors (Roberts 1997b). The larval longevity of most fishes is probably best viewed as a measure of the range of distances over which dispersal can occur, because of other factors, such as current speed and direction which will affect dispersal in practice (e.g. Carr and Reed 1993).

14.3.2 Impacts on fisheries yield

The evidence for greater yield in fisheries adjacent to MPAs is based on few studies, in contrast to the evidence for greater abundance and body size of target species in MPAs (Table 14.3). The empirical work has been on reef fisheries in Kenya and the Philippines (Alcala and Russ 1990; McClanahan and Kaunda-Arara 1996), and demersal shelf species such as plaice in the North Sea (Borley et al. 1923; Margetts and Holt 1948), and shrimp in Florida (Klima et al. 1986). McClanahan and Kaunda-Arara (1996) showed that although catch per unit effort increased within 2 km of the boundary of the Mombasa Marine Park, total catch declined because the MPA consituted a large part of the ground and fishing effort per unit area increased; seven years after closure, the catch was still reduced (T.R. McClanahan and S. Mangi, unpublished data). The yield of pink shrimp (*Penaeus duorarum*) following establishment of a fishery MPA in the Tortugas of Florida was greatly affected by recruitment, but compliance by fishermen with the closure was also poor (Klima et al. 1986). One of the most striking examples of the effects of closure are those of the 'great fishing experiments' based on fisheries yield before and after both world wars in the North Sea (Smith 1994 and Smith, Chapter 4, this volume). Although there are problems with interpretation of the effort data, the evidence for these demersal fisheries is that with large-scale closure of entire grounds tens to hundreds of kilometres across, substantial increases in catch rate and total catch occur over time-spans of much less than 10 years (Borley et al. 1923; Margetts and Holt 1948). Other more recent examples of large-scale closures in the North Atlantic include those of herring (*Clupea harengus*) and capelin (*Mallotus villosus*) (ICES 1990; Bailey 1991), but the North Sea plaice (*Pleuronectes platessa*) box had failed to produce an increase in yield or stock biomass four years after permanent closure following earlier seasonal closure (ICES 1999). Another example of a large-scale temperate demersal fishery closure is that of the extension of the seasonal ban on trawling off the coast of Cyprus, where the MPA substantially increased yield within two years of the extension because the fishing mortality on fish in the first few months post-recruitment had probably been very high (Garcia and Demetropoulos 1986).

In the absence of extensive data both on spillover and recruitment through increased egg and larval output, modelling studies have provided predictions of yield under different MPA and fishing conditions, taking account of varying biological features of the animals involved (Table 14.3). With increase in MPA size, the spawning stock biomass per recruit can be expected to increase, but the yield per recruit outside the MPA will not increase, unless there is a decline in fishing effort; in fact, if the fishing effort remains the same, the yield will decline, because the effort per unit of fished habitat will have increased. MPAs can scarcely be expected greatly to increase yield (DeMartini 1993), except where they are large and fishing mortality is very high (e.g. Russ et al. 1992). The simplest yield-per-recruit models do not take account of recruitment variations in relation to stock (Shepherd and Pope, Chapter 8, this volume). This was true of the models used by Russ et al. (1992) and DeMartini (1993). When Guénette and Pitcher (1999) included both Schaefer and Beverton–Holt stock–recruitment relationships in a model as well as transfer across a hypothetical MPA boundary, they showed that at the fishing mortality corresponding to maximum sustainable yield (MSY), the yield is likely to be less when part of the ground is protected from fishing. However, when fishing mortality was double that producing the MSY, the yield was maintained in the presence of the MPA and exceeded that without a protected area (Guénette and Pitcher 1999). The suggestion is that the recruitment effects of MPAs will be more important for enhancement of yield than the spillover effects, but as yet there are no data about recruitment dynamics at the scale typical of MPAs.

Intense fishing should often increase year-class variability by making stock biomass more prone to annual recruitment (but see, e.g. Rijnsdorp et al. 1992). As a result MPAs may under certain circumstances reduce this variability by building spawning stock biomass. Only modelling results are currently able to provide specific predictions of the extent to which this will happen. Thus in a simulated cod (*Gadus morhua*) stock, the number of years with poor recruitment is likely to be reduced when some 10% or more of the ground is closed to fishing (Fig. 14.2). Using a simple logistic model, Lauck et al. (1998) have shown that the likelihood of maintaining a stock above, say, 60% of carrying capacity for at least 20 years, is likely to fall as the temporal variability in the catch increases. The proportion of a ground that must be protected to maintain the stock in this way is likely to be more than 50%.

14.3.3 Under what conditions will fish and fisheries benefits be detected?

The science of MPAs will no doubt be long in the development. Except in broad outline, extrapolation of data from one site to another is unwise, but it is reasonable to ask what general factors may affect the likelihood of detecting fish and fisheries effects.

Proper demonstration of fish abundance changes or fishery effects of MPAs requires comparison of the state before and after introduction of

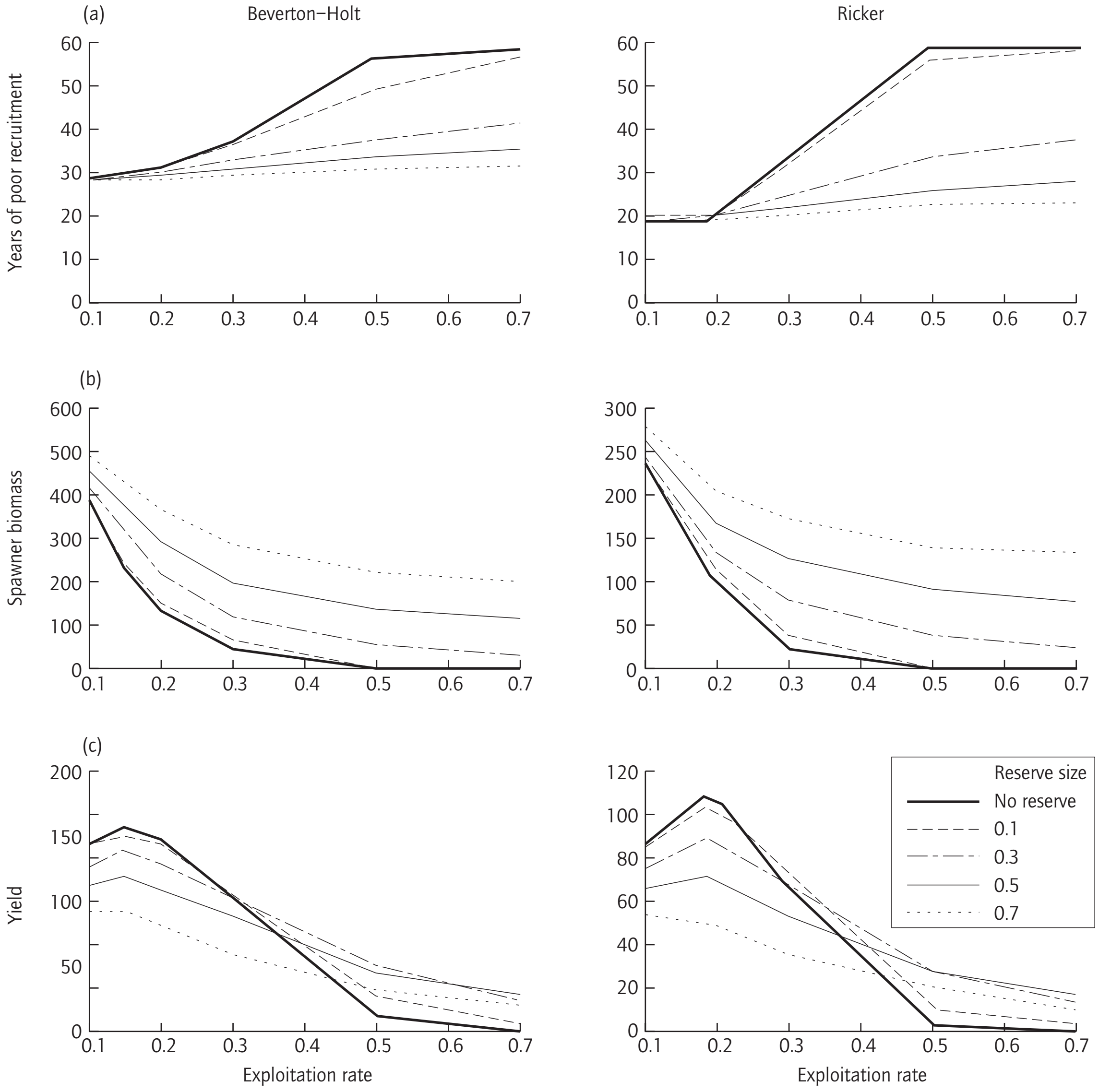

Fig. 14.2 Changes in (a) the number of years with poor recruitment, (b) spawner biomass, and (c) yield, of an Atlantic Cod (*Gadus morhua*) fishery as a function of exploitation rate and the proportion of the fishing ground ('reserve size') set aside as an MPA. Exploitation rate u is given by the equation $u = 1 - e^{-F}$, where F = the fishing mortality. (Source: from Guénette and Pitcher 1999, p. 299.)

the management regime and with unmanaged controls for comparison. This has seldom been possible. In both tropical and temperate waters, the data on changes in abundance are few, and those pertaining to yield itself fewer still. Warmer waters provide the opportunity of direct visual underwater surveys (e.g. Polunin and Roberts 1993; Russ and Alcala 1996 a point also mode by Jones et al., Chapter 16, Volume 1), but, at least in clear waters elsewhere, video is being recognized as a means of discriminating spatial differences in abundance (Willis et al. 2000) and size (Harvey and Shortis 1996) data. In many cases, including many fishery species, abundance and size estimation has to rely on sampling techniques such as fishing gears, including traps and nets (Jones et al., Chapter 16, Volume 1). Catch-per-unit-of effort data offer a relative measure of abundance, but the precision of this will typically be low (Appeldoorn 1996; Schnute and Richards, Chapter 6, this volume; Sparre and Hart, Chapter 13, this volume).

Given spatial and measurement sources of variability, statistical power for detecting most differences when they exist is small, where statistical power is the probability of correctly rejecting a null hypothesis of no difference between MPAs and unprotected areas. Put another way, only when large differences exist will they be detected (Fairweather 1991). It follows that in many cases, lesser but significant differences will not be detected. High spatial variability, small sample areas and numbers, differences in life history and behaviour, and high measurement error, perhaps caused by differences in procedure or acuity between divers, help to explain apparent differences among species in response to the creation of MPAs (e.g. Polunin and Roberts 1993). Yet, as noted by the meta-analysis of Mosquera et al. (2000), in MPA assessments to date, even basic statistics such as variances in means are sometimes not reported. There has also been very little attention to sources of measurement error, and full details of sample design are rarely given, yet the latter is crucial to defining spatial and temporal variability as a basis for assessing management effects. Differences in abundance between areas subject to different levels of management have been much more readily detected when species abundance data have been aggregated into trophic or taxonomic groups (e.g. Russ and Alcala 1996; Polunin and Jennings 1998).

Assessments of yield from fished areas are possible through several means. Surplus production models are simple, but preferably require long time series including good contrasts between catches and effort (Hilborn and Walters 1992; Appeldoorn 1996, Chapter 2.6; Schnute and Richards, Chapter 6, this volume). Yield-per-recruit models rely on catch, mortality and age data (Sparre and Hart, Chapter 13, this volume; Shepherd and Pope, Chapter 8, this volume). However, confident estimation of the underlying growth and mortality data is difficult in many areas (Appeldoorn 1996). Such data tend to be even more highly aggregated biologically and spatially than the best results from underwater visual work, and there is therefore a difference in spatial size of the sampling unit involved between using yields and using visual methods.

14.3.4 When and where can fisheries benefits be expected to occur?

Many factors will affect the likelihood of fisheries benefits occurring, but given the number of unknowns, it is worthwhile focusing on a few which might act as useful predictors. These factors include biological characteristics of the organisms, features of MPAs and their environments, and modes of exploitation.

One factor affecting MPA success in terms of fisheries benefits is the mobility of the species concerned. As mobility of species is a key determinant of the build-up of biomass within MPAs, it is clear that it will affect the likelihood not only of spillover effects, but also of the recruitment functions of MPAs. This can be simply expressed by comparing species that are highly mobile with those that are not (Table 14.4). Where species are highly mobile, the probability of movement out of MPAs will be high and biomass will not build up within them; this means not only that recruitment effects, will be small, but also that spillover will be small, on the grounds that it is a function, of biomass and the probability of movement (Table 14.4). Conversely, for sedentary species, the recruitment function of MPAs will be maximal, but the spillover effects will be small; on this basis, the greatest spillover is likely to be brought about by species of 'intermediate' mobility. This is supported by modelling, where the greatest yield per recruit occurred in a fish of intermediate mobility, although only the most mobile species exhibited

Table 14.4 Consequences of species mobility for recruitment through increased egg output and spillover functions of MPAs in intensively fished areas.

	High mobility	Moderate mobility	Low mobility
Biomass accumulation in MPA	Low	Medium	High
Recruitment function	Minimal	Intermediate	Maximal
Spillover function	Intermediate	Maximal	Intermediate

increase in yield with increasing MPA size, provided the fishing mortality was sufficiently high (DeMartini 1993). In the case of Sumilon Island in the Philippines, increases in yield were supported especially by fusiliers (Caesionidae), but also by jacks (Carangidae) and mackerels (Scombridae) (Alcala and Russ 1990), which are relatively mobile species for reefs (e.g. Holland et al. 1996).

Other biological characteristics may also help predict fishing impacts and the likelihood for recovery from exploitation in MPAs. For the North Sea, age at maturity, maximum size and potential rate of population increase are useful predictors of fishery depletion (Jennings et al. 1997), while in reef fisheries, maximum size can help predict decline in target-fish abundance (Jennings et al. 1999). Where a stock is depleted through direct effects of fishing alone, body size may help to predict recovery in MPAs. Body size is clearly related to a number of other characteristics, including potential longevity, natural mortality, growth rate and recruitment, and thus does not of itself provide an explanation for variations in recovery rate among organisms (Russ and Alcala 1998b).

On tropical reefs, very few studies have examined changes over time, and it appears that only two to date have determined effects on yield, and produced different results, from intensive fisheries (Table 14.3). In Kenya, a fishery with an MPA 10 km^2 in area, which is about 60% of the ground, had produced no increase after seven years in a total catch contributed to mostly by rabbitfish (Siganidae), parrotfishes (Scaridae), octopus and squid (McClanahan and Kaunda-Arara 1996; T.R. McClanahan and S. Mangi, unpublished data 1999). In the Philippines, a reef catch predominantly of fusiliers (Caesionidae), jacks (Carangidae) and mackerels (Scombridae) was greater with an MPA much less than 1 km^2 in area (*c*. 25% of the ground) than without (Alcala and Russ 1990). In temperate waters, measurements of yield effects come principally from MPAs spanning 10 000–>500 000 km^2 (Table 14.3), but results at the lower end of this spatial scale are equivocal, as in the case of the North Sea 'plaice box', and Cyprus and Georges Bank (2500–6000 km^2) closures (Piet and Rijnsdorp 1998), although the seasonal closure in Cyprus had a dramatic effect on yield (Garcia and Demetropoulos 1986). While these data contrast the effects of MPAs in reef and temperate demersal fisheries, the indication is that absolute size is not a good predictor of fishery effects. Modelling studies help to emphasize that it is the proportion of whole fishing grounds which is important (e.g. Guénette and Pitcher 1999), rather than absolute size, and, further, that fishing mortality relative to natural mortality is going to be important.

The time-scales over which MPA benefits can be expected have been examined in a few empirical and modelling studies. For some large vulnerable reef predators in the Philippines, spillover effects may take about ten years to become evident (Russ and Alcala 1996). The accumulation of biomass within MPAs of site-attached species vulnerable to fishing can occur within 10 years (Fig. 14.3) (see also Borley et al. 1923; Margetts and Holt 1948; Polunin and Roberts 1993), if the MPA is large enough to accommodate the mobility and vulnerability of the species concerned. In spite of the fact that the scientific basis for it is better understood than for other strategies such as spillover and larval recruitment through spawning biomass accumulation, pulse fishing of MPAs is considered by some not to be a feasible option. This is on the

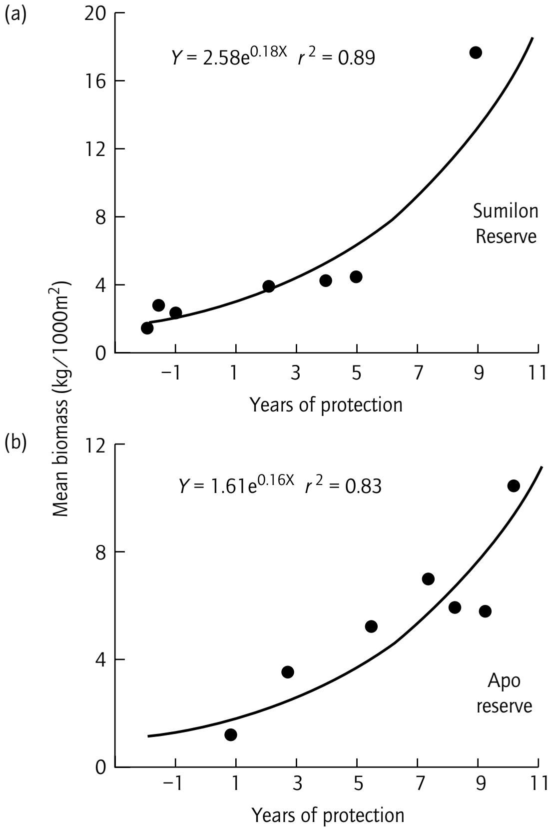

Fig. 14.3 Increase in biomass of large predatory fishes [19 species of groupers (Epinephelinae), 11 species of snappers (Lutjanidae), 6 species of emperors (Lethrinidae) and Carangidae] estimated by underwater visual census in two Philippine MPAs, showing a curvilinear pattern consistent with likely patterns of recruitment and growth: (a) Sumilon MPA and (b) Apo MPA. (Source: from Russ and Alcala 1996, p. 956.)

grounds that the accumulation of biomass takes a long time, but is quickly dissipated (e.g. Bohnsack 1994).

From what has been reviewed above, it can be seen that the siting of MPAs will influence the performance of their ecological and fishery functions. With the exception of a few fisheries closures, existing MPAs have been sited almost exclusively in relation to recreational diving and habitat conservation according to criteria which are mostly aesthetic. These criteria have served implicit purposes of attracting tourism, educating the public or signalling the presence of sensitive communities in particular areas (see below). However, the science of reserve design and location in relation to issues such as larval supply to depleted fisheries has scarcely progressed beyond an elementary modelling stage (e.g. Man et al. 1995; Guénette and Pitcher 1999; Sladek Nowlis and Roberts 1999; Planes et al. 2000; Sánchez Lizaso et al. 2000). Some general guidelines on the design of MPAs can be offered (e.g. Carr and Reed 1993; DeMartini 1993). In practice, the actual condition of particular sites is unknown. For example, the recruitment source or sink status of sites is rarely established, and this is especially so over long time-scales.

14.4 WHAT ELSE DO MPAs OFFER?

Fishing has effects on the marine environment other than direct impacts on target species (Kaiser and Jennings, Chapter 16, this volume). These include effects on species which interact with the target species and are thus secondarily affected, and impacts on habitat, where destructive gears such as trawls are used. The latter may have consequences for fish and fisheries if the habitat is important in recruitment.

MPA management tends to increase abundances of site-attached species which have been depleted by fishing. Through this MPAs can play a role in the conservation of biological diversity, and in creating greater species richness, expressed as the total number of species. Other measures of diversity have been reported in many MPAs (e.g. Cole et al. 1990; Jennings et al. 1995). Such increases do not invariably occur, and there are a number of reasons for this. In the Philippines, species richness rose in one MPA (Sumilon), which was enforced between bouts of intensive fishing, but not in another (Apo) (Russ and Alcala 1998a), although differences in the biomass of target species were significant. In both cases, the principal fishery targets contributed greatly to community biomass but little to overall numerical abundance. As a consequence species richness was a poor indicator of the presence or absence of fishing even though this was intense, albeit somewhat non-selective (Russ and Alcala 1998a). Since most data on abundance of target species in MPAs are derived by visual means, the sample areas are small, and observer presence can affect them (Kulbicki 1998). In reality effects of MPAs on biological diversity are poorly known; for example, species which are rare and those with large home ranges will be undersampled. Given such sampling constraints, use of a phrase such as 'local extirpation', in the context of a small-scale fishery, needs to be classed as provisional until the wider distribution of the species is known. The contention that species extinction is comparatively less common in the sea than on the land tends to be upheld (e.g. McKinney 1998), but there are points of vulnerability. For example, species of large size with slow growth and low reproductive rates, such as many turtles, large serranids and elasmobranchs, are vulnerable (Dulvy et al. 2000; Reynolds et al. 2001). Hotspots of endemism are places where MPAs may play a conservation role. Given the mobility of the larger species often involved, lack of knowledge of their life histories, and competing uses of marine habitat, mean protection of whole populations is unlikely, while planning for piecemeal inclusion of vulnerable stages and habitats will be difficult.

The role of MPAs in biodiversity conservation could be increased by species interactions, such as those between predators and prey, and among competitors for space. Shifts in community structure have occurred in many intensively exploited systems in the tropics and in temperate waters, and there is much debate about the exact nature and causes of these changes (e.g. Hughes 1994; Christensen 1998; Fogarty and Murawski 1998). Although food webs and models of carbon fluxes are obvious places to look for synoptic overviews of systems (e.g. Pauly et al. 1998; Pauly and Christensen, Chapter 10, this volume), in fact they provide pictures only of how species are trophically linked, and may not be good predictors of change in community structure where processes such as recruitment, control prey organisms rather than predation (Chapter 14, Volume 1). This may explain why prey fishes are no more abundant in fished sites than in MPAs in the Seychelles (Jennings et al. 1995) and the Philippines (Russ and Alcala 1998a), or grounds in Fiji with very high fishing pressure when the abundance of predators is greatly reduced (Polunin and Jennings 1998). However, there are cases where linkages between species are tighter, and predators may play keystone roles, such that community effects of fishing may be reversed in MPAs, as for triggerfish (Balistidae) feeding on sea urchins in Kenyan lagoonal reefs (McClanahan and Shafir 1990). Other implications of food webs for changes in communities in MPAs are addressed elsewhere (Chapter 14, Volume 1).

Recreational diving is a point of significant growth in tourism and thus a major source of revenue of marine origin around the world (e.g. Dixon et al. 1995). Although there seems scarcely to have been any systematic study of the fact, fishes are undoubtedly a major focus of much diving and snorkelling, and in some cases they greatly influence perceptions of the underwater experience (e.g. Andersson 1998; Polunin and Williams 1999). MPAs, where they increase the abundance or size of fishes which are of interest to divers, may therefore help to generate local revenue through increased expenditure on diving, accommodation, entrance fees and other means (e.g. Dixon et al. 1995). Estimates of the market value of the standing stock of fishery target fish in a Belize MPA (Polunin and Roberts 1993), when compared with the direct revenues to MPAs that are intensively used by divers (e.g. Mattson and DeFoor 1985), indicate that marine habitat, in this case reef, can be hundreds of times more valuable per unit area to tourism than to capture fisheries. A substantial part of this tourism revenue is unlikely to reach the local communities involved, and is derived from particular dive sites of limited total area. Conversely, fishing is a more extensive activity than most diving, but the value of the reef as source of catch is lower still when the costs of fishing are considered. On balance, recreational diving has to be a major potential financial benefit to be derived from MPAs. Where this is focused on large or rare species in particular, the implications for enforcement need to be carefully considered. The evidence from reef fishes is that maximum biomass is built up and large fishes are abundant only if there is minimal fishing; a small amount of fishing is likely to lead to rapid decline in biomass (Fig. 14.4) (see also Russ and Alcala 1996).

MPAs have additional value to recreational divers such as through the presence of fragile hard corals and gorgonians. These can be destroyed by fishing (e.g. Shaffer et al. 1998). In addition, recovery from the effects of damaging gears such as trawls on benthic organisms and on habitat structure (e.g. Engel and Kvitek 1998; Thrush et al. 1998; Kaiser et al. 2000) can be expected to occur in MPAs, especially where natural disturbance is minor (Jennings and Kaiser 1998). This may have significant consequences for fishery species and for biodiversity (Auster et al. 1996). Further, in large MPAs, bycatches will no longer be discharged back into the environment, and any effects this has on abundance of scavengers and predators (e.g. Hall 1999) will be reversed.

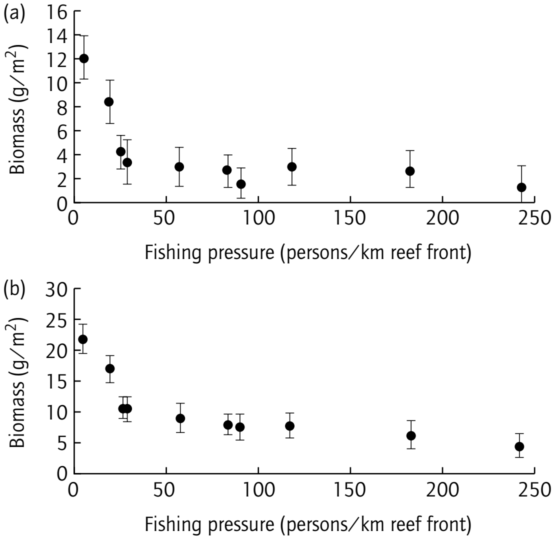

Fig. 14.4 Biomass assessed by underwater visual census of (a) epinepheline groupers (genera *Anyperodon, Cephalopholis, Epinephelus, Gracila, Plectropomus* and *Variola*) and (b) all piscivorous fishes >30 cm in length on reefs in 10 Fijian traditional fishing-grounds varying 600-fold in fishing pressure index from very low levels. Error bars are 95% CL. (Source: after Jennings and Polunin 1996a.)

14.5 REALITIES, ADVOCACY AND IMPLEMENTATION OF MPAs

As in so much environmental literature, there is an inclination in many of the general reviews that have been written about MPAs to list only known advantages of MPAs (e.g. Plan Development Team 1990; Ballantine 1991, 1999; Roberts and Polunin 1991; Russ et al. 1992; Bohnsack 1993). These can be read as promotional statements of benefits that can be expected from MPAs generally. Costs and uncertainties are inherent in all MPAs (e.g. Dugan and Davis 1993; Allison et al. 1998) and many of these are expressed in Table 14.5. Conflict between potential costs and potential benefits can of course be overplayed, but the water being muddied is a vast middle ground between advocacy and science, and consequences of unbalanced judgements can be far-reaching, as evinced by the existence of many protected areas on land. It is true that scientific methods of data gathering and inference are not the best means alone to address urgent demands of growing human impacts on the marine environment. In developing countries in particular, advocacy for MPAs does not necessarily solve the underlying problems of seemingly hopeless growing social and economic deprivation (e.g. Polunin 1990). In developed regions such as the North Sea or the northeast shelf of North America, it is hard to see how politicians will legislate for even more draconian measures than those already in place and derived from conventional fisheries science. These measures have led to the extensive closure of fishing-grounds decided on the basis of available data and scientific common sense. It is worth noting that closures have been applied in areas such as the North Sea where potential benefits for particular stocks such as plaice and cod

Table 14.5 Advantages and disadvantages of permanent or long-term MPAs for site-attached fishes, fisheries management, conservation, science and other stakeholder activities.

Advantages/Likelihoods	Disadvantages/Uncertainties
Fisheries	
Fisheries yield maintained or enhanced through larval dispersal	Benefits may be only long term
Fisheries yield maintained or enhanced through spillover	Higher catch rates confined to a small adjacent area
Fluctuations in catch potentially reduced	Most of ground closed, yield likely to be reduced
Chances of recruitment overfishing reduced by maintained spawning stock	Fishing effects increased because only part of stock exploited
Fisheries management	
Undisturbed spawning and/or nursery grounds	Unlikely to be useful for migratory species
Temptation of fishermen to violate laws reduced	Incentive for deliberate poaching increased
Data collection needs of management potentially reduced	More research needed because of uncertainty as to MPA design
Surveillance and enforcement simplified	Increased poaching: increased need for surveillance and enforcement
Resources potentially available for mariculture and restocking	Potential vulnerability to recruitment failure
Conservation	
Habitat protected from damaging fishing techniques	Use of damaging methods may be increased outside
Endangered/vulnerable species protected	Protection unlikely to be for whole life cycle
Biodiversity may be increased	Most species unaffected
Science	
Areas provided for research on unfished systems	Uncertain baselines, pollution uncontrolled
Community protected, biodiversity maintained or enhanced	Recruitment and system-level effects (e.g. reversibility) unsure
Other stakeholders	
Increased diver use	Negative impacts of visitor use and tourism development
Management concept more easily understood by public	Local resistance to MPA: detailed research needed to justify
Areas provided for nature-educational purposes	Costs of interpretive facilities and access
Economic benefits through tourism	Failure of some to benefit economically

have been indicated. The example of the plaice box emphasizes that wisdom and objective advice will not guarantee successful management, but mostly they are sensible preconditions for it. Many have touched on matters of design (e.g. Carr and Reed 1993; Dugan and Davis 1993; Rowley 1994; Allison et al. 1998; Ballantine 1999), and I do not intend to elaborate these further here, beyond what is explicit from the empirical and other evidence that I have presented. Rather I wish to explore the wider values and implications of the planning and implementation of MPAs.

MPAs have positive, negative and unknown impacts, and it is surprising that MPAs have rarely been subject to the environmental impact analyses that are now widely required for most other developments of any size in areas of natural beauty. The fact is that not only have few MPAs been established in many regions, but where many MPAs have been gazetted, they have often not been properly managed and so have not met their objectives (e.g. Stanley 1995; McClanahan 1999). There are many reasons for this, including lack of interest, personnel and money, and opposition from other stakeholders. This comes particularly from those who are disadvantaged, as are the fishers by loss of ground. Given the patchy evidence for increased yields of many important resource species arising from MPAs, it is difficult to promise future fishery benefits. This is so in developing countries for reasons of rural poverty, but it is also difficult for small-scale fisheries in developed countries. If the weak evidence for fisheries benefits is considered, there should be little surprise that scepticism exists; it is well justified on scientific grounds.

Declines over time in several of the world's marine fish stocks (FAO 1995; Hart and Reynolds, Chapter 1, Volume 1) may constitute a global crisis in capture fisheries (Roberts 1997a), yet, although excessive fishing effort has contributed to decline (e.g. Myers and Barrowman 1996), variation in environmental conditions constitutes a source of great uncertainty for the science, for suitable political decision making and for effective management (e.g. Caddy and Gulland 1983; Botsford et al. 1997). Fluctuations in recruitment have been studied for over a century at higher latitudes (Smith 1994; Smith, Chapter 4, this volume), but substantial variations in year-class strength are now being recognized in some tropical species (e.g. Ferreira and Russ 1995), although probably concealed in most fisheries through aggregations of species into broad categories. The arguments that have been presented with respect to the maximization of spillover and recruitment effects (Table 14.4) highlight the fact that for MPA-orientated fisheries management to be rational, more science is required, just as modern fisheries management has been underpinned by vigorous investigation and reasoned debate (e.g. Smith 1994; Smith, Chapter 4, this volume). It is ironic that MPAs should be confidently advocated as fisheries management measures on the basis of failures in conventional fisheries science, when the science underpinning MPAs is in its infancy. This is best illustrated by the example of recruitment to and from MPAs, which can clearly be crucial to achievement of management objectives (e.g. Carr and Reed 1993; Allison et al. 1998; Planes et al. 2000). What is required is a clearer picture of how MPAs relate to the wider panoply of fishery management measures, but one difficulty is that, at least in developed countries, the MPA proponents are very different from those responsible for fisheries management. This may not always be so, but it is worth noting that, in contrast, many less-developed countries such as Malaysia, have fisheries and MPA management under the same governmental roof, which may facilitate communication, although interdisciplinary work is no doubt easier when the variety and volume of information are lower (e.g. Caddy 1999). This is commonly the case in the tropics. In more temperate settings, the social and economic impacts of MPAs and consequences of fishery science, which is considered by some to have failed (e.g. Roberts 1997a), are surely similar, and will need similarly to be addressed by politicians and managers if measures in either case are to be a success.

Small MPAs set up in reef habitats for nature conservation and not for fishery purposes, mostly in tropical and subtropical areas (Tables 14.1–14.3), have provided much of the impetus for the advocacy of MPAs (Bohnsack 1993; Roberts 1997a). However, the overwhelming evidence is that MPAs should typically be a large portion of a fishing-ground if it is to benefit fisheries (e.g. DeMartini 1993; Guénette and Pitcher 1999; Lundberg and Jonzén 1999; Sladek Nowlis and Roberts 1999). Some of the evidence from site-attached species on reefs suggests that increased yields can occur as a result of small MPAs (Table 14.3). Yet the impacts which large-scale oceanic events can have on major fisheries (Hofmann and Powell 1998) highlight the vulnerability of small MPAs, and the findings and inferences from studies of site-attached species, mostly at low latitude, and of temperate demersal species, contrast markedly with each other. There are several likely reasons for this, including differences in ecology, and different perceptions of scientists studying them. It is hard to escape the conclusion that MPAs will not everywhere do the same job. They will need therefore to be designed differently and appropriately, but further research is needed to predict the outcomes.

The uncertainties of fisheries outcomes from MPA-orientated management have surely to be treated with openness if such management is to be widely adopted. One means towards open dialogue, particularly with those who stand most to be disadvantaged by large-scale area closure, is through participation by fishers in 'comanagement' (Hart and Reynolds, Chapter 1, this volume). One argument in favour of comanagement derives from the contention that in many parts of the world local communities have traditionally managed their resources in areas over which they have tenure (Johannes 1978; Ruddle et al. 1992). Sophisticated tenure does not go hand in hand with a conservation ethic (e.g. Carrier 1987) and the abundant evidence is that such ownership arose for reasons of conflict resolution rather than of resource restraint (e.g. Polunin 1984). The adaptability of traditional management to modern management is thus in question, but it should be the case that local users have potential roles to play in resource monitoring and management, and there is some evidence that this is so. For example, in Chile, 'management and exploitation areas' owned by local communities have been beneficial in a mollusc fishery (Castilla and Fernandez 1998). This case, together with work in Samoa, highlights the potential uses of cooperative arrangements for knowledge building and promotion of MPAs (e.g. Castilla 1999; King and Faasili 1999). Local management on its own would seem typically to be unwise for a number of reasons. From work in the Philippines, it is evident that local institutions may be politically vulnerable (e.g. Russ and Alcala 1999), while experience in Fiji indicates that without help local institutions may not be good at discerning significant changes in the status of their resources (Fig. 14.5). Further, the Chilean case study points to looming conflict between the sustainability of resources and wider management objectives (e.g. Castilla and Fernandez 1998). Rather, the essence of comanagement is that there are some inputs which are best provided by central authorities, and others which are most appropriately delivered by the local group concerned.

In the field of nature conservation, where the concern is to protect biodiversity, vulnerable organisms and fragile habitats, the concept of MPAs enters different territory. One reason for this is that the financial value of fragile habitats such as reefs can be so much greater on the basis of tourism than that of fisheries. This linkage with tourism of course brings a danger of visitor-related damage. Then, revenue is not the only benefit to consider, although it is an important outcome recognized by politicians and welcomed by the poor. It is evident that MPAs can contribute much towards such income: well-managed visits to pleasing seascapes must surely increase the likelihood of a wealthy diver returning to a site and of others visiting and enjoying the environment in turn. And in fact it would appear that in many regions, such as the Caribbean and Southeast Asia, MPAs have been set up with tourism in mind. The most obvious thing that MPAs will do in this respect is to increase the abundance of site-attached species which are vulnerable to fishing, and these are an important part of what divers and snorkellers come to see (Williams and Polunin 2000). Fishes of large size are, however, especially vulnerable to fishing, and these valuable attributes of dive sites need to be conserved, by employing a strict protection regime. It is also probably true that just the hint that MPAs are close, or closer, to the natural state will be sufficient for many ecotourists to visit and dive in them. In relation to biological diversity, the openness of local marine populations and thus their susceptibility to recruitment variability emphasize that the future of biotic assemblages is not best assured by small MPAs. Either much larger areas are needed or networks of areas are required

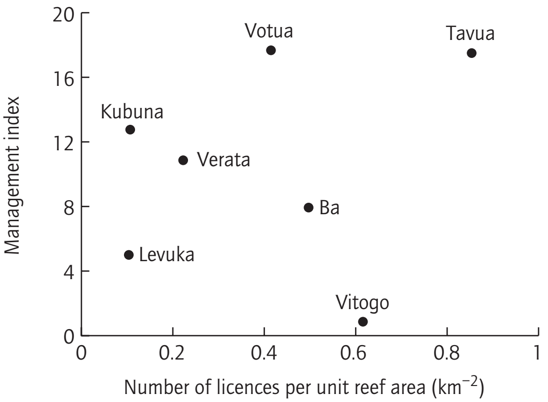

Fig. 14.5 Traditional fishing-grounds (*qoliqoli*) of Fiji: variations in management regime ('yes' or 'no' responses to 26 questions relating to the structure of management, the marshalling of information for management, approach to goodwill payments for licensing, management measures taken or contemplated, and patrolling and enforcement) among the seven *qoliqoli* which varied in access pressure (number of licences issued per ground). (Source: Cooke et al. 2000.)

to do the job, but the underlying science needed is poor (e.g. Carr and Reed 1993; Allison et al. 1998).

14.6 CONCLUSIONS

In the marine environment, human exploitation is ahead of its time; the environment is different and management is relatively new (Allison et al. 1998). Fisheries management science has been conducted under conditions that are unfavourable to sound science (e.g. Hilborn and Walters 1992; Caddy 1999). Fisheries management science may be derided for the 'global fisheries crisis' (Roberts 1997a), but other uncertainties adversely affect the uptake of scientific advice by management (e.g. Hall 1999), and it would be surprising if an unsophisticated and inflexible management concept, such as represented by MPAs, were to supersede fisheries management with its more detailed scientific underpinnings. An important question for the advocates of MPAs is how the gap can honestly be bridged between the small areas protected (Fig. 14.1) and the large areas required for the delivery of benefits from MPAs to fisheries, ecotourism and biodiversity. In spite of the socioeconomic circumstances, the spatial scale involved is one which might more easily be spanned in developing countries than in developed nations. In many developing countries, the evidence for economic benefits from MPAs is greater, and in some cases it seems that the government structures are less resistant to the type of interdisciplinary thinking required. Benefits of ecotourism are widely recognized while plentiful relevant resources remain, and lesser sophistication in scientific knowledge probably facilitates discussion at an interdisciplinary level. In contrast, the evidence for benefits being derived from MPAs in developed countries is minor, government structures seem cumbersome, and there is a widespread perception that the resources are in many cases unredeemably tainted.

The big unknown in all this is, of course, public opinion. If the public voice becomes loud enough, then that of the rump fishing community typical of developed countries may scarcely be heard. The public perception of the urgency of conserving rare organisms and biodiversity as a whole might then outweigh the lingering doubts about retaining the capacity to exploit the oceans in ways that in principle have not changed for centuries. In the case of some, such as trawling, there is much waste by crude methods. It could happen: liberalization and globalization of markets have increased, allowing some to embrace consumption of marine products based entirely on imports. As aquaculture shows signs of taking off, it could perhaps replace the supply of marine products from capture fisheries, albeit with environmental consequences of its own. But caution dictates that options should be kept open, and, in the meantime, it seems wise to consider MPAs as one of a range of measures which are available for management of the seas, and tourism has to feature strongly in that consideration. Apart from reef fish and fisheries, the overwhelming evidence is that management has to be large scale, and this implies much more sophisticated planning and implementation structures than those required for MPAs.

ACKNOWLEDGEMENTS

The research and other field experience which underlie my writing of this chapter have been funded from several sources, most notably the Department for International Development for the benefit of developing countries and the Natural Environment Research Council of the UK. I especially thank Simon Jennings, Nick Dulvy and Adriaan Rijnsdorp for their comments.

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15 Exploitation and other Threats to Fish Conservation

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15.1 INTRODUCTION

The traditional goal in fisheries management has been to obtain continuing yields from a living 'resource'. Concerns are raised when populations fall below levels that provide adequate yields or which fail to meet other specified reference points (Shepherd and Pope, Chapter 8, this volume). Unfortunately, fishers and fisheries biologists have had a lot to be concerned about lately, as maximum sustainable yields have been exceeded for many fisheries (Jennings et al. 2001b) with many stocks now in decline. There have been some spectacular declines of species with a wide spectrum of life histories and habitats, including various stocks of Atlantic cod, *Gadus morhua*, Peruvian anchoveta, *Engraulis ringens*, southern bluefin tuna, *Thunnus maccoyii*, swordfish, *Xiphius gladius*, and sablefish, *Anoplopoma fimbrae* (Fig. 15.1).

The economic and social hardships caused by population declines in so many fisheries around the world have received a great deal of deserved attention. The poorest of the world's countries (with a per capita gross domestic product <US$5000) rely on fisheries to supply approximately 40% of their protein (Kent 1998). In richer countries, while diminished fisheries may not lead to starvation, the disruptions to livelihoods can still be enormous, as shown by the loss of 40 000 jobs in eastern Canada when the northern cod stock collapsed and was finally closed to fishing in 1992 (Hutchings and Myers 1994). Clearly, with such economic issues at stake, politics has played a large role in the uptake of management advice, often erring on the side of continued employment rather than more stringent, less socially palatable management measures (Hart and Reynolds, Chapter 1, this volume).

Until recently, such failures of fisheries management policy have remained outside the mainstream conservation movement. Indeed, conservationists have generally taken much less interest in marine and freshwater environments than in terrestrial habitats. For example, a survey of papers published in the journal *Conservation Biology* found that only 5% were for marine species and habitats, 9% were freshwater, and 67% were terrestrial (Irish and Norse 1996). While there have been some notable public concerns about selected issues such as whaling, declines in fish populations have dwelt in the domain of 'management failures' rather than 'conservation problems' (Reynolds and Jennings 2000). This inattention to conservation issues in fishing has started to change during the past decade as conservationists have begun to worry about the possibility that fish populations may be unable to recover from severe declines (Reynolds and Mace 1999; Roberts and Hawkins 1999; Hutchings 2001a). Perhaps fishes may become extinct as a result of fisheries. We already know that they can be virtually eliminated from large parts of their ranges (Brander 1981; Casey and Myers 1998; Dulvy et al. 2000; Dulvy and Reynolds 2002). Thus, after swimming quietly in the backwaters of the environmental move-

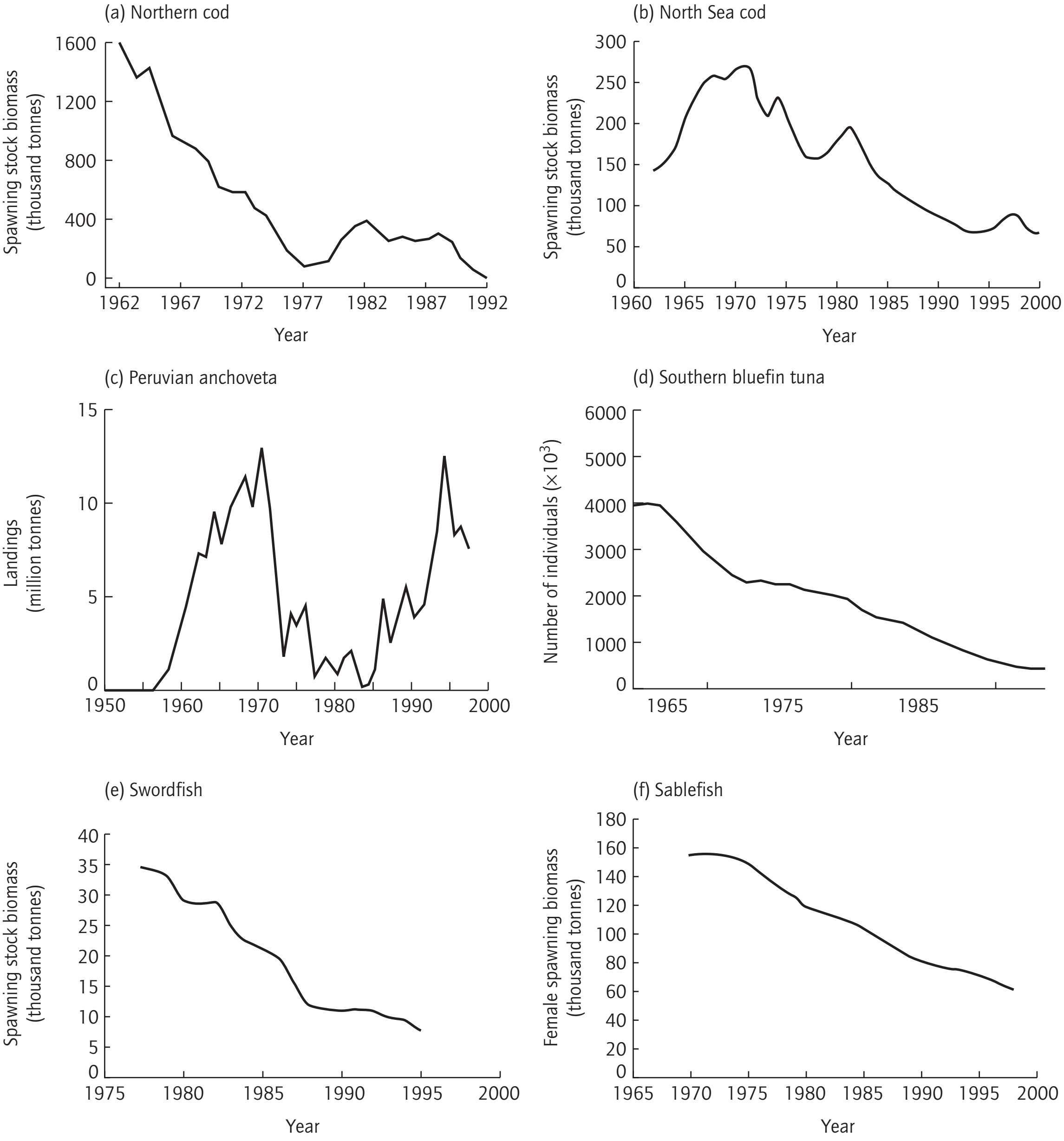

Fig. 15.1 Fish stock declines: (**a**) northern cod, *Gadus morhua* (Hutchings and Myers 1994); (**b**) North Sea cod, *Gadus morhua* (ICES 2001); (**c**) Peruvian anchoveta, *Engraulis ringens* (FAO 1999); (**d**) southern bluefin tuna, *Thunnus maccoyii* (Matsuda et al. 1998); (**e**) swordfish, *Xiphius gladius*; (**f**) sablefish, *Anoplopoma fimbrae* (*http://www.mscs.dal.ca/~myers/welcome.html*).

ment during the 1970s and 1980s, fishes are now featuring alongside other taxa as the public and scientists ask questions about links between exploitation and conservation (e.g. Mace and Hudson 1999; Hutchings 2001a; Reynolds et al. 2001a).

The goal of this chapter is to review the role of exploitation in causing conservation problems for fish species. We will review the evidence for severe declines in freshwater and marine fish populations which could lead to extirpation or extinction. We examine biological attributes of fishes and socio-economic aspects of fisheries that render species vulnerable. This leads to a consideration of how 'conservation' of exploited species means different things to different people, as shown by difficulties in assessing the threatened status of marine fishes. We hope that this discussion will help to bridge the scientific gap between different approaches to 'conservation' of exploited species.

15.2 GLOBAL STATUS OF EXPLOITED FISH POPULATIONS

The fallacy that there are always more fish in the sea has officially ended. Marine capture fisheries produced 86 million tonnes in 1998, valued at US$76 billion. The global marine fish catch was thought to have levelled out in the 1990s, but a predictive catch model suggests the global marine fish catch peaked in 1988 at 78 million tonnes and has since declined to 69 million tonnes (Watson and Pauly 2001; see Hart and Reynolds, Chapter 1, Volume 1). These figures omit the highly variable Peruvian achoveta catch and correct for massive misreporting by China (Watson and Pauly 2001). The FAO report that approximately half of the major fish stocks are fully exploited and very close to their maximum sustainable limits, with another quarter overexploited or depleted (Fig. 15.2). Only the remaining quarter of the world's fish stocks are considered to be under- or moderately exploited (FAO 1999).

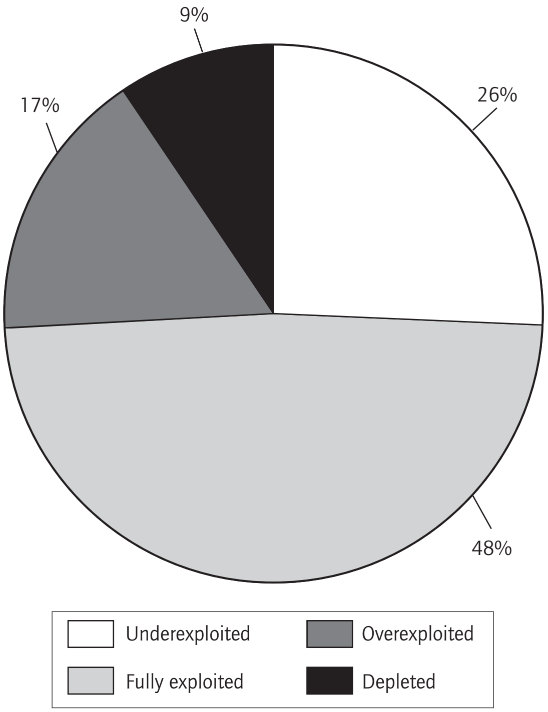

Fig. 15.2 Percentages of the world's fish stocks that range from underexploited to depleted. (Source: from FAO 1999.)

15.3 EXTINCTION

15.3.1 Recent extinctions

There are severe problems in estimating how many fish species have become extinct because of the difficulties of sampling aquatic habitats sufficiently well to be sure that a fish has truly disappeared from its entire range (Smith et al. 1993; Carlton et al. 1999; McKinney 1999). It is no longer fashionable for funding agencies to pay for basic taxonomy and collecting trips. Thus, lack of sampling effort as well as taxonomic uncertainties raise real difficulties in assessing accurately whether or not species have become extinct.

These problems are illustrated by an attempt to convey the strength of evidence for extinction of freshwater fishes, which has led to ongoing refinements of criteria and a database showing the level of support for apparent recent (since AD 1500) extinctions of fishes (Harrison and Stiassny 1999; *http://creo.amnh.org/*). Examples of criteria that have been proposed include that the species' name should be taxonomically valid, and that attempts to collect the species during appropriate surveys have failed. Both of these requirements are often sticking points in conservation assessments of aquatic species. There has also been debate about whether one should wait some arbitrary period of time (e.g. 50 years) to be sure that a species has truly gone, but this requirement has been dropped by the World Conservation Union (IUCN's) *Red List* rules, as well as by the American Museum of Natural History's Committee on Recently Extinct Organisms (*http://creo.amnh.org/*).

Table 15.1 shows 34 fish species whose taxonomic status is clear and for which surveys have been adequate to be reasonably certain that they are extinct. This list does not include Lake Victoria cichlids, largely because of inadequate surveys (Harrison and Stiassny 1999). When these species are included, along with other cases of unresolved extinctions, the database includes a total of 164 species.

It is noteworthy that all known cases of recent extinctions of fishes (since AD 1500) have happened to be freshwater species, despite the fact that marine taxa account for roughly 60% of described species (Gill and Mooi, Chapter 2, Volume 1). While the compilation by Harrison and Stiassny (1999) focused on freshwater taxa, our own survey of the literature and discussions with colleagues did not reveal any marine species that we could add to the list with complete confidence. However, there are at least three reasonable candidates that may well be extinct (Roberts and Hawkins 1999; Hawkins et al. 2000). The Galapagos damselfish (*Azurina eupalama*) is a planktivorous species which disappeared during the 1982–3 El Niño in the eastern Pacific, one of the most intense El Niños for the last several hundred years (Glynn 1988). The warming associated with the El Niño shut down the upwellings that fuelled plankton production for nearly one year and the Galapagos damselfish has not been seen since, despite thorough surveys. The green wrasse (*Anampses viridis*) was described from shallow waters around the island of Mauritius in 1839 but has not been seen since. It may have suffered from degradation of reefs in the area, due to sedimentation and nutrient pollution. Similarly, the deepwater angelfish, *Apolemichthys guezi*, endemic to the nearby island of La Réunion, seems also to have disappeared, though further sampling will be necessary to confirm this. Morris et al. (2000) also noted that several species of tropical groupers have not been seen for long periods since their first description. Although general rarity and poor sampling are probably to blame for their 'disappearance', groupers are highly vulnerable to overfishing (Coleman et al. 1996). Thus, while some of these marine taxa may rise from the dead, extinction of highly localized species in areas subject to detrimental human activities cannot be ruled out.

15.3.2 Palaeoextinctions

The fossil record may shed some light on whether extinction rates in marine habitats are really lower than in non-marine habitats. McKinney (1998) showed that in a variety of non-fish taxa, marine lineages have persisted on average for five times longer in the fossil record than have non-marine lineages. However, it is not clear whether these differences are due to differences among habitats per se, or due to differences among the taxa themselves, since none of the taxa analysed had representatives in both environments. If these broad taxonomic comparisons also apply to fishes, they would support the impression of lower rates of recent extinctions in marine habitats.

McKinney (1998) also looked at how duration of species in the fossil record related to the fraction of a taxon that was listed as threatened by the World Conservation Union (IUCN 1996). Fishes represented one data point among a number of broad taxonomic groupings. There was a positive relationship between extinction rates in the geologic past and the percentage of species currently threatened. Of course, these data are confounded because the most threatened taxa also tend to be the largest and best known, and the best-known species do

Table 15.1 Species of fish for which there is strong evidence of extinction. This list does not include Lake Victoria cichlids, nor many other species, due to uncertainties about taxonomic status or incomplete surveys of appropriate habitat.

Family	Genus	Species	Common name	Former distribution	Extinction year	Extinction cause
Adrianichthyidae	*Adrianichthys*	*kruyti*	duck-billed buntingi	Indonesia	>1983	P – IN – D
Aplocheilidae	*Leptolebias*	*marmoratus*	ginger pearlfish	Brazil	>1944	HM – P
Catostomidae	*Chasmistes*	*muriei*	Snake River sucker	United States	>1927	HM
Catostomidae	*Moxostoma*	*lacerum*	harelip sucker	United States	1893	HM
Cyprinidae	*Cephalakompsus*	*pachycheilus*		Philippines	>1921	HM – IN – OE
Cyprinidae	*Chondrostoma*	*scodrensis*		Yugoslavia	>1881	P – OE
Cyprinidae	*Cyprinus*	*yilongensis*		China	>1977	HD
Cyprinidae	*Evarra*	*bustamantei*	Mexican dace	Mexico	>1957	HM – P – HD
Cyprinidae	*Evarra*	*eigenmanni*	plateau dace	Mexico	>1954	HM – P – HD
Cyprinidae	*Evarra*	*tlahuacensis*	endorheic dace	Mexico	>1957	HM – P – HD
Cyprinidae	*Gila*	*crassicauda*	thicktail chub	United States	>1957	HM – IN
Cyprinidae	*Lepidomeda*	*altivelis*	pahranagat spinedace	United States	>1938	IN
Cyprinidae	*Mandibularca*	*resinus*	bagangan	Philippines	>1922	HM – IN – OE
Cyprinidae	*Notropis*	*amecae*	Ameca shiner	Mexico	>1969	HM – P – IN
Cyprinidae	*Notropis*	*aulidion*	Durango shiner	Mexico	>1961	HM – P – IN
Cyprinidae	*Ospatulus*	*palaemophagus*		Philippines	>1924	HM – IN – OE
Cyprinidae	*Ospatulus*	*trunculatus*	bitungu	Philippines	>1921	HM – IN – OE
Cyprinidae	*Pogonichthys*	*ciscoides*	Clear Lake splittail	United States	>1970	HM – P – IN
Cyprinidae	*Rhinichthys*	*deaconi*	Las Vegas dace	United States	>1940	HM
Cyprinidae	*Sprattelicypris*	*palata*	palata	Philippines	>1922	HM – IN – OE
Cyprinidae	*Stypodon*	*signifer*	stumptooth minnow	Mexico	>1903	HM – P
Cyprinodontidae	*Cyprinodon*	*ceciliae*	pupfish	Mexico	>1988	HM
Cyprinodontidae	*Cyprinodon*	*inmemoriam*	cachorrito del la Presa	Mexico	>1984	HM
Cyprinodontidae	*Cyprinodon*	*latifasciatus*	Parras pupfish	Mexico	>1903	HM – P
Cyprinodontidae	*Orestias*	*cuvieri*	Lake Titicaca orestias	Bolivia, Peru	>1937	IN
Fundulidae	*Fundulus*	*albolineatus*	whiteline topminnow	United States	>1889	HM – IN
Gastoresteidae	*Pungitius*	*kaibarae*	Kyoyto ninespine stickleback	Japan	>1959	HM – P
Gobiidae	*Weberogobius*	*amadi*	Poso bungu	Indonesia	>1985	P – IN – D
Goodeidae	*Characodon*	*garmani*	Parras characodon	Mexico	>1880	HM – P
Goodeidae	*Empetrichthys*	*merriami*	Ash Meadows killifish	United States	>1948	HM – IN
Poeciliidae	*Gambusia*	*amistadensis*	Amistad gambusia	United States	>1968	HM – IN
Retropinnidae	*Prototroctes*	*oxyrhynchus*	New Zealand grayling	New Zealand	>1923	HM – IN – D
Salmonidae	*Coregonus*	*johannae*	deepwater ciscoe	Canada, United States	>1952	IN – OH – HY
Salmonidae	*Salvelinus*	*agassizi*	silver trout	United States	>1930	HM – IN – OE

Notes: Codes for cause of extinction: HD, habitat destruction; HM, habitat modification; HY, hybridization; IN, introduced species; OE, overexploitation; P, pollution; D, disease.
(Source: American Museum of Natural History's Committee on Recently Extinct Organisms (*http://creo.amnh.org/*).)

not live in the sea. We are therefore most likely to identify a species as threatened if it lives in a non-marine habitat. Nonetheless, McKinney concluded that the perception that marine species are less extinction prone is valid. Subsequent work has argued that the extinction rate of poorly known taxa in well-studied regions equals that of the best studied taxa – mammals (McKinney 1999). Thus, the appearance of relatively low extinction rates of fishes and other marine organisms may simply stem from artefacts of sampling biases and undersampling.

15.3.3 Causes of extinction

Human activities have been held responsible for all known cases of recent extinction (Fig. 15.3). Remember that, so far, all known extinctions have occurred in freshwater fishes (Section 15.3.1). Habitat alteration is the most important problem, and includes construction of dams and channels, as well as siltation and water extraction (e.g. Minkley and Deacon, 1991; Miller et al. 1999). The World Conservation Union's most recent *Red List* (Hilton-Taylor 2000) also lists habitat destruction as the most important cause of threats to birds, mammals and plants.

Introduced species pose a major threat to native fishes (Courtney and Sauffer 1984; Froese and Torres 1999). They rank as the second most important threat to freshwater fishes, again mirroring the threats posed to birds, mammals and plants, where introduced species rank as either the third or fourth most important threat, depending on the taxon. Over a decade ago, Welcomme (1988) was able to compile data on 1354 introductions of 237 alien fish species into inland waters. For 72 species, it was possible to document the outcome of the introduction in terms of impacts on the environment, including native fish species. Twenty-five of these introduced species had harmful impacts, including reduction or elimination of native fish populations, introductions of parasites to native fishes, physical disturbance of habitats, or severe depletion of native fishes due to predation.

Introductions can also cause problems through direct and indirect interactions with native populations of the same species (Ward, Chapter 9, Volume 1). Escapes of farmed fishes are widespread; for example 20–30% of spawning Atlantic salmon (*Salmo salar*) in Norway are of farmed origin. Various studies have shown genetic differences between farmed and wild salmon in important

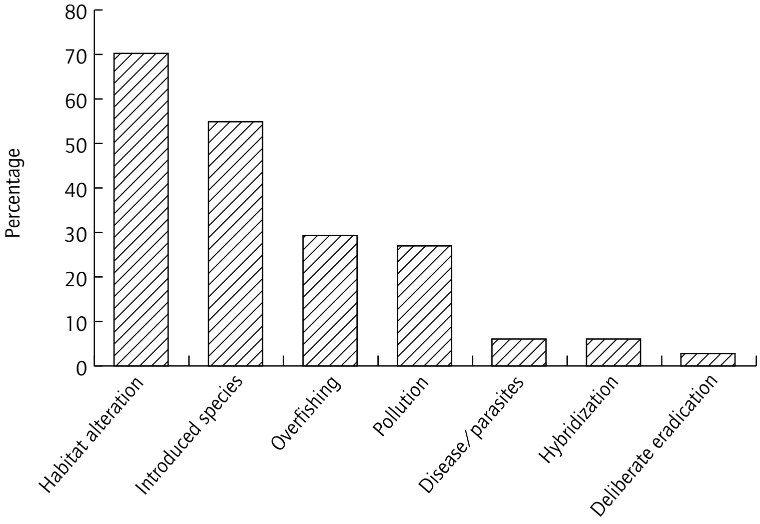

Fig. 15.3 Percentages of fish extinctions attributed to specific causes. The percentages pertain to a total of 70 species of fish, all occurring in freshwater habitats (see text) but excluding Lake Victoria cichlids. Many species were affected by more than one problem. (Source: from Harrison and Stiassny 1999.)

fitness traits (e.g. Einum and Fleming 1997; Fleming and Einum 1997). An ambitious field study in Norway showed that farm fish were competitively inferior to wild fish, with a lifetime reproductive success of 16% of that of wild fish (Fleming et al. 2000). Males were particularly inferior, courting females about one-third as often as did wild males, and obtaining only 24% of the breeding success of wild males. Thus, the main route of gene flow was from wild males mating with farm females. Overall, farm fish contributed to a reduction in productivity by wild fish by over 30%.

Pressures to farm genetically modified fishes have brought concerns about introduction of alien species and genes into uncharted waters. For example, transgenic salmonids have been created with the objective of enhancing growth rates of fish used in aquaculture (e.g. Devlin et al. 2001). The environmental impacts of escapes to the wild are unknown, but the lessons from studies of farmed fish described above suggest that concerns would be well founded (Hedrick, 2001). Thus, while no species is known to have become extinct as a result of competition with non-native populations of the same species, hybridization between wild and domesticated fishes has certainly led to the loss of genetically distinct native populations, which we expect to accelerate with the use of transgenic fishes. There may be impacts on wild populations through competitive interactions, as well as genetic introgression, because it is doubtful that sterility can be achieved with 100% success.

Overfishing ranks as the third most important cause of extinction of fishes (Fig. 15.3). The importance of exploitation in general rises if we consider secondary activities related to it, such as introductions of alien species. The most notorious case has been the introduction of the Nile perch (*Lates niloticus*) to a fishery in Lake Victoria (Witte et al. 1992). This predatory species has had a devastating impact on rock-dwelling haplochromine cichlids, though estimates of the exact number of species lost are severely hampered by uncertainties about taxonomic relationships, incomplete sampling, and the role of additional threats such as ecosystem alterations due to eutrophication and introduced macrophytes (Harrison and Stiassny 1999).

The problems faced by Lake Victoria cichlids exemplify the typical situation whereby fish populations are rarely threatened by a single process. Instead, the direct impacts of fishing, as well as indirect impacts related to fishing, often combine with various forms of habitat degradation to threaten species (Beverton 1992). These problems are particularly acute in freshwater bodies and in coastal zones, as these waters are the recipients of virtually every form of human waste (Moyle and Leidy 1992). In North America, multiple factors were implicated in 82% of extinctions of 27 species and 13 subspecies during the past 100 years (Miller et al. 1999).

Although there is a paucity of known extinctions of marine fish species, we can gain some insights into differences between marine and freshwater environments in processes that may lead to extinction by making comparisons among taxa. A comparison of threatened species of freshwater fishes confirms the findings for extinction risk, with species most heavily threatened by habitat loss and introductions (Froese and Torres 1999). Indeed, there is a correlation between the number of introductions and the number of IUCN threatened species at a national level. In contrast, marine introductions have not been linked to any extinctions of native fauna. An analysis of the relative importance of different causal factors of extinctions in the Wadden Sea over the past 2000 years suggested that overexploitation was responsible for the loss of six species of fishes, with habitat loss responsible for the loss of four additional species (Wolff 2000). These two factors together are thought to have contributed to the loss of two more fish species, and pollution together with habitat loss has caused the loss of one more species.

15.4 EXPLOITATION AS A CAUSE OF DECLINES AND EXTINCTION

Comparatively little is known of the disappearances of some fishes. For example, declines of the endemic New Zealand grayling (*Prototroctes oxyrhynchus*) were first noted in the year in which the species was described, 1870. This species is presumed to have become extinct by 1930 from a combination of habitat degradation due to deforestation plus the impacts of introduced salmonids. Exploitation may not have been a major culprit here, though neither of the two proposed explanations is conclusive (McDowall 1996).

15.4.1 Targeted species

The common sturgeon (*Acipenser sturio*) is now captured only rarely in Europe. Historically this species was highly regarded as a food fish, contributing 70% of the fish consumed around the southern Baltic Sea during the 7th–8th century. By the 11th century this species was extinct in the Netherlands and by the 12th century sturgeon were so rare that all captures in the United Kingdom and France were reserved for kings. So by the 14th century sturgeon had been reduced from a common to a quantitatively insignificant portion of the fish catch (Hoffmann 1996). International trade in this species has been restricted under the Convention on International Trade in Endangered Species (CITES) since 1983 and the species is listed under the IUCN *Red List* as critically endangered and it is protected under Appendix III of the Berne Convention. All other species of sturgeons and paddlefishes (Acipenseriformes) are threatened by multiple factors including overexploitation for caviar, habitat loss through dams, channelization, degradation of spawning habitat and pollution. To date one species and one population of Acipenseriformes are listed as extinct, 6 species are critically endangered, 10 species are endangered and 7 are listed as vulnerable (Hilton-Taylor 2000). Two species, *Acipenser sturio* and *A. brevirostrum*, are listed in Appendix I of CITES. At the time of writing, Russia, Kazakhstan and Azerbaijan have declared a complete moratorium on the capture of sturgeon species from the Caspian Sea, and Iran exercises strict controls.

Direct exploitation has caused the collapse of many targeted fish stocks. There are some cases where fishing alone has caused the collapse, such as the Georges Bank haddock and various cod stocks on both sides of the Atlantic (Fig. 15.1). The decline of the sablefish (*Anoplopoma fimbrae*) off the west coast of the United States provides another example, with stocks reduced by half over a period of 27 years (Fig. 15.1f).

Declines have often been assisted by unfavourable environmental conditions, as illustrated by the short-lived early maturing herring-like fishes – clupeoids. For example, Peruvian anchoveta stocks crashed dramatically in 1972 as a result of a strong El Niño event that moved warmer waters nearshore and led to the shutdown of upwelling, consequently reducing availability of their planktonic food (Fig. 15.1c) (Glantz 1979). Intense fishing continued on the now more vulnerable schools that had been pushed shorewards. The anchoveta has taken 25 years to recover, and this process was hindered by smaller El Niño events after the initial collapse. There are numerous other examples of combinations of exploitation and environmental problems causing collapses of stocks, such as the Monterey Bay sardine fishery (Chapter 1, this volume) and the southern North Sea herring fishery.

A marine fish that is listed under the United States Endangered Species Act is the the totoaba (*Totoaba macdonaldi*). The plight of this species highlights several impacts of exploitation and the ways in which they interact with other environmental problems. The totoaba is a huge species of croaker (Sciaenidae) which is restricted entirely to the northern half of the Gulf of California. In the early 20th century, when directed fishing on the species first began, each year the fish migrated in huge shoals, following the coast north to their spawning grounds at the mouth of the Colorado River. The fish were enormous, reaching lengths of more than 2 m and weights upwards of 100 kg (Cisneros-Mata et al. 1995, 1997). Initially, they were caught simply for their swim bladders, which were sent to the Far East for thickening soups. The bodies were piled on the shore to rot or were used as fertilizer. It was only in the 1930s that a market developed in California for the meat and the fishery prospered, peaking at 2300 tonnes per year in 1942 (Cisneros-Mata et al. 1995).

Totoaba were just too easy to catch. Sometimes the shoals ran so thick and close to the coast that the fish could be pitchforked out of the water. But gill-net fisheries began the real decline and the fishery soon crashed, falling to just 59 tonnes in 1975. Fishing for totoaba has been banned in Mexico since 1975, but the species has continued to decline due to bycatch in gill-nets set for other species, and increasing bycatch of juveniles by shrimp trawlers near the Colorado River estuary (Roberts and Hawkins 1999). Added to the problems of bycatch, the estuarine nursery habitat has been transformed over this period from brackish to predominantly saline, a consequence of abstraction of water upstream for irrigation. The case of the totoaba demonstrates how marine species can be reduced from prolific abundance to the edge of extinction just as surely as terrestrial animals.

It is relatively easy to track declines of important target fishery species such as the totoaba. It is much more difficult to document declines in non-target species, or species of minor commercial importance. For example, the smalltooth sawfish has never been of much commercial interest. Like the totoaba, this estuarine species has been badly hit by bycatch in fish nets and habitat degradation. It has been extirpated sequentially from estuaries on the Atlantic and Gulf of Mexico coasts, and is now largely restricted to a few lagoons off the Florida coast (Anon. 2001).

Another example of severe population declines involves rockfishes (Scorpaenidae) off the west coasts of Canada and the United States. This complex of 72 species supports important commercial and recreational fisheries (Yoklavich 1998; Glavin 2001). However, only a few are common enough for the US National Marine Fisheries Service or the Canadian Department of Fisheries and Oceans to be able to collect reliable data on their rates of capture. Those data show such steep declines in abundance for several species that extinction is possible. One of them, the bocaccio (*Sebastes paucispinis*), has been added to the World Conservation Union's *Red List of Threatened Animals*, but it is far from being the least common rockfish, or the most threatened. We simply lack good data on the status of the many species that are rarer than bocaccio.

Artisanal fisheries are often thought to be less damaging than industrial ones, but there is extensive evidence that they also cause species extirpations, which may be the first steps on the road to extinction (Roberts 1997). What is important is not the fishing methods employed, but the intensity of fishing. Tropical reef fisheries are often pursued at a subsistence level and may be the last resort of poor people in developing countries (Polunin and Roberts 1996). The rapid expansion of human populations in coastal areas has driven enormous increases in exploitation rates. In the Caribbean, for example, several of the larger species of groupers have been extirpated from intensively fished islands such as St Lucia and Dominica (Hawkins and Roberts, unpublished data; see also Section 15.5.2, below). Such extirpations have also been documented in the Indo-Pacific, especially in southeast Asia where the growing live-food fish trade targets larger species like groupers (Bryant et al. 1998). Extirpations have even been recorded in subsistence fisheries, where fish and other organisms are captured solely for local consumption. Extirpations of the giant clam (*Tridacna gigas*) and the bumphead parrotfish (*Bolbometopon muricatum*) have been documented from subsistence fisheries of the isolated Lau Island group, Fiji (Lewis et al. 1988; Dulvy and Polunin unpublished data). Human populations on these islands have not expanded significantly and they still have poor trade links (Zann 1992).

So widespread is overexploitation on coral reefs that even species with large geographic ranges may be at risk of extinction. Morris et al. (2000) recently examined the status of 85 species of epinephelinae groupers (Serranidae) that inhabit coral reefs. They found evidence for serious declines in 37 species, two of which they proposed for 'endangered' status in the World Conservation Union's *Red List* and a further 35 as 'threatened'.

Hawkins et al. (2000) drew attention to the fact that there are far more species of small island endemics than had been believed previously. They found that nearly 10% of a sample of 1677 coral reef fish species had geographic ranges $<50\,000$ km^2

(equivalent to an area of reef habitat of perhaps as little as a few hundred square kilometres). Many restricted-range species are small, like damselfish and wrasses, but direct exploitation for the ornamental fish trade may put some of them at risk. For example, the Banggai cardinalfish (*Apogon kauderni*) has an extremely limited distribution in central Indonesia, where it has been heavily collected for the aquarium trade (Allen 2000). As it can be bred in aquaria, it is unlikely to go extinct, but it could disappear from the wild.

15.4.2 Non-target species

Many other species of vertebrates, fishes and invertebrates are captured alongside the target species in the relatively non-selective fishing gears commonly used, predominantly trawl nets on temperate shelves and encirclement nets, traps and hook-and-line gears in reef fisheries. In the north Australian prawn trawl fishery there are 411 species of fish bycatch alone (Stobutzki et al. 2001). Many species are simply thrown back, while others are retained as they have some commercial value, such as skates. The North American barndoor skate (*Dipturus laevis*) (Casey and Myers 1998) and the European common skate (*D. batis*) (Rijnsdorp et al. 1996; Walker and Hislop 1998) have similar problems due to bycatch in trawl fisheries directed at groundfish stocks. Brander (1981) conceded that we may have to accept the possible extinction of such low-value bycatch species as a consequence of capturing more valuable species. It was suggested that the barndoor skate may be close to extinction, although recent surveys suggest a comeback, restricted to large, no-trawl areas on Georges Bank (S. Murawksi, personal communication). The common skate is restricted to a few de facto refuges where the bottom is too rough to fish. Dulvy et al. (2000) argued that the problem of skate extirpations is more general than for these species alone, but the problems of detecting declines and extirpations of individual species have usually been masked by the lumping of different species into general categories in fishery statistics – a common practice for low-value fishes. We are only just beginning to look into how many other species are threatened by industrial-scale fisheries.

15.4.3 Ecosystem impacts

Exploited species are connected to many others by reticulate webs of behavioural and trophic interactions, the simplest of which are direct interactions such as predation, competition and mutualisms (Chapters 11–16, Volume 1). Furthermore, there are many less direct interactions through which exploitation, pollution and dam construction may have profound and less predictable consequences (Menge 1995; Pinnegar et al. 2000). In freshwater systems eutrophication can lead to phase shifts from macrophyte- to phytoplankton-dominated production systems (Strong 1992; Pace et al. 1999; Scheffer et al. 2001). Such phase shifts can stem from trophic cascades, where the removal of a top predator, which controls the abundance of a herbivore, affects the abundance of key basal species, such as algae (Pinnegar et al. 2000; Kaiser and Jennings, Chapter 16, this volume). In hard substrate marine ecosystems trophic cascades have been found to control coral–algal abundance in tropical systems and kelp–coralline algal abundance in temperate systems. One of the key problems is that there is currently no way of predicting which species have critical ecosystem roles.

Fishing down food webs, the removal of top predatory fishes, and subsequent targeting of species further down the food chain, is globally widespread; although the details can be disputed, the pattern is consistent (Caddy et al. 1998; Pauly et al. 1998a,b). Unfortunately, the ecosystem implications of removing top predators (such as sharks) is at best unclear and at worst may be idiosyncratic or unpredictable (Stevens et al. 2000). One suggested consequence of fishing down food webs is that it could lead to ecosystems dominated by microbial loops (Jackson 2001). There have been various pathogen outbreaks resulting in the die-offs of Caribbean seagrass beds, corals and remaining herbivores, which may be connected with overexploitation of megafauna, such as manatees, turtles, large predatory fishes and herbivores (Jackson 1997; Wing 2001).

Recent attention has focused on the disturbance effects of trawl gears on the benthos. Heavy, mobile trawl gears resuspend sediments and kill or injure benthic invertebrates, which are then eaten by scavengers (Hall 1994; Kaiser and Spencer 1996; Jennings and Kaiser 1998). This has resulted in declines of benthic invertebrates (Collie et al. 2000). Recently, an analysis of benthic invertebrate community production : biomass ratios along a fishing gradient has demonstrated that trawling has negative impacts on secondary benthic production (Jennings et al. 2001a).

Habitat degradation is responsible for estuarine species topping the list of threatened species in the sea, largely through human development and pollution (Roberts and Hawkins 1999). Estuarine and nearshore habitats like salt-marshes, mangroves and seagrass beds provide critical spawning and nursery habitats for a wide range of species, including many that we exploit. Such habitats have been cleared extensively for aquaculture, agriculture, development and timber. The US has lost more than 50% of its salt-marshes during the last century (Agardy 1997), while many countries in southeast Asia have cleared as much as 80% of their mangroves in recent decades (Spalding 1998). By interrupting critical phases of the life cycles of species, habitat destruction has caused many species to decline. Estuaries are also foci for introductions of invasive species that may threaten native fauna (Cohen and Carlton 1998). For example, the spotted handfish (*Brachionichthys hirsutus*) is restricted entirely to the Derwent River estuary in Tasmania and may be threatened by predation on its benthic egg clusters by starfish (Roberts and Hawkins 1999).

Other marine habitats are also being damaged and destroyed at accelerating rates. For example, the widespread use of highly destructive blast fishing in southeast Asia is converting diverse and complex habitats to rubble (Cesar et al. 1997). Local impacts and habitat loss such as the construction of a military airbase in Castle Harbour, Bermuda, has led to the local extirpation of 10–14 species of reef fishes (Smith-Vaniz et al. 1999). Furthermore, habitat destruction is sufficiently widespread that it could cause global extinctions, especially for species with small ranges. Many of the restricted-range coral reef fish species documented by Hawkins et al. (2000) had ranges overlapping regions where reef habitats are under growing pressure. For example, the damselfish (*Chromis pelloura*) is restricted entirely to the far northern Gulf of Aqaba in the Red Sea, where it is hemmed in by intensive coastal development. The splendid toadfish (*Sanopus splendidus*) occurs only on reefs around the island of Cozumel in the Mexican Caribbean, an area undergoing rapid tourism development.

Recently, it has become clear that coral reef environments are highly sensitive to seawater warming associated with global climate change (Reaser et al. 2000). The year 1998 saw the most widespread coral bleaching and subsequent mortality so far documented. Coral mortality reached 70–90% throughout large regions of the Indian Ocean (Wilkinson 2000). Such large-scale habitat degradation, especially if combined with other human pressures such as overfishing, could trigger extinctions. Indeed theoretical estimates of the number of extinctions likely to have been caused by coral bleaching have been calculated using the species–area curve method. This approach indicates that about 1000 species may already have been lost if we accept the most conservative estimate of a loss of 5% of the world's reefs (Carlton et al. 1999). The key caveat is that bleaching causes hard and soft coral loss alone, rather than complete loss of all reef microhabitats. There are bound to be species thriving on reefs with little or no remaining coral as a consequence of bleaching.

15.5 WHAT RENDERS SPECIES SUSCEPTIBLE TO OVERFISHING?

From the foregoing discussion and various reviews (e.g. Beverton 1992; Roberts and Hawkins 1999; Reynolds et al. 2001b), we have picked out five key features of the biology of fishes and the motivations of fishers that render fish populations susceptible to overfishing.

15.5.1 Catchability remains high as population size decreases

Species that form shoals can still be targeted profitably by fishers even as the total population sizes decline (Pitcher 1995; Mackinson et al. 1997). Thus, species such as herring and Peruvian anchoveta can still be caught effectively by purse seines as populations decline. This continuing efficiency works against the old concept that as fish became rare, they would become unprofitable and therefore subject to lower mortality (see also next section).

Species that migrate through physical bottlenecks, such as diadromous salmonids, shads and sturgeons, are susceptible to high mortality due to focused fishing effort and pollution outputs associated with the dense human populations of river mouths (McDowall 1992). The impact of dams on freshwater fish populations, particularly the Atlantic salmon (*Salmo salar*), has been known since before 1214, when a Scottish statute required that all dams be fitted with an opening (Hoffmann 1996; unpublished data). Damming and the introduction of dikes also contributed to the decline of the common sturgeon. This was confirmed by the revival of catches after floods destroyed barriers in the southern Baltic in the 1400s.The catches remained high until new reclamation works in the 1800s (Hoffmann 1996; unpublished data). Conservation of salmonids remains a serious concern, as their discrete freshwater spawning populations remain subject to a variety of threats, including forestry and damming (Jonsson et al., 1999). To date, 55 evolutionarily significant units (ESUs) are recognized for the seven anadromous species of Pacific salmon, of which 23 ESUs are listed as endangered under the US Endangered Species Act (R.S. Waples, personal communication).

Species with limited physiogeographic ranges, living in small catchments, with specific breeding and feeding habitats appear to be particularly vulnerable to extinction in freshwater habitats (Angermeier 1995; Parent and Schriml 1995). In the sea critical habitats such as locations where groupers aggregate to spawn are vulnerable. The loss of subpopulations may result in the loss of behavioural resilience in the population as a whole. There is growing evidence of assortative mating and genetic substructuring on even spatially diffuse breeding grounds of more wide-ranging species such as cod (Hutchings et al. 2000; Nordeide and Folstad 2000; Ruzzante et al. 2000). Such aggregations are easily targeted.

The classic example of vulnerability due to fishers targeting spawning aggregations concerns the Nassau grouper (*Epinephelus striatus*) (Sadovy and Eklund 1999). In some areas of the Caribbean approximately 90% of commercial and recreational landings of this species came from spawning sites. Aggregations no longer form at some previously known traditional sites in Belize, the Dominican Republic, Honduras, Mexico and the Bahamas, while none of the previously known aggregations remain in Bermuda, Puerto Rico, or the US Virgin Islands. In Cuba, 21 aggregations were known in the 1800s. Today, however, only one of these sites is known to remain in use. The status of many other spawning aggregations is unknown.

15.5.2 Fish are highly valuable

Some fish derive their value not only as a source of protein, but also from cultural or social values leading to premium prices. Buyers capable of paying for rare species may advertise their wealth and social status. The reservation of caviar and sturgeon for English and French nobility in the 14th century is testament to the deep-rooted existence of this behaviour, which continues today in fine restaurants. Raw tuna or *sashimi* is highly coveted by rich restaurant-goers in Japan. The most prized species is the southern bluefin tuna. It set a new price record early in 2001, when US$178 000 was paid for one individual (Watts 2001). Western Atlantic bluefin tuna (*Thunnus thynnus*) has sold for up to US$83 500 for a single individual. It provided 2400 servings of sushi, worth US$180 000. Another expensive fish is the giant yellow croaker (*Bahaba taipingensis*), which has been exploited for its swimbladder in the South and East China seas from Shanghai to Hong Kong. In recent years the swimbladder, or maw, has been called ‘soft gold’ due to market prices of US$20 000–64 000 per kg

(Sadovy and Leung 2001). It is highly valued for its medicinal properties, and as a health tonic, and is typically boiled and drunk as a soup. Despite the near extinction of this species, 100–200 boats still target its historical spawning sites in the hope of netting a windfall (Sadovy and Leung 2001).

Unfortunately for conservation efforts the high prestige and price of rare species often widen the geographical net to meet demand, thereby threatening even those species that have large ranges. The humphead, maori or Napoleon wrasse (*Cheilinus undulatus*) is a highly valued commodity in the live reef fish trade centred in Hong Kong and reaching Taiwan, Singapore and China. It is worth a retail price of up to US$130 per kg, with parts of this fish reaching much higher prices (Lau and Parry-Jones 1999). As southeast Asian sources have been overfished, demand has led to fishing explorations and export operations as far away as the Seychelles, Fiji and Kiribati (Bentley and Aumeeruddy 1999). This increasing price associated with biological and market rarity has meant that it is economically viable to fly fish to markets from such distant sources. This species is now listed as threatened under IUCN criteria (Donaldson and Sadovy, 2001). Given the role that increasing 'rarity value' has had in depleting terrestrial species such as African elephants, rhinoceroses, tigers and musk deer, it is difficult to see how current aquatic conservation methods can protect such species. International trade can be prevented through CITES Appendix I listing, if enforcement is adequate. However, this would not prevent trade within countries, and this measure would only be introduced after species had already declined seriously.

15.5.3 Fish are susceptible to capture as non-target species

If fish are caught as a byproduct of other activities, they again defy the hope that unprofitability at low population sizes might protect their populations. We have already described several examples of this problem for species such as skates and rays (Section 15.4.2). Stevens et al. (2000) noted that roughly 50% of elasmobranchs are taken as bycatch without any regulations, and these species rarely appear in catch statistics. Non-target species thus inhabit the poorly known underworld of fisheries conservation. They are either discarded at sea or, if landed, they often fetch a lower price than the species being targeted. Therefore they do not attract much attention from assessment biologists or managers.

15.5.4 Life histories result in low productivity

Species with long generation times, low natural mortality rates and slow body growth are expected to be less able to withstand elevated mortality (reviewed by Musick 1999b; Reynolds et al. 2001b). This has been shown on theoretical grounds (e.g. Adams 1980; Kirkwood et al. 1994; Pope et al. 2000), and it has been borne out by comparisons among diverse taxa (e.g. Jennings et al. 1998, 1999a, 1999b; Dulvy et al. 2000). Thus, sharks and rays feature prominently in the *Red List of Threatened Animals* (Hilton-Taylor 2000), on the basis of severe population declines under exploitation. Other examples of species with life histories that are incompatible with elevated mortality include sturgeons, rockfishes (*Sebastes*) (Section 15.4.1) and orange roughy (*Hoplostethus atlanticus*) in New Zealand, which reaches maturity in its twenties to thirties and may live to a maximum age of 150 years (Smith et al. 1995; Horn et al. 1998). The coelacanth (*Latimeria chalumnae*) also fits this category. While most details of its life history remain unknown, this species has the lowest metabolic rate known for any fish (Fricke and Hissmann 2000). This suggests a very slow life history, which would render the species susceptible to the mortality that individuals suffer as a result of bycatches in deepwater artisanal fisheries in the Comoros and in Indonesia (reviewed by Fricke 2001).

15.5.5 Per capita recruitment decreases as population size decreases

Depensation, called the 'Allee effect' in terrestrial systems, occurs when there is a positive relationship between individual productivity and population size (Myers, Chapter 6, Volume 1). In fisheries, depensation can occur due to a reduced ability to aggregate and find mates, reduced fertilization success, or increased predation rates (reviewed by Petersen and Levitan 2001). The concern here is that as fish stocks are pushed downwards, they may fall over a cliff of recruitment from which they cannot climb back. A Bayesian analysis of various fish stocks by Liermann and Hilborn (1997) showed that scatter in relationships between stock sizes and recruitment cause considerable difficulties in detecting depensation, if it exists. For a number of species of cod relatives (Gadiformes), flatfishes (Pleuronectiformes) and herring relatives (Clupeiformes), the authors found that the tails of probability distributions for the likelihood of depensation extended well into the depensation range. However, attempts to quantify the prevalence of depensation based on current stock–recruitment (S–R) models may be too conservative. This is because current models assume that recruitment is zero *only* when the stock is extinct. However, Allee effects, by definition, involve low recruitment despite the continued presence of spawners. Therefore, future assessments of the existence of depensation in fishes may need a new family of S–R models, which do not necessarily have their origin at zero (Frank and Brickman 2000).

15.6 CONSERVATION MEETS SUSTAINABLE USE

Conservationists traditionally worry about preventing extinction, whereas resource managers in fisheries and forestry traditionally ignore extinction risk, and worry instead about obtaining high sustained yields (Mace and Hudson 1999). Of course, if the yield objective is achieved, we won't have to worry about extinction! However, most of the world's exploited fish species are not being assessed or managed. Therefore, extinction cannot be ruled out for many species that have the vulnerable characteristics listed in the previous section, especially if exploitation exacerbates other problems such as habitat degradation, pollution and introductions of alien species. These problems are particularly acute in freshwater habitats. Furthermore, many conservationists point to the repeated failure of fisheries management to maintain adequate populations, even when fisheries are under the 'control' of single nations or unions of member states. The northern cod stock(s) off Newfoundland, which has still not shown convincing signs of recovery since a ban on fishing was imposed in 1992, is the most recent notorious example. Some resource managers counter that there are still millions of Atlantic cod in the sea, and that you couldn't kill off this species if you tried. At this point, conservationists tend to bring up the fate of the passenger pigeon (*Ectopistes migratorius*), which once numbered between 3 and 5 billion in the mid-1800s, but became extinct in 1914. The debate continues from there.

How did we come to this? We blame cod and haddock. Specifically, it was their listing as 'vulnerable' (to extinction) by the *Red List of Threatened Species* (IUCN 1996) that triggered a confrontation between some conservationists and some resource biologists. The species were listed on the basis of their population declines within the previous three generations. Rate of decline is one of five criteria under which a species can be listed as threatened. The others are small distribution combined with declines or fluctuations, small populations combined with declines, very small or restricted ranges, and quantitative population models that yield pessimistic outcomes. A caveat was published with the *Red List*, which noted that its designations may not be appropriate for fish species that are subject to management by fisheries. However, this did not save the *Red List*'s rate-of-decline criterion from criticism by many fisheries biologists (e.g. Musick 1999a; Butterworth 2000).

One criticism of the *Red List*'s treatment of exploited fishes is that traditional management practice suggests that populations should decline to about 50% of virgin population sizes in order to maximize productivity (e.g., Schnute and Richards, Chapter 6, this volume). So in theory, a perfectly well-managed abundant species could be brought quickly to 50% of its population size and provide a maximum yield, only to be listed by a globally recognized conservation body as threatened with extinction. In practice, of course, one could suggest that this is all a moot point, because there are few examples of any virgin population of fishes being brought down to 50% (and not beyond) in the controlled way envisaged by this hypothetical scenario. But even if this situation is only hypothetical, it does suggest an anomaly, which the IUCN has been trying to fix (see below).

Another problem that has been raised is that it is difficult to distinguish between 'real' declines and population fluctuations in many marine fishes (Butterworth 2000). A recent study by Hutchings (2001b) suggested that fish populations do not fluctuate more than populations of terrestrial animals. So, while the problem certainly deserves to be taken seriously, it is not unique to fishes.

Finally, the high fecundity of many exploited fish species has been taken to imply that such stocks have high potential to bounce back from low numbers (Musick 1999a). The theory and evidence in support of this assumption have been questioned (Sadovy 2001). Indeed, Hutchings (2000) found little evidence of recovery for most of the 90 stocks that he has examined. Although his analyses did not take fishing mortality following population declines into account explicitly, subsequent analyses have shown that recoveries remain slower than generally expected even when the data are restricted to stocks in which fishing mortality during the recovery phase is extremely low (Hutchings 2001b).

After the uproar over the listing of commercially exploited fishes, there was a careful rethinking of the *Red List*'s main criteria for listing species. CITES has also been grappling with these issues, with advice from the FAO (Butterworth 2000), as have the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the Australian Society for Fish Biology and the American Fisheries Society (Musick 1999a). The American Fisheries Society has adopted a two-step listing process, under which species with life history characteristics that imply high productivity and resilience would be allowed to decline more steeply than the IUCN suggests before triggering a listing. Elsewhere, we have argued that the high rates of decline required for a listing under this proposal are not sufficiently precautionary (Reynolds et al. 2001b). For example, a species deemed to have high productivity would be allowed to decline by 99% over 10 years or three generations, whichever is longest, before it would be listed as 'vulnerable' (Musick 1999a).

In the meantime, after a series of scientific workshops, the World Conservation Union brought out a refined set of criteria in 2001. Among various refinements there were two key changes. First, for any taxon to be listed as 'vulnerable' (the lowest threat status), the species must have declined by 30% (formerly 20%) over the previous 10 years or three generations (whichever is longest). Second, and particularly relevant to exploited species, higher declines are allowed before triggering a listing if the causes of the decline are understood, clearly reversible, and have ceased (IUCN 2001). Now, the species in our hypothetically controlled fishery can decline by at least 50% before being listed as 'vulnerable' (formerly 20%), 70% for 'endangered' status (formerly 50%), and 90% for 'critically endangered' status (formerly 80%).

The *Red List* has taken on the ambitious task of combining versatility with practicality so that the same criteria can be applied to a wide variety of plant and animal taxa. Thus, the aim is to draw attention to species when they show at least one of the symptoms of vulnerability towards extinction, including severe population declines (Mace and Hudson 1999). Defenders of this approach argue that the *Red List* is intended as precautionary flag, not a prescription for action, though it is hoped that it might lead to careful assessment, and management if required.

Perhaps the best way to bridge this divide between conservationists and resource managers is to incorporate extinction risk explicitly into population models, so that traditional fisheries reference points such as maximum sustainable yield (MSY) can be compared with the probability of extinction. Several researchers have begun to build this bridge. Matsuda et al. (1998) used three methods to evaluate the probability that the southern bluefin tuna would become extinct (less than 500 individuals) within the next 100 years: a simple simulation model, a model that used a diffusion approximation of births and deaths, and a fluctuating age-structured model. None of these found support for a high probability of extinction under current circumstances, contrary to the IUCN's 1996 and 2000 listing of this species as critically endangered. This was largely due to the large current population sizes of these fish, despite their high rates of decline. Matsuda et al. (1998) concluded that the decline criterion should be linked to population sizes to give a better reflection of extinction probability.

A direct comparison of traditional fisheries reference points with extinction risk has been made by Punt (2000). He used a deterministic population model that compared the level of fishing mortality that achieves maximum sustainable yield (F_{MSY}) with that which causes the population to become extinct, defined as 1/1000th of initial population size (F_{crash}). At this point, depensation might occur, whereby per capita recruitment might decline, thus potentially spiralling the population downwards to extinction (Section 15.5.5; see also Myers, Chapter 6, Volume 1). The analyses confirmed the expectation that F_{crash} was highest for highly productive populations, and that depensation greatly reduced the ratio of $F_{crash} : F_{MSY}$. In tests with case studies, Punt found that in two shark species F_{crash} was only about twice F_{MSY}. This is worrying because F_{MSY} cannot be estimated with much precision in many fisheries, so one cannot be certain how far above or below it the actual fishing mortality is.

A third approach towards bridging conservation and sustainable use has examined the effects of various exploitation strategies on yields and long-term risks of population collapse and extinction in populations that undergo strong natural fluctuations (Lande et al. 1995, 1997; reviewed by Lande et al. 2001). These studies suggest that if the goal is to maximize the cumulative yield before extinction or population collapse, the best approach is to use threshold exploitation, whereby populations are fished only when they overshoot their carrying capacities. A more prudent strategy, appropriate when there is considerable uncertainty about population sizes, is to use proportional threshold exploitation, whereby only a fraction of the estimated surplus above the threshold is taken, rather than aiming for maximum exploitation of the surplus. These models are noteworthy not only for their contributions to the theory of exploitation of fluctuating populations, but also because they explicitly incorporate extinction risk, unlike traditional models such as yield-per-recruit, which are in widespread use (see Shepherd and Pope, Chapter 8, this volume, and Sparre and Hart, Chapter 13, this volume).

15.7 WHAT IS NEEDED TO SAFEGUARD FISH BIODIVERSITY?

It should be clear from this review that freshwater and marine biodiversity is seriously threatened. The bright side is that although many populations have undergone steep declines no species of marine fishes is known for certain to have become extinct. As we have argued in Section 15.3, there is good reason for thinking that we are less able to detect extinctions in marine environments. But at least we can say that no fisheries manager goes to bed at night with a conscience laden with the guilt of having seen a species of targeted marine fish become extinct during their watch.

The situation for freshwater fishes is far more dire in many parts of the world. Direct and indirect effects of exploitation, habitat destruction and degradation loom large among the drivers of decline. As demand for freshwater increases, and technologies for catching fish have improved, so the areas free from exploitation and habitat loss have diminished. We treat inland water bodies as sources of irrigation and hydroelectric power, at the expense of aquatic biodiversity.

15.7.1 Marine reserves

Marine reserves are often championed as one mechanism for protecting marine biodiversity (Watling and Norse 1998; NRC 2000; Roberts and Hawkins 2000). The evidence for and against this viewpoint is reviewed critically by Polunin

(Chapter 14, this volume). Syntheses of research from around the world have shown that the creation of reserves closed to fishing does yield rapid increases in abundance, body size and diversity of marine communities (Mosquera et al. 2000; Côté et al. 2001; Halpern, in press). Reserves can therefore provide an important fishery management tool by putting back the refuges that fishing has eroded away during the last century. Furthermore, fully protected reserves can begin the process of habitat recovery from fishing disturbances such as trawling or blast fishing.

Because of their promising role in fishery management, reserves are viewed as a potential ecological–economic win–win tool (Pezzey et al. 2000; Rodwell and Roberts 2000), providing an economic rationale for doing what is also sensible from a conservation perspective. Current understanding of marine reserves suggests that they will deliver maximum benefits when they cover between 20% and 50% of every habitat and biogeographic region of the oceans (NRC 2000). Theoretical studies suggest that they will be most effective when established in dense networks consisting of areas of a few to a few tens of kilometres across, and which are separated by a few to a few tens of kilometres (Roberts et al., in press).

Of course marine reserves will not be sufficient to protect high seas and migratory fish stocks like swordfish, marlin and tuna, and their use in freshwater has barely been explored. Furthermore, their implementation needs to be augmented by overall reductions in fishing effort and other technical measures (Murawski et al. 2000; Wabnitz and Polunin 2001; Polunin, Chapter 14, this volume). Otherwise, reserves may simply cause a redistribution of fishing effort, without leading to reduced mortality.

15.7.2 The precautionary principle and reference points

The precautionary principle is now being implemented in fisheries management in many parts of the world (FAO 1995). The elements of this principle are simple, such as taking account of uncertainty, being cautious with new fisheries, not using lack of information as an excuse for inaction, and using reference points. Reference points include benchmark population sizes or mortality rates that are not to be exceeded ('limit reference points') or which are desirable ('target reference points') (see also Shepherd and Pope, Chapter 8, this volume). However, for precautionary reference points to be successful it is critical that once a benchmark is agreed upon the conservation goalpost is not shifted. Powles et al. (2000) outlined the continuum and overlap of both fisheries management and conservation benchmarks. As some species have declined management has shifted from one benchmark to the next, allowing populations to go from growth overfishing to recruitment overfishing, and up the scale to a critically endangered listing under IUCN criteria.

15.7.3 Targeted management at key points in the life history

Identifying key points in the life history of organisms could prove to be a fruitful approach for focusing often-limited management efforts. However, identification of critically important ages, stages, habitats or even sexes is still in its infancy. Guesses can be made based on experience; salmon are clearly more vulnerable in estuaries than in the open sea, and females usually limit populations more strongly than do males. However, we still have a lot to learn. For example, at present managers are unsure as to whether is it better to protect juvenile skates or mature females. While control of mortality in either life stage would be difficult, one can imagine that closed areas could be applied to nursery areas or locations that are primarily used by adults.

One way forward is the application of elasticity analyses, based on demographic matrix models (e.g. Kokko et al. 2001). These can be used to determine the relative importance of various stages of the life cycle for the population growth rate. One of the first uses of this method was to examine the conservation method of 'head starting', which is widely applied to a bycatch turtle species. This involves enhancing the hatching and survival rate of turtles, which was previously assumed to be the critical stage for population growth. However, demographic modelling and elasticity analyses demonstrated that this life stage contributed little to population growth rate compared to the subadult and adult stages (Heppell et al. 1996). Similarly, while fishery scientists often focus on understanding what determines survival in the first year of life, elasticity analyses hint that it is more critical to protect fishes between the first year and maturation (Heppell et al. 1996). For example, in the North Sea haddock survival in the first year of life contributes only approximately 30% to the overall population growth rate, whereas survival from the first year to maturity contributes approximately 60%. We should therefore focus conservation effort on allowing juveniles to reach maturity rather than focusing on first-year juveniles (Heppell et al. 1999). Though such approaches are data-intensive, the information should be generally applicable to species that have similar life histories to those studied so far.

There is a critical need for more precautionary and ecosystem-based approaches in fishery management (NRC 1999). What has become clear is that present approaches to fishery management are too risk-prone, failing to take adequate account of irreducible uncertainties in fishing mortality rates or future environmental conditions (Ludwig et al. 1993; Mangel 2000; Roberts 2000). In combination, reduced fishing effort, extensive use of reserves in both marine and freshwater habitats and management focused on critical life stages will do much to secure the future of fish species.

15.8 CONCLUSIONS

For too long, fisheries biologists and conservation biologists have been attending different conferences, publishing in different journals, and worrying about different things. Extinction risk has not usually been a concern in marine fisheries, but the collapses of fish stocks, extirpations and damage to ecosystems, combined with considerable uncertainty about risks of cryptic extinctions, are causing conservationists to ask resource biologists awkward questions. Furthermore, there is no question about the vulnerability of freshwater fishes to extinction, and the potential for exploitation to exacerbate the threats. There have been positive developments in the field of fisheries conservation, including studies of marine reserves, ecosystem-based analyses, adoption of precautionary reference points that embrace the uncertainty that pervades fisheries, and theoretical studies that bridge between management targets and risks of extinction. We look forward to further progress in all of these fields, which should lead to more prudent use of fishes as resources while protecting them and the environment.

ACKNOWLEDGEMENTS

We thank Yvonne Sadovy and Richard Hoffmann for providing unpublished manuscripts and comments. This chapter is dedicated to the memory of Don McAllister, a committed environmentalist and an inspiration to all those who knew him. NKD was supported by the UK's Natural Environment Research Council.

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16 Ecosystem Effects of Fishing

M.J. KAISER AND S. JENNINGS

16.1 INTRODUCTION

Humans are extremely effective predators. As a result we have seen at various times throughout history the sequential overexploitation of many target species (FAO 1994). Traditional fisheries management focused on these single species with a recent move towards multispecies approaches. It has proved difficult enough to manage stocks of single species successfully, and so it is not difficult to understand why relatively little effort has been devoted to trying to predict ecosystem responses to target-species removal. Nevertheless, the wider ecosystem effects of fishing activities are becoming more apparent, which emphasizes our need to understand the consequences of exploiting marine resources (Hall 1998; Jennings and Kaiser 1998; Auster and Langton 1999). Although we reviewed this topic in detail several years ago (Jennings and Kaiser 1998), there have been new and exciting developments in the interim period, some of which have confirmed our previously unsubstantiated theories.

16.2 EFFECTS OF HARVESTING TARGET SPECIES

A target species is just one component of an ecosystem; hence it may perform a variety of functions as it interacts with other species. Target species may be predators, grazers, prey, scavengers and competitors. Some species may form habitat structures (Lenihan 1999) or maintain habitat patchiness through their feeding activities (Van Blaricom 1982). The consequences of harvesting a particular species will depend on its role and dominance within an ecosystem and also the complexity of the species interactions in that system (Pauly and Christensen, Chapter 10, this volume). Hence intensive harvesting of one species might relieve predation on its prey species while harvesting prey species might increase predation pressure on alternative prey types. When they exist, such ecosystem responses to single-species removal are known as 'trophic cascades' (Pace et al. 1999). Later in this chapter we give some examples where trophic cascades have resulted from fishing activities. However, a recent study by Yodzis (1998) demonstrated that even when dealing with a well-quantified ecosytem such as the Benguela system, the predicted outcome of culling large top predators such as seals can be highly variable (see Section 16.5).

While intensive fishing has led to well-documented population reductions of many target species (e.g. Davis et al. 1996; Myers et al. 1996), it has also caused changes in the species composition structure within fish communities (e.g. Greenstreet and Hall 1996). Whereas in the past fish assemblages had a broad range of size classes, exploited assemblages tend to be dominated by a much higher proportion of small-sized individuals (Kirkwood et al. 1994; Pauly et al. 1998). Jennings et al. (1998) used a comparative approach based on phylogenetic comparisons to examine the differential effects of fishing on individual species that have contrasting life histories. They found that those fishes that decreased in abundance relative to their nearest phylogenetic relative matured later and at a greater size, grew more slowly towards a greater maximum size and had lower rates of potential population increase (Table 16.1). For example, common skate (*Raja batis*) have the steepest slope for the decline in catch rates through time, whereas the smaller starry rays (*Raja radiata*) actually show an increase in population numbers. While both halibut (*Hippoglossus hippoglossus*) and long rough dabs *Hippoglossoides platessoides* have decreased with time, the rate of decrease is three times greater for the halibut that attains a much greater maximum size.

Patterns observed in these North Sea studies are also typical of those in exploited reef fish communities. Russ and Alcala (1998a,b) looked at changes in a Philippine reef fish community during periods of exploitation and protection from fishing. Large predatory species with slow life histories, such as snappers (Lutjanidae), emperors (Lethrinidae), sea basses (Serranidae) and jacks (Carangidae) declined in abundance rapidly as fishing pressure increased and recovered slowly when fishing ceased. During periods when the community was most intensively exploited, they formed a smaller proportion of the total abundance of the community and the community was dominated by smaller species with faster life histories (see also Polunin, Chapter 14, this volume).

Thus the response of fish populations to exploitation follows a consistent pattern, with the progressive removal of the largest body-sized fauna from the system leading to dominance by smaller-bodied individuals. Consequently, the sustained harvesting of fish populations has led to a gradual decline in their body-size spectrum (Rice and Gislason 1996). This has important considerations for predator–prey interactions. For example, juvenile cod, *Gadus morhua*, are preyed upon by adult whiting, *Merlangius merlangus*, while the latter are consumed by adult cod. A decrease in the body-size spectrum of cod populations could mean that they are exposed to proportionately greater levels of predation. Conservation measures designed to reduce bycatches of whiting in the cod fishery could further exacerbate this problem by further reducing the body-size spectrum of cod through harvesting while conserving the population struc-

Table 16.1 Abundance trends and life-history parameters for selected species in the North Sea fish community.

Species	Common name	Trend	L_∞ (cm)	$K\,(y^{-1})$	T_m (y)	L_m (cm)
Raja batis	Common skate	–0.030	254	0.06	11.0	130
Raja naevus	Cuckoo ray	–0.027	92	0.11	9.0	59
Raja radiata	Starry ray	+0.013	66	0.23	4.0	46
Squalus acanthias	Spurdog	–0.051	90	0.15	6.5	67
Scyliorhinus canicula	Lesser-spotted dogfish	+0.002	88	0.20	5.0	58
Trisopterus minutus	Poor cod	–0.007	20	0.51	2.0	15
Trisopterus esmarkii	Norway pout	+0.012	23	0.52	2.3	19
Hippoglossus hippoglossus	Halibut	–0.015	204	0.10	5.8	83
Hippoglossoides platessoides	Long rough dab	–0.005	25	0.34	2.6	15

Notes: Trend: slope of linear relationship between standardized catch rate (numbers h^{-1}) in standard fisheries surveys and time (years); L_∞: asymptotic (maximum) length; K: growth rate; T_m: age at maturity; L_m: length at maturity. The sequence and grouping of species reflects their phylogenetic relationship. The species are shown in phylogenetically linked couplets or triplets and the first species is the one for which catch rate has declined the most. (Source: adapted from Jennings et al. 1999.)

ture of whiting through technical conservation measures.

In the next few sections we give some examples of where cascade effects have and have not been observed in marine systems in response to the selective removal of target species.

16.2.1 Exploitation of target species on tropical reefs

Most tropical reefs are fished intensively since they provide the main sources of protein and income for fishers who have few other means of generating a living. Many trophic groups are targeted, and the abundance of herbivorous, piscivorous or invertebrate feeding fishes is often reduced by an order of magnitude or more on fished reefs (Russ 1991).

Fishes and sea urchins are the most abundant herbivores on most tropical reefs. Sea urchin abundance is regulated by recruitment success, food supply and natural mortality due to predation by fish and disease. The main predators of sea urchins are invertebrate feeding fishes such as emperors (Lethrinidae) and triggerfishes (Balistidae) and, on reefs in the Caribbean and East Africa, fish predation strongly regulates urchin populations (McClanahan 1995a). As a result, on reefs where populations of emperors and triggerfishes have been reduced by fishing, there is good evidence that urchins have proliferated (McClanahan and Muthiga 1988; McClanahan 1992, 1995b).

When urchins dominate herbivore biomass, they will graze the majority of algal production on a reef. Because urchins have low consumption and respiration rates they can survive and reproduce when their food supply is greatly reduced by their own feeding activities. In contrast, herbivorous fishes have higher consumption and respiration rates and are unable to tolerate low levels of food availability. As a result, urchins outcompete herbivorous fishes and reach maximum biomass levels an order of magnitude higher (McClanahan 1992). Since the herbivorous fishes are poor competitors, they may be unable to achieve their former abundance when fishing is stopped (McClanahan 1995a).

Urchins erode the reef matrix as they graze and this prevents the settlement and growth of coral recruits. Occasionally recruitment failure or urchin disease may lead to a collapse of urchin populations. In the absence of such occurrences, intervention may be required to promote recovery of the reef ecosystem by the deliberate removal of urchins. McClanahan et al. (1996) found that when they removed urchins from unfished experimental plots on Kenyan reefs, there were significant increases in algal cover and fish abundance within one year. However, on fished reefs, herbivorous fishes were less abundant, and the algae rapidly overgrew corals as they proliferated in the absence of herbivores.

While many studies have shown that the abundance of piscivorous reef fishes is greatly reduced by fishing, there is little evidence for a corresponding increase in the abundance of the fish species that are their prey (Bohnsack 1982; Russ 1985; Jennings and Polunin 1997). Why is the response of prey fish communities so weak? The reasons for this are probably linked to reef fish community structure, in which phylogenetic groupings of fish contain many species, with a wide range of life history traits, behavioural differences and feeding strategies (Hiatt and Strasburg 1960; Parrish et al. 1985, 1986; Hixon 1991). Moreover, most fish species alter their feeding behaviour and hence diet as they grow and can act as both prey and predators of other species. Hence, while the collective impacts of predatory fish are large, the impacts of individual predator species on the dynamics of their prey are minor (Hixon 1991).

Notably, at smaller scales (m^2 compared with km^2) there is some evidence for the role of predation as a structuring force, particularly when habitat or refuge space is directly limited. Thus experimental reductions in piscivore abundance led to detectable decreases in the abundance and diversity of their prey (Caley 1993; Hixon and Beets 1993; Carr and Hixon 1995).

16.2.2 Removal of predatory fish in temperate marine fisheries

Even in the most intensively fished marine ecosystems such as the Benguela upwelling, Georges Bank, Bering Sea and North Sea, piscivorous fish are more important consumers of fish biomass than the combined removal by humans, marine mammals and birds (e.g. Bax 1991; Yodzis 1998). Long-term studies have demonstrated that the intensive removal of predators has allowed other species to proliferate. One such example showed that population explosions of sandeels (*Ammodytes* spp.) in the northern Atlantic coincided with the depletion of predators such as the herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) (Sherman et al. 1981). Although coincident changes in predator and prey populations might infer causality, it is just as likely that such changes could be driven by a range of environmental factors.

Elsewhere, we have concluded that there are relatively few circumstances in which changes in the abundance of piscivorous fishes in marine ecosystems has had cascading impacts on other parts of the system (Jennings and Kaiser 1998). Most fish species can act as both predators and prey in the course of their life history and adult predators are capable of switching diet and their feeding behaviour in response to prey availability (Mittlebach, Chapter 11, Volume 1). Hence high fish consumption rates do not necessarily imply that predation is a structuring force of fish populations within a particular system. Indeed, in temperate systems, the strongest evidence for the predator-based control of prey species comes from the impact of humans on their target species. The strength of this relationship is likely to result from the conservative fishing strategies employed by humans. In the majority of commercial fisheries, fishers are unwilling to be flexible in their aims and target a relatively small proportion of the total fish fauna. Most predatory fish, conversely, are very generalist feeders, often switching to invertebrate prey or cannibalism and eating many species of fishes at different stages in their life history (Fig. 16.1).

16.2.3 A comparison with freshwater systems

Unlike in many marine systems, the occurrence of cascading trophic effects is much more prevalent following the exploitation of target fishes in freshwater lakes and streams (Marten 1979; Carpenter et al. 1987; Persson, Chapter 15, Volume 1). For example, Flecker and Townsend (1994) and McIntosh and Townsend (1996) demonstrated that the presence of a brown trout (*Salmo trutta*) predator in a New Zealand stream led to increased predation of herbivorous mayfly larvae. The mayfly larvae responded by spending more time sheltering beneath rocks and less time feeding on their upper surfaces. This change in mayfly larval behaviour led to a proliferation of epilithic algae. Conservation or fisheries management action that affects the trout population would therefore have knock-on effects on other aspects of ecosystem function.

Carpenter et al. (1987) examined the possibility that species at higher trophic levels could regulate the abundance, productivity and community structure of phytoplankton and zooplankton. In order to do this, they manipulated the fish populations of three entire lakes. Productivity varied annually in the control lake, predominantly in response to climatic factors. The addition of piscivorous largemouth bass (*Micropterus salmoides*) and hence potentially the removal of planktivorous fish from one of the lakes, led to an increase in zooplankton biomass and a shift from a copepod and rotifer zooplankton assemblage to one dominated by cladocerans. As a result, algal biomass decreased and hence primary productivity also fell. In the lake where most largemouth bass were removed, thereby relieving the predation pressure on the planktivores, zooplankton biomass and the dominance of large cladocerans increased. At first this seems surprising, but it appeared that the planktivorous fish remained within refuges despite lower predator numbers, and thus allowed the larger zooplankton to increase. Carpenter et al. (1987) had thus provided convincing evidence that fish populations could be important regulators of primary productivity and that predator avoidance behaviour also has important consequences for other trophic levels in a system.

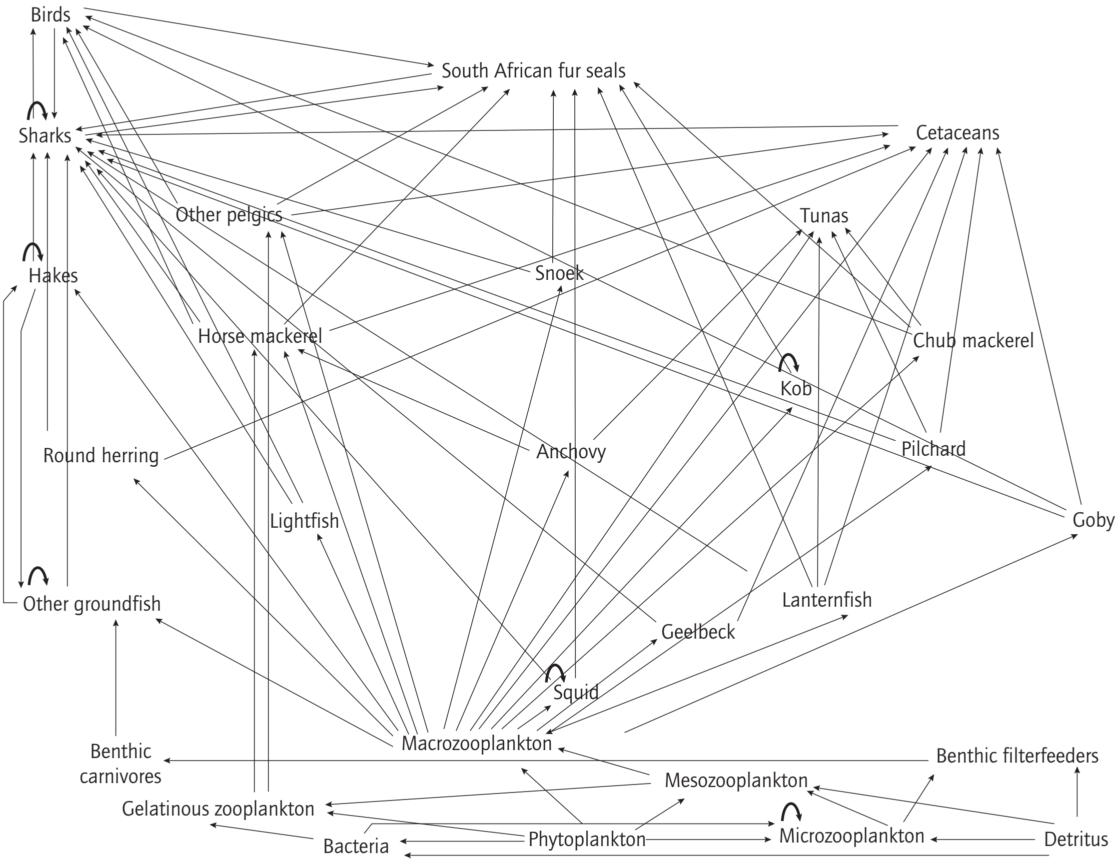

Fig. 16.1 Schematic diagram of the Benguela food web adapted from Yodzis (1998). Many of the linkages and some of the species have been removed for clarity. What is clear is that there are many linkages between the different trophic levels in the system and cannibalism (indicated by the circular arrows) occurs often.

16.2.4 Why systems respond differently to predator removal

The removal of fish predators in marine ecosystems often has limited consequences for prey species, whereas in many freshwater ecosystems there are much closer links between predator and prey dynamics (Persson, Chapter 15, Volume 1). We attribute this to general differences in the structure of many marine and freshwater ecosystems and suggest that the indirect effects of fish predator removal in marine systems are smaller and less predictable than in freshwaters (Jennings and Kaiser 1998). Within lake ecosystems most biomass is aggregated into a few size classes. These loosely correspond to phylogenetic groupings such as algae, crustaceans or fish with a limited range in their biomass spectrum (Sprules et al. 1983; Sprules and Goyke 1994; Sprules and Stockwell 1995). Conversely, in the marine environment the biomass spectrum is often extended and there is more variance in size within the main phylogenetic groupings. Moreover, phylogenetic groupings tend to contain more species, with a wider range of life history traits, behaviours and feeding strategies (Jennings and Kaiser 1998).

16.2.5 The collective effects of fishing

Designing experiments to study fishing effects has always been difficult because it is never clear whether areas subject to different fishing pressure can be treated as replicates that respond more or less independently to fishing. Spatial designs have often been used to investigate the effects of fishing in the tropics, with reefs or islands treated as replicates. This approach was adopted by Samoilys (1988) and Jennings and Polunin (1996) to examine the effects of fishing on the structure of fish communities, and by McClanahan to look at the fish, algal and urchin interactions described previously.

The assumption that different reefs could be treated as semi-independent replicates was thought to be reasonable because small (km^2) areas protected from fishing, such as marine reserves, would harbour a diverse and abundant fish community when adjacent reefs were heavily fished. In addition, fish communities on reefs that were separated by a few km would respond differently to local fishing pressure. It was also assumed that the migrations or movements of adult reef-associated fishes between replicate areas were limited, and this was later confirmed with tagging studies (e.g. Holland et al. 1993; Zeller and Russ 1998). However, the major weakness in understanding the level of connectivity between reefs was associated with the planktonic egg and larval stages (Jones et al., Chapter 16, Volume 1; Polunin, Chapter 14, this volume). These could return to their natal reef, making the effects of fishing localized, or be transported to reefs that were many tens to hundreds of km away, making the effects of fishing collective. Clearly, if the majority of larvae recuited to sites away from the natal reef, then spatial studies of fishing effects gave little insight into the longer-term impacts of fishing. Moreover, if we do not know the scale on which we should test for fishing effects, it is equally difficult to know the scale on which to impose management strategies.

Two recent studies made direct assessments of larval dispersal rates. Both concluded that rates of dispersal between reefs were low and that most larvae were retained close to the natal reef. Swearer et al. (1999) looked at the evidence for larval retention of bluehead wrasse (*Thalassoma bifasciatum*) at St Croix (US Virgin Islands) in the Caribbean. They used isotopic signatures in the otoliths to identify the source of larvae that were recruiting to the reefs, and showed that many had been retained close to the area where they were spawned. Jones et al. (1999) marked the otoliths of approximately 10 million developing Ambon damselfish (*Pomacentrus amboinensis*) eggs with tetracycline, a marker that fluoresces when the otolith is examined under ultraviolet light. All the eggs were marked on a reef at Lizard Island on the Great Barrier Reef, and they comprised 0.5–2.5% of total Ambon damselfish egg production on this reef. Later in the year, juveniles recruiting to the reef were caught, and their otoliths were removed and viewed under ultraviolet light. The frequency of otoliths with marks suggested that 15–60% of juveniles returned to the natal reef and that long-distance dispersal was not usual.

Thus there is some evidence to suggest that fish populations are largely self-sustaining on reefs that are separated by >10 km. This suggests that spatial designs can be useful for looking at long-term fishing effects and that even small and isolated marine reserves may be useful conservation tools for some reef fish species. (See also Polunin, Chapter 14, this volume, for further commentary on the degree to which fish move away from small areas.)

16.3 EFFECTS OF PREY REMOVAL ON SEA BIRDS

Piscivorous sea birds feed primarily on small shoaling fish. In the North Atlantic, these prey species include herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and sandeels (*Ammodytes* spp.). Sandeels are particularly important prey during the breeding and chick-rearing season, whereas clupeoid and gadoid fish become more important dietary components during the winter period. The International Council for the Exploration of the Sea (ICES) working group on sea bird ecology (Anon. 1994) estimated that the annual consumption of fish by 18 sea bird species, based on sea bird

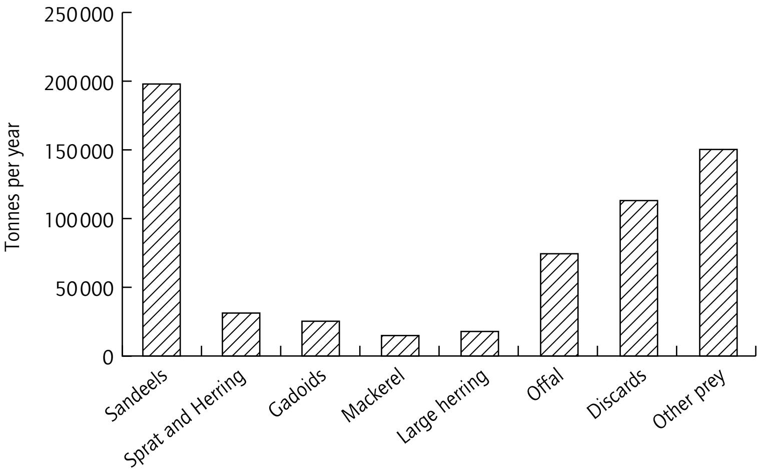

Fig. 16.2 Estimated total annual consumption of fish and discarded materials by 18 sea bird species in the North Sea. (Source: data from Anon. 1994.)

abundance estimates and their energetic requirements was 600000 tonnes y^{-1} (Fig. 16.2). Of this figure the total consumption of small fish, consisting of sandeel, sprat, young herring and small gadoids, by sea birds is approximately 250000 tonnes y^{-1}, which is about one-tenth of the small fish consumed by larger predatory fish (Anon. 1994).

It is thought that the abundance of immature fish in the North Sea has increased due to the overfishing of larger size classes of piscivorous fish (e.g. Furness and Monaghan 1987; Daan et al. 1990). Similarly, congruent shifts in sandeel abundance in the western and eastern North Atlantic ecosystems were also explained by predator removal by fisheries (Sherman et al. 1981). Although the increase in the amount of small fish intuitively must have resulted in a larger potential resource for piscivorous sea birds, the availability of prey may not have changed quite that dramatically. Shifts in the localized availability of small fish may negatively affect sea birds even when the wider fish stock is relatively unaffected. For example, the reproductive output of puffins (*Fratercula arctica*) that nest on the Lofoten islands off Norway was reduced over a 20-year period following the collapse of local herring stocks, even though, elsewhere, herring stocks remained at relatively high levels (Anker-Nilssen 1992).

16.3.1 Effects of industrial fisheries on sea bird populations

Industrial fisheries in the North Sea have increased substantially since the early 1960s. These fisheries target species such as sandeels, which are then converted into animal feed, fertilizer or are even used as fuel. This fishery has caused concern among conservationists because many top predators such as seals, cetaceans and sea birds, rely on sandeels as the main part of their diet (Furness 1990). The direct impacts of fisheries impacts on prey availability can easily be overlooked as sea birds are able to compensate for food shortages by working harder, allocating more time to foraging, switching to alternative prey types, or abandoning nesting attempts. Ultimately the impacts of significant reductions in prey populations become apparent as sea birds starve to death.

During the 1980s, the breeding success of several sea bird species in the Shetland Islands declined markedly, coincident with a marked decline in landings of sandeels from an industrial fishery that operated close to the Shetland coast (Monaghan et al. 1992). The sea bird species affected most severely were surface feeders such as Arctic terns (*Sterna paradisaea*), black-legged kittiwakes (*Rissa tridactyla*) and great skuas (*Catharacta skua*) that fed predominantly on O-group sandeels.

The kleptoparasitic Arctic skuas (*Stercorarius parasiticus*) were also affected, as was the puffin. The diet of gannets changed from predominantly sandeels to clupeoid and gadoid fish. After a few years of poor breeding success, significant declines occurred in breeding populations of Arctic terns, black-legged kittiwakes and common guillemots. The numbers of Arctic terns increased dramatically again in 1991, coincident with the appearance of a large year class in the sandeel population.

These population shifts led to suggestions that the industrial fishery competed for the same resource as the sea birds and was responsible for the decline in their food supply. However, other studies indicated that the decline in sandeel abundance was the result of poor recruitment to the Shetland stock. Hence, natural fluctuations in sandeel survival and recruitment may have been the main cause of the decline in prey availability for sea birds breeding on the Shetland Islands (Anon. 1994).

16.4 HOW FISHERIES AFFECT ENERGY SUBSIDIES

16.4.1 Terrestrial systems

At first glance, the ecosystem consequences of fishing in the marine environment might seem to have little relevance to ecosystem processes in terrestrial ecosystems. However, there is a substantial literature that has examined the importance of the contribution of nutrients and energy to aquatic and terrestrial ecosystems by salmon carcasses (See also Persson, Chapter 15, Volume 1, for a discussion of the role of fishes in nutrient cycling within freshwater systems.). Pacific salmon (*Oncorhynchus* spp.) migrate to sea where they grow to maturity before migrating back to their native rivers to spawn and in many cases die (Cederholm et al. 1999). Thus Pacific salmon are important vectors of marine-derived nutrients that are moved upstream. Energy subsidies, such as those provided by salmon carcasses, are only likely to have a significant ecological contribution if they occur frequently enough and in large concentrations (Polis and Strong 1996). Mass spawning aggregations of salmon are important sources of food for many terrestrial animals and bird species that inhabit the relevant watersheds. Studies that have examined $^{15}N/^{14}N$ ratios in food webs of systems with anadromous salmon and those without indicate that the decomposing carcasses of salmon are remineralized by primary producers that are consumed by fish predators (Kline et al. 1993; Cederholm et al. 1999).

Salmon carcasses can supply a critical source of energy for some terrestrial vertebrates and provide nutrients for riparian vegetation along some spawning streams. They are now viewed by some as keystone species in certain terrestrial vertebrate communities (Willson and Halupka 1995). The reproduction cycle and seasonal distribution of species such as bald eagles (*Haliaeetus leucocephalus*) is tied directly to a spawning run of salmon (McClelland et al. 1982). Salmon stocks are, in general, overexploited (Nehlsen et al. 1991). Hence the present-day inputs of marine nutrients from salmon carcasses are probably much lower than they were prior to overexploitation. While it is not possible to attribute differences in past and present-day community structure to decreases in the amount of energy and nutrient subsidies passing into watershed systems, the importance of the role of salmon carcasses has prompted management action to ensure their continued presence. For example, timber debris on which salmon carcasses become snagged is introduced into river systems to avoid loss of the carcasses through wash-out, and salmon carcasses from fish farms are used to supplement nutrient inputs in some systems (Cederholm et al. 1999).

16.4.2 Energy subsidies from discarding practices

While some fishing techniques are highly specific, such as pelagic fisheries and single hook and line fisheries, others yield bycatches or incidental catches of species that are not utilized by the fishers. These bycatches are usually discarded and are composed of animals that are dead, dying or injured (Kaiser and Spencer 1995). Bycatches may be discarded for legal reasons, in the case of commercially valuable species that are undersized. Alternatively, bycatches are discarded because there is insufficient money to be gained by sorting or landing them. There are even instances when fishers will discard commercial species that are greater than the minimum landing size so as to enable them to fill their quota with a larger average size of fish. This phenomenon is known as high-grading (Pascoe 2000). Global energy subsidies in the form of bycatch material dumped back into the ocean totals approximately 27 million tonnes per annum which is almost equivalent to a quarter of the global annual landings of fish (Alverson et al. 1994). However, this figure does not account for those animals that are never landed on board vessels but remain dead on the seabed. Thus, fishing activities redirect energy in marine ecosystems by the production of carrion that then becomes available to scavengers on the seabed and those that feed at the surface of the sea.

16.4.3 Changes in sea bird populations

Anyone who has witnessed a fishing boat returning to port will have observed the scrum of sea birds that contest for the offal and discarded fish as they are thrown overboard. In the North Sea alone, approximately 235 000 tonnes of discarded fish are consumed by sea birds each year and this partly explains the increases in the populations and distribution of some species (Furness 1996; Camphuysen and Garthe 2000). Sea birds are very choosy, preferring to eat offal that gives the greatest energetic reward in preference to flatfishes or invertebrates that yield lower energy returns or that are more difficult to swallow. Relatively high consumption rates for these less-preferred discard types occurs in areas of the sea where the resource needs of the sea birds at sea exceeds the amount of material discarded (Table 16.2). This suggests that competition for fisheries discards is intense in some areas of the sea, but not in others.

The northern fulmar (*Fulmarus glacialis*) is one of the most common scavenging sea birds that are observed following fishing vessels in the North Sea, and has shown the most spectacular increase in numbers (Fig. 16.3) and breeding range of any sea bird found in the North Atlantic (Lloyd et al. 1991). The expansion of the fulmar population has been attributed mainly to its success as an offal scavenger, firstly associated with whalers in northern polar regions, and later in association with commercial fishing fleets. Field studies have ranked fulmars at the apex of the interspecific dominance hierarchy, hence they are able to obtain the best quality food: offal or fish livers (Hudson and Furness 1988). While Tasker et al. (1987) concluded that fishing activities were an important deter-

Table 16.2 The energetic requirements of sea birds at sea and the energetic content of available discards. (Source: from Camphuysen and Garthe 2000.)

Subregion of the North Sea	Energetic requirements of scavengers ($\times 10^6$ kJ)	Energetic equivalents of discards and offal ($\times 10^6$ kJ)	Index of required/available discards	Potential shortage or surplus if discards were only prey
Northwestern	899 000	463 000	1.9	shortage
Northeastern	312 000	456 000	0.7	surplus
Central-western	364 000	269 000	1.4	shortage
Central	322 000	659 000	0.5	surplus
Central-eastern	120 000	698 000	0.2	surplus
Southern	175 000	871 000	0.2	surplus
Total	**2 192 000**	**3 216 000**	**0.6**	**surplus**

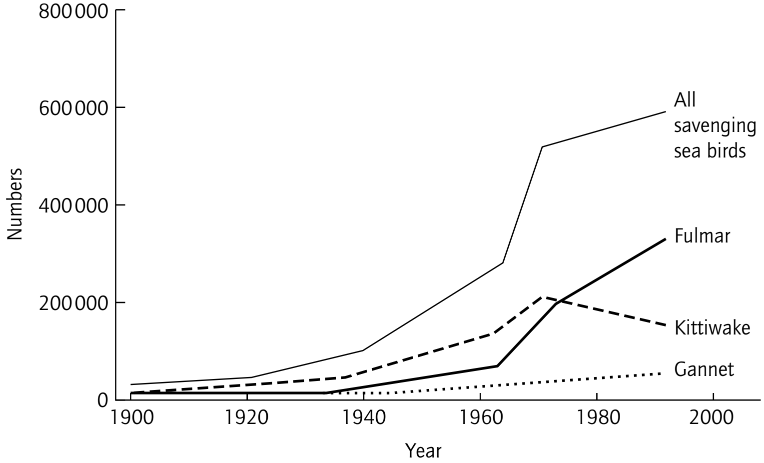

Fig. 16.3 Increases in the numbers of breeding pairs of a selection of scavenging sea birds breeding on North Sea coasts. (Source: adapted from Camphuysen and Garthe 2000.)

minant of fulmar distribution at sea, more recent studies, conducted at different scales, were less conclusive and suggested that, although fulmars were evidently attracted by fishing vessels, the spatial distribution of the main fisheries and fulmars did not coincide as well as was expected (Camphuysen et al. 1995; Stone et al. 1995). Also, recent investigations have shown that the position in the dominance hierarchy at fishing vessels was not so high in other parts of the North Sea, as compared with studies that had concentrated on the Shetland Islands (Camphuysen et al. 1993).

In light of these findings, Camphuysen and Garthe (1997) re-examined the distribution and scavenging habits of northern fulmars in the North Sea using a large set of recently gathered data. They calculated the availability of discards and offal per km^2 for each subregion in the North Sea (Table 16.2). They found negative correlations for northern fulmar densities at sea versus the availability of offal and all types of fisheries wastes. There was no correlation between numbers of fishing vessels at sea and densities of northern fulmars at this scale, but the numbers of fulmars observed at the stern of fishing vessels were highly correlated with the overall densities of northern fulmars at sea. These results suggested strongly that commercial fisheries were not the prime determinant of fulmar distribution at sea. Further investigations indicated that fulmars had a northerly, offshore distribution, over waters with a rather strong Atlantic influence and high concentrations of zooplankton. This observation suggested that the distribution of zooplankton, their natural prey, was a much more important parameter that influences their distribution at sea.

While offal and discards would appear to present sea birds with high-energy food that is easily obtained, this does not always equate to higher reproductive output as might be expected. Hamer et al. (1991) demonstrated that the chick growth index of great skuas on Foula (Shetland Islands) declined considerably when more than half of the prey delivered by the parents was comprised of discards and offal. When smaller proportions (20–30%) of offal and discards were included in chick diets, growth rates were relatively high.

The insights into the dominance hierarchies that exist between different scavenging sea birds have important implications for fisheries managers as they suggest that measures to reduce the amount of discards would affect the lower ranked sea bird species first. Increases in trawl-net mesh size would increase the mean length of discarded fish and this in turn would lower the handling efficiency of smaller scavenging sea birds that are less well adapted to consuming large fish (Furness, Ensor and Hudson 1992). A total ban of discards and offal would lead to major changes in current sea bird diets. An overnight introduction of such a ban would certainly increase the predation risk for smaller birds from larger predators such as great skuas (Camphuysen and Garthe 2000).

16.4.4 Energy subsidies for marine benthic communities

Food-falls of carrion can have a profound effect on local diversity and production processes of deep-sea benthic communities (Dayton and Hessler 1972). Although fishing activities occur in oceanic waters, the majority of fishing activities are confined to more shallow coastal waters that are less than 100 m deep. Hence the energy subsidies to deep-sea communities from current levels of fishing activities are likely to be less significant than for shallow waters.

The greatest energy subsidies to benthic communities are generated by towed bottom fishing gears. These trawls and dredges are specifically designed to remain in close contact with the seabed and thereby maximize catches of bottom-dwelling species such as flatfishes and scallops (Misund et al., Chapter 2, this volume). Not surprisingly, these gears are particularly heavy and robust; a typical beam trawl fished in the North Sea will weigh up to 10 tonnes in air. Most bottom fishing gears are fitted with chains or toothed bars across the mouth of the net or dredge (Fig. 16.4; see also Misund et al. Chapter 2, this volume). These modifications are designed to dig out or disturb the target species from the substratum whereupon they are caught in the following net. Although these fishing gears are very effective at catching the target species (Cruetzberg et al. 1987), they also catch, damage or kill in situ a large number of non-target fish and invertebrates (Bergman and Van Santbrink 2000). The odours emitted from this carrion rapidly attract mobile scavenging species into areas of the seabed that have been trawled (Kaiser and Spencer 1994; Ramsay et al. 1996, 1997). Fishers have known of this phenomenon for many years and it is not uncommon to see trawlers fishing one after the other along the same navigational plot. The density of scavenging fishes attracted into the areas of trawl disturbance often exceeds their initial density before trawling started by between 4 and 10 times (Ramsay et al. 1996; Fonds and Groenwold 2000). Examination of the gut contents of scavenging fish reveals that they eat a wider variety and larger rations of prey in areas of trawl disturbance (Kaiser and Spencer 1994; Kaiser and Ramsay 1997). Furthermore, they are able to consume prey such as burrowing sea urchins and large bivalve molluscs that normally would be unavailable to them (Kaiser & Spencer 1994). In addition to scavenging fishes, a wide variety of invertebrate scavengers are attracted into areas of trawl disturbance. The most commonly observed taxa that

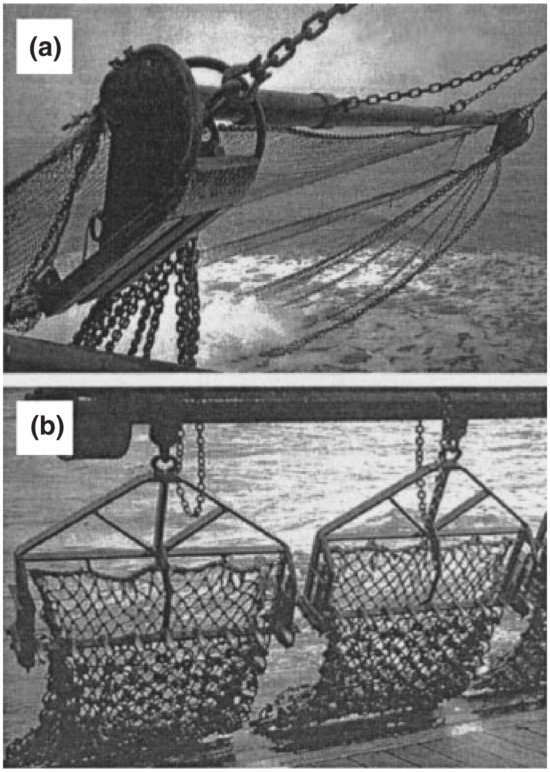

Fig. 16.4 Towed bottom fishing gears are designed to remain in close contact with the seabed: (a) 12-m wide commercial Dutch beam trawls can be fitted with up to 27 tickler chains that are attached between the two beam shoes, (b) scallop dredges are fitted with toothed bars that dig scallops out of the seabed.

feed upon fisheries carrion are starfishes (Asteroidea), hermit crabs (Paguridae), crabs (Decapoda) and gastropods (Gastropoda) (Hill and Wassenberg 1990; Kaiser and Spencer 1996a; Ramsay et al. 1997). When hermit crabs are found in high background densities, they can locate carrion within minutes of its arrival on the seabed and can reach densities in excess of 300 m^{-2} (Kaiser and Spencer 1996a; Ramsay et al. 1997). It is not surprising therefore that dominance hierarchies occur among the scrum of scavenging invertebrates such that smaller conspecifics are excluded from the food resource as are other less competitive species (Ramsay et al. 1997; Kaiser et al. 1998). The amount of carrion generated on the seabed by bottom fishing is at least equivalent to the amount of material discarded at the surface of the sea (Bergman and Van Santbrink 2000). However, this carrion is calculated to supply only 7% of the maximum annual energy requirements of invertebrate scavenging megafauna in the southern North Sea (Fonds and Groenwold 2000).

While the responses of populations of scavenging sea birds have been correlated in part with subsidies from discarding practices, the responses of fish and invertebrate scavenger populations to fisheries subsidies are far less clear (Ramsay et al. 2000). Several studies indicate that populations of flatfish species that are known to be facultative scavengers have increased in abundance or increased their growth rate in response to increased fishing effort. For example, the growth rates of plaice (*Pleuronectes platessa*) and sole (*Solea solea*) have increased in relation to the increase in bottom fishing effort and hence disturbance of the seabed (Millner and Whiting 1996; Rijnsdorp and Leeuwen 1996). However, there are many alternative explanations for the increased growth of plaice and sole, which include the reduction of the populations of their main predators and the enhancement of polychaete communities due to the effects of eutrophication.

Why should there be such large differences in the responses of scavenging sea birds and fishes and invertebrates to energy subsidies? Sea birds are able to actively search for fishing vessels over large areas and hence discards from trawlers are a relatively reliable and constant source of high-quality food (Camphuysen et al. 1993). Furthermore, we now know that sea birds will often choose not to feed on fisheries discards especially when rearing chicks (Camphuysen and Garthe 2000). In contrast, benthic invertebrates are unable to actively search for sources of fisheries-generated carrion and rely on its chance occurrence on the seabed. Thus, at present, this source of carrion may be too unpredictable to give significant benefit to most invertebrate scavenger populations. In line with our rationale for the relative lack of cascade effects observed in marine systems as a result of fishing activities, it is perhaps not surprising that we only see population effects of subsidies at higher trophic levels (sea birds) whereas they are not apparent, or are less obvious, at lower trophic levels.

16.5 EFFECTS OF REMOVING PREDATORS

16.5.1 The 'krill surplus' hypothesis

Commercial whaling dramatically reduced the abundance of baleen whales in the Antarctic Ocean, and these whales were the main consumers of krill (mostly *Enphausia superba*). The reduced predation on krill was expected to release krill production for species that formerly competed with whales. This was known as the 'krill surplus hypothesis'. Predicted krill production in the southwest Atlantic is 28.6 to 97.6 million tonnes yr^{-1}, while sea bird, seal, whale and fish consumption in the same area was estimated as 32.6 million tonnes yr^{-1} (Trathan et al. 1995). If the distributions and feeding behaviour of krill feeders overlapped in space and time then competition could reasonably be expected. However, a recent analysis by Murphy (1995) suggests that many krill predators cannot compete because they feed in different areas at different times. As a result, the effects of competitive interactions between krill predators are minor in comparison with the oceanographic factors that determine krill abundance on feeding grounds. In general, temporal and spatial variation in krill abundance appears to drive the dynamics of krill consumers. The variation is due to recruitment fluctuations and the differential transport of krill by ocean currents. In the waters around South Georgia, for example, krill abundance fluctuates by a factor of twenty between years, and in years of low abundance krill predators suffer catastrophic breeding failures (Croxall et al. 1988; Brierley et al. 1997; Murphy et al. 1998). The early models that predicted the existence of a 'krill surplus' were based on a homogeneous view of the food chain and assumed that krill were equally vulnerable to predators when in fact they were not (Murphy 1995).

16.5.2 Culling mammals to boost fishery yields

Fishers see marine mammals eating fish and often treat them as competitors. Indeed, there are many examples of fishers culling marine mammals in an attempt to boost fishery yields (Earle 1996; Hutchinson 1996). There are similar traditions in freshwater systems, where by anglers sometimes remove predatory birds and fishes in the hope that this will increase their catches (Cowx, Chapter 17, this volume).

Traditionally, the simple logic that marine mammals and fishers competed directly was followed, and the debate focused on how much the mammals ate and whether this consumption was significant in relation to catch (Beddington et al. 1985; Crawford et al. 1992). This argument assumes a simple food web as perceived by many fishers, in which fishers compete with a marine mammal for a prey. However, such systems are embedded in a much more complex system in which the interactions between fishers and marine mammals do not follow the rules predicted by simple models (Beverton 1985; Yodzis 1998; Pauly and Christensen, Chapter 10, this volume).

A recent analysis by Yodzis (1998) considered the potential effects of a fur seal cull on fishery yields from the Benguela upwelling ecosystem off West Africa. Here, the simple model, where seals and fishers compete for fish that feed on everything else, was discarded, and Yodzis described the system using a food web containing 29 species or species groups (Fig. 16.1). Probability distributions were calculated for the outcomes of interest, such as changes in yields of different species following a seal cull. Contrary to the prediction of the simplistic models, Yodzis showed that a cull of seals was more likely to be detrimental to total yields than beneficial.

16.6 EFFECTS ON BENTHIC COMMUNITIES AND HABITATS

All continental shelf areas are subject to fishing using towed bottom-fishing gear. Fishing in the marine environment is perhaps the best example of a method of harvesting animals that can lead to habitat change. In a recent article, Watling and Norse (1998) compared the effects of fishing with towed bottom-fishing gears to clear-cutting of forests in terrestrial systems. This is perhaps understandable, given the manner in which towed bottom fishing gears operate (see section 16.4 and Misund et al., Chapter 2, this volume). Watling and Norse's (1998) assertion was that the incidental or even deliberate removal of topographically complex seabed habitats would have detrimental effects on the associated species assemblage as in terrestrial systems. This is perhaps not surprising and there is good evidence to demonstrate these effects in some marine systems. For example, Sainsbury (1987; 1998) reported that as sponges and soft-coral communities were removed as bycatch in trawls off the northwestern shelf of Australia, the associated fish species were greatly reduced in abundance. Only after these areas were protected from bottom fishing did they observe slow regeneration of the habitat as sponges and corals began to recolonize and grow. Once this process had begun, then the populations of associated fish species began to increase once again. In temperate estuarine systems, oysters are important reef-forming organisms that add structural complexity to the seabed and increase species and habitat diversity. Oysters also improve water quality through their filtration activities as they bind particulate organic matter and remove pollutants and nutrients from the water column. The functional role of oysters in coastal ecosystems is now deemed to be of such importance that in many areas large sums of money are spent attempting to re-establish degraded oyster reefs (Lenihan 1999).

Many fisheries that use towed bottom gears occur over coarse sediments in relatively shallow waters. The species that live in these habitats are adapted to physical disturbance as they are regularly subjected to wave action, strong currents and tidal scouring (Kaiser 1998). Hence, it might be expected that the effects of fishing disturbance in such habitats would be relatively minor in comparison with other more stable environments. The ecological significance of fishing disturbance will vary according to the intensity, frequency and history of disturbance that has occurred over a particular area of the seabed. This implies that in some habitats a certain level of physical disturbance may be sustainable, whereas in others it may have long-lasting ecological effects. This is probably the most relevant question for current research as the implicit assumptions would form the basis for predicting the likely outcome of bottom-fishing practices in different habitats.

There now exists an extensive literature on manipulative experiments designed to ascertain the immediate effects of fishing disturbance on benthic community structure. The majority of these studies demonstrate significant short-term reductions in species number and counts of individual organisms as a result of fishing disturbance (Jennings and Kaiser 1998; Auster and Langton 1999). While these studies have been important for understanding the mechanism of community change and ascertaining those species that are most vulnerable to disturbance, they are unable to replicate the intensity, frequency or long-term disturbance history associated with the fishing activities of an entire fleet of fishing vessels. A better approach to studying the long-term effects of fishing disturbance at the scale of the fishing fleet is to compare areas subjected to different known intensities of fishing disturbance. A number of studies have employed this approach and have independently shown similar findings (Collie et al. 1997; Thrush et al. 1998; Bradshaw et al. 2000; Kaiser et al. 2000a,b).

Using a combination of fishing effort data and direct observations from side-scan sonar surveys, Collie et al. (1997) were able to identify comparable substrata that experienced different intensities of scallop dredging on the Georges Bank, northwest Atlantic. Areas that were less frequently fished were characterized by abundant bryozoans, hydroids and worm tubes which increased the three-dimensional complexity of the habitat. Furthermore, examination of evenness within the community suggested dominance by these structural organisms, which indicated that this environment was relatively undisturbed. In contrast, the more intensively dredged areas had lower species diversity, lower biomass of fauna, and were dominated by hard-shelled bivalves (e.g. *Astarte* spp.), echinoderms and scavenging decapods. The higher diversity indices observed at the less intensively dredged sites were attributable to the large number of organisms, such as polychaetes, shrimp, brittle stars, mussels and small fishes, that were associated with the emergent sessile fauna (Collie et al. 1997). Many of these associated species were also important prey for commercially exploited fishes such as cod (Bowman and Michaels 1984). This study emphasizes how fishing activities can degrade habitat characteristics on which commercial fish species depend for successful growth and survival (see Benaka 1999).

Bradshaw et al. (2000) were able to take advantage of the creation of an area closed to fishing to monitor subsequent changes in benthic community structure. The closed area was located off the south of the Isle of Man, Irish Sea, in an intensively fished scallop ground. After several years surveyed plots within the closed area had become significantly different to similar plots of seabed in the adjacent seabed that remained open to fishing. Bradshaw et al. (2000) then tested the hypothesis that these changes had occurred as a result of the lack of fishing disturbance. Within the area closed to fishing, experimental plots were fished with the same scallop dredges that are used by the commercial fleet. As a result of their experimental fishing, Bradshaw et al. (2000) altered the benthic community in the experimental plots within the closed area such that it became similar to that in the adjacent commercial fishing ground. This manipulation convincingly demonstrated that the seabed surrounding the closed area was maintained in a permanently altered state by bottom-fishing disturbance.

In a similar study, Kaiser et al. (2000a) investigated differences in benthic community structure and habitat complexity in areas exposed to differing levels of bottom-fishing activity according to the restrictions imposed by a voluntary management agreement. This agreement exists between fixed-gear and towed bottom-gear fishers that operate off the south Devon coast in England. The agreement was instigated in 1978. All fishing by scallop dredgers and trawlers is prohibited in areas reserved for the setting of pots or fixed bottom gear. Some areas are open to towed bottom gears for limited periods of the year. The closed areas extend out to 6 nautical miles from the shore, beyond which there are no operational restrictions on bottom-fishing activities. This management system permitted Kaiser et al. (2000a) to compare areas of the seabed that had been exposed to differing levels of fishing disturbance over a prolonged period. The areas open to pot fishing only were considered to have experienced only infrequent bottom disturbances for 20 years. Standard benthic surveys of the infauna and epifauna within the different areas revealed that the areas that had been closed to towed bottom-fishing gears were dominated by emergent sessile epifauna that had a relatively high biomass. In contrast, the areas of seabed subjected to either seasonal or continuous towed bottom-fishing activities were dominated by small-bodied opportunistic species and mobile scavenging fauna (Fig. 16.5).

The resolution of fishing-effort data sets remains a major obstacle to comparative studies of the long-term effects of repeated bottom-fishing disturbance. The simplest solution is to install tracking devices to fishing boats that would record their precise position. These devices are now fitted to a proportion of certain fleets for the purpose of monitoring compliance with fisheries regulations (Rijnsdorp et al. 1998). However, these schemes are in their infancy and do not yet provide a long-term historical record of seabed disturbance. Kaiser et al. (2000b) were able to partly overcome some of these problems to compare areas of the seabed off the Isle of Man that are subjected to either high or low levels of scallop-dredging disturbance. They chose this fishery as the subject

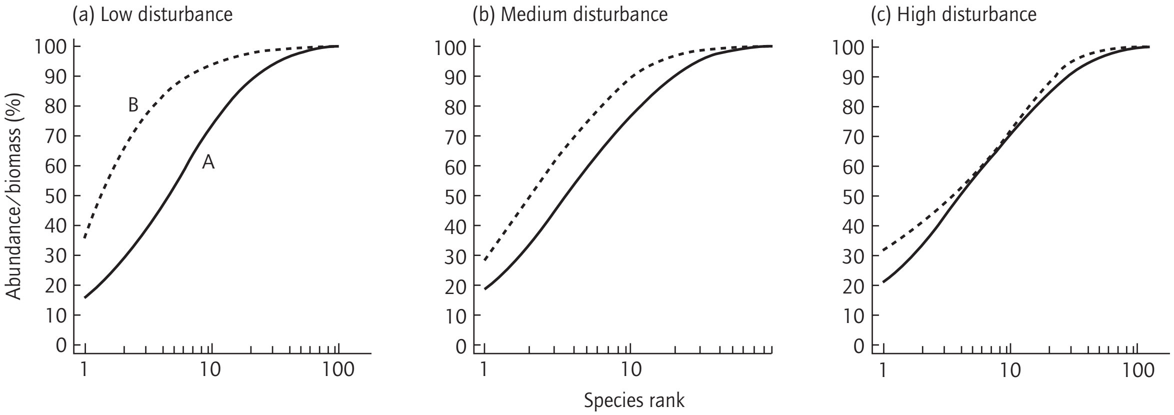

Fig. 16.5 Abundance/biomass curves of samples collected from (a) areas protected from towed bottom-fishing gear (low disturbance), (b) areas open seasonally to towed bottom-fishing gear and those areas (c) that are fished all year with towed bottom-fishing gear (high disturbance). As the level of bottom-fishing disturbance increases the biomass curve (B) converges with the abundance curve (A), which is a typical response in stressed communities. (Source: adapted from Kaiser et al. 2000a.)

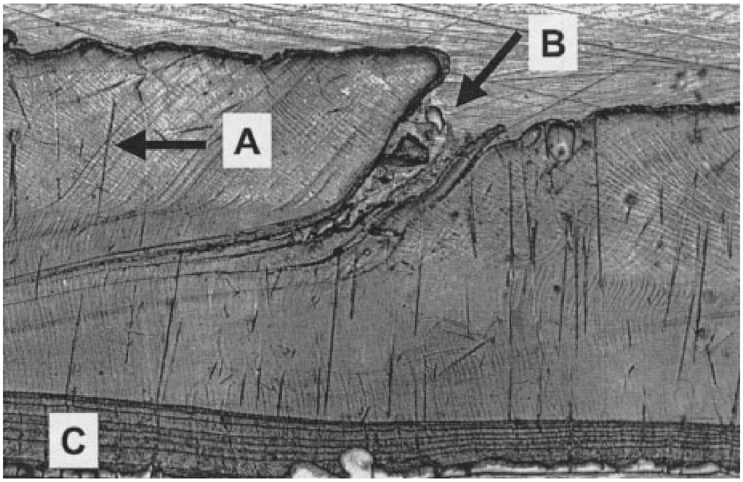

Fig. 16.6 An acetate peel of a section through the shell of the bivalve *Glycymeris glycymeris* collected from a commercial scallop fishing ground. (A) Growth bands in the shell matrix are laid down each year, enabling the age of the bivalve to be determined; (B) physical damage from passing fishing gears is recorded as a fracture in the outside portion of the shell which has then continued to grow; (C) the inner side of the shell that is in direct contact with the bivalve's tissues. (Source: adapted from Ramsay et al. 2000.)

of their investigation because fishing effort has been recorded at a relatively small spatial scale since the early 1980s (5 × 5 nautical miles). Nevertheless, even this relatively fine scale of fishing-effort data presents problems of sampling at the appropriate scale when one considers that the sampling devices used collect organisms from areas of 0.1 m^2 (grabs) to approximately 1 m^2 (dredges). Kaiser et al. (2000b) were able to corroborate the disturbance history of the specific areas of seabed sampled from the disturbance scars that occurred in the shells of a long-lived bivalve, *Glycymeris glycymeris.* Bivalves lay down annual growth rings, hence it was also possible to determine the year in which the disturbance occurred. Fishing gears that come into contact with bivalves leave distinctive scars in the shell matrix when the animal's mantle withdraws in response to physical injury (Fig. 16.6). The occurrence of these scars in the shells of *G. glycymeris* confirmed that the chosen heavily fished areas had experienced significantly higher levels of fishing disturbance consistently over many years compared with low mean levels of disturbance experienced in the chosen areas of low fishing effort. An examination of the benthic communities in these areas showed that large biomass emergent epifauna were more prevalent in the areas of seabed that had been fished sporadically over many years, whereas those areas that had experienced constantly high levels of fishing disturbance were dominated by more opportunistic and scavenging species.

16.6.1 Meta-analysis: a basis for better management

As we have seen, the magnitude of the impact of bottom-fishing activities on benthic fauna and their habitat varies according to factors such as habitat stability, depth, disturbance frequency and presence of biogenic structures. Thus, the results from any one experiment or comparative study are limited in their scope for extrapolation to other situations, and such extrapolations may be entirely misleading. A far better approach is to take all the data from these studies and undertake what is known as a meta-analysis of the data, which increases the power for the analysis of general trends and patterns that might provide the basis of predictive models (Collie et al. 2000; Myers Chapter 6, Volume 1). Collie et al. (2000) undertook such an analysis and identified those gears that cause the greatest initial impact on benthic habitats. Note this does not equate to long-term impact. Not surprisingly they found that intertidal dredging activities caused the greatest initial impacts, followed by scallop dredging and then trawling. The most consistently interpretable result was with respect

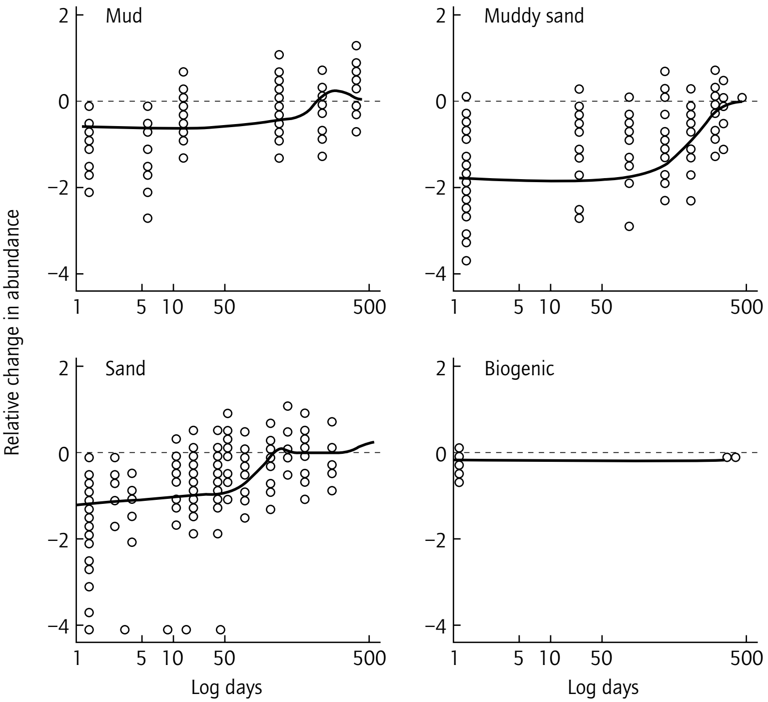

Fig. 16.7 Results from a meta-analysis of the effects of fishing disturbance on benthic communities. The scatter plots of the relative change of all species (each datapoint represents the relative abundance of a different species on each different sampling date) in different habitats at time intervals after the occurrence of a fishing disturbance. The fitted curves show the predicted time trajectory for recovery to occur. On the y-axis, 0 shows no relative change in abundance, negative values show a relative decrease in abundance.

to faunal vulnerability, with a ranking of initial impacts that matched expectations based on morphology and behaviour.

More importantly, Collie et al. (2000) were also able to model recovery rate and speculated about the level of physical disturbance that might be sustainable in a particular habitat. Their results suggested that sandy sediment communities are able to recover within 100 days (Fig. 16.7), which implies that they could perhaps withstand two to three incidents of physical disturbance per year without changing markedly in character. This is the average predicted rate of disturbance for the whole of, for example, the southern North Sea. However, we know that effort is patchily distributed and that some relatively small areas of the seabed are disturbed approximately eight times per year (Rijnsdorp et al. 1998). If these recovery rates estimates for sandy habitats are realistic then we would predict that the communities in these heavily fished areas are held in a permanently altered state. Although Collie et al.'s (2000) analysis shows recovery in biogenic habitats to occur after 500 days, there were few data on which to base this analysis. We now know that recovery rates in some biogenic habitats take from 5 to 10 years (Sainsbury et al. 1998).

16.7 BYCATCHES AND GHOST-FISHING

In their comprehensive review of world bycatches, Alverson et al. (1994) extracted data from over 800 published records. Although this represents the most authoritative text written on this subject, it is certainly by no means entirely comprehensive. Bycatch and discard data are best documented for nations that monitor fisheries and have sufficient resources to operate observer programmes on fishing vessels, which are beyond the means of poorer nations. Trawl fisheries accounted for most of the records of bycatches (966) followed by drift-nets and gill-nets (232), line fisheries (150), pot (83) and purse seine (82) fisheries. An investigation of which target species or target groups were associated with most records of bycatches revealed that shrimp and groundfish species headed the list. In particular, shrimp fisheries accounted for approximately 35% of the global commercial fisheries discards wasting approximately 27 million tonnes per annum.

16.7.1 Sea birds

There are numerous reported incidents of sea birds captured and drowned in fishing gears (Dayton et al. 1995). In general, set-net, drift-net and longline fisheries take the most birds (see also Misund et al., Chapter 2, this volume). These fisheries often target large fish species such as adult tunas and salmonids that do not occur in the diet of sea birds. Diving sea birds are particularly vulnerable to capture by drift- and set-nets and longlines. The nylon meshes of drift- and set-nets are designed to be invisible underwater, hence birds have little chance of avoiding any nets set in the area where they are feeding.

The number of sea birds killed annually is quite staggering for some fisheries. It is not possible for us to list all the recorded instances here, but it is sufficient to say that the examples given are probably repeated elsewhere around the world. For example, an estimated 210 000–760 000 sea birds were killed every year by Japanese drift-nets fishing in the North Pacific Ocean (Northridge 1991). Subsequently, the use of these nets was banned in the early 1990s. Although such high incidental catches are undesirable, they are not necessarily unsustainable if they constitute a relatively small (<1%) proportion of the population. However, in some circumstances bird deaths associated with nets can constitute the greatest source of mortality for some local populations. For example, a small population of 1600 razorbills (*Alca torda*) breeds in Newfoundland, Canada and from 1981 to 1984 approximately 200 birds were killed in nets each year. This was slightly more than the 10% of the population that died each year through natural causes. As a result, this population was considered under threat of extinction as nearly a quarter of the adult population was lost each year to a combination of natural and fishing mortality (Piatt and Nettleship, 1987).

Albatrosses, and in particular the wandering albatross, have been severely affected by the activities of the southern bluefin tuna (*Thunnus maccoyii*) and Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries. Birds are attracted to the baited lines as they are paid away from the vessel and dive after the baited hooks as they pass into the water. The Southern Ocean bluefin tuna fleet deployed 107 million hooks annually and was estimated to have killed 44 000 albatrosses up to 1989 when conservation measures were introduced. Nevertheless, modelling studies of wandering albatross populations predict that unless fishing is reduced by more than 50%, this species will soon be extinct (Weimerskirch and Jouventin 1987; Brothers 1991). Currently, there are only 13 breeding pairs of the Amsterdam albatross, *Diomedia amsterdamensis*, and only 158 pairs of the short-tailed albatross, *D. albatrus.* Both of these species are known to encounter longline fisheries and the latter have already been caught as incidental catch in Hawaiian waters. With so few remaining breeding adults in these populations the loss of even a few birds will jeopardize survival (Weimerskirch et al. 1997).

16.7.2 Marine reptiles

Captures of sea turtles have been recorded in longline, set-net and towed-gear fisheries. The survival of some turtle species is also threatened by loss of suitable habitat in which to lay their eggs through coastal tourist developments, egg stealing and illegal fishing for wild turtles. Turtles are particularly vulnerable to entanglement and drowning in gillnets and associated ghost-fishing gear as the rough skin on their head and flippers catches easily on the meshes of these nets (Carr 1987). Baited longlines set for swordfish in the Mediterranean take approximately 20 000 endangered species of turtles every year. Similarly shrimp trawl fisheries are a significant source of mortality for turtles (Poiner et al. 1990).

To date, relatively little information exists on the biology or population dynamics of sea snakes. As a result, it is difficult to gauge whether the estimated 120 000 sea snakes, comprising 10 different species, caught in the prawn trawl fisheries in the Gulf of Carpentaria, Australia, represents a significant threat to the survival of these species. Post-capture mortality varies from 10% to 40% depending on species, and in common with sea turtles, increases with tow duration (Ward 1996a,b; Brewer et al. 1998).

16.7.3 Marine mammals

It is an inescapable fact that wherever fishers pursue prey fish species they are likely to encounter larger predatory organisms such as marine mammals. As industrialization of fisheries has replaced less intensive forms of fishing, so incidental catches of species that are closely associated with the target fish species has increased. Such was the case in the eastern Pacific tuna purse-seine fishery that began in the late 1950s (Misund et al. Chapter 2, this volume). This fishery replaced the highly species-specific pole and line fishery that had operated previously. It is thought that schools of tuna follow herds of dolphin as they pursue smaller fish species, but the exact reason for the association is not entirely understood (Hall 1998). In the early days of this tuna fishery dolphin were inevitably captured since their presence within the purse seine net ensured the capture of the tuna. Crude estimates of the number of dolphin killed during the 1960s indicated fatalities of hundreds of thousands per year, which caused a population decline until the late 1970s. This sparked the 'tuna–dolphin' debate that culminated in the Marine Mammal Protection Act of 1972 passed by the US Congress. This act necessitated the adoption of good fishing practices that involved 'backing-down', which is a process to release dolphins from the net, and the provision of independent observers aboard tuna vessels to record dolphin mortality (Hall 1996).

Gill-nets are also used to catch tuna in inshore areas. United Nations legislation has banned the use of high-seas gill-nets. Although highly selective with respect to the size class of animals captured, gill-nets are associated with high numbers of incidental captures of cetaceans. In the Sri Lankan gill-net fishery, one dolphin is caught for every 1.7 to 4.0 tonnes of tuna landed. This compares very poorly with one dolphin for every 70 tonnes landed in the eastern Pacific purse-seine fishery. Hence, while the use of gill-nets may have conservation benefits for target fish stocks, the negative aspects of bycatches of larger organisms may be counterproductive (Hall 1998).

16.7.4 Ghost-fishing

Static fishing gear, such as pots and set-nets, are usually deployed and then left unattended for periods of up to several days (Misund et al. Chapter 2, this volume). During this time the gear is vulnerable to damage from bad weather or can be snagged accidentally by passing vessels or even deliberately vandalized. Once fishing gear has been lost it could continue fishing indefinitely. This phenomenon is termed 'ghost-fishing'.

Just how long a gear is likely to continue ghost-fishing depends upon the circumstances of its loss. Gear that has been dragged off by trawlers or lost in rough weather is likely to become tangled and will fish less effectively when it is eventually cut free and allowed to sink back to the seabed. In other circumstances, the gear may be held in an open fishing position when it becomes snagged on rocks or similar seabed features. In sheltered or deep-water situations, lost gear is likely to continue fishing for many years as it will not be subjected to damage by wave action and abrasion (Carr et al. 1992). In contrast to the numerous records of incidental catches in drift-nets and other set gears few incidents of 'ghost-fishing' are reported or studied (Dayton et al. 1995). The few studies that have been undertaken reveal large differences in the behaviour of lost gear according to the circumstances and environment in which the gear is lost. Kaiser et al. (1996) reported that a net that was snagged on rocky substrata in the Irish Sea continued to catch crustacea and fish for over a year. In the shallow clear waters off the Algarve, Portugal, Erzini et al. (1997) observed that similar lost nets were over-grown by algae, thus increasing their visibility and reducing their ability to catch fish.

Pots or traps tend to be constructed of robust man-made materials and incorporate a rigid structure. This means that pots are likely to maintain their shape and hence capture efficiency for much longer than lost nets. Animals that are trapped and die within pots act as bait that attracts yet more scavengers into the lost pot. The 'ghost-fishing' potential of pots also varies according to their design. For example, Parrish and Kazama (1992) found that the majority of Hawaiian spiny lobster (*Palinurus marginatus*) and slipper lobster (*Scyllarisdes squammosus*) were adept at escaping traps. In contrast, Smolowitz (1978) studied mortalities of lobster (*Homarus americanus*) in parlour-type traps that have non-return entrances to minimize animal escape. They found that 12–25% of trapped individuals died in these pots (Smolowitz 1978).

Little is known about the frequency of net or pot loss, which no doubt results from the reluctance of fishers to report such incidents and the difficulty in undertaking quantitative surveys to estimate the prevalence of lost gear. Estimates of gear loss would indicate that these are substantial in some fisheries. The fact that fishers have complained about the problem of ghost-fishing certainly indicates the scale of the problem. These complaints prompted a grapnel survey of the seabed on Georges Bank, which yielded 341 actively fishing ghost nets from 286 tows (Brothers 1992). The phenomenon of ghost-fishing was clearly perceived to have negative effects on commercial stocks of Greenland halibut (*Reinhardtius hippoglossoides*) by commercial fishers involved in this fishery. As a result, they instigated their own voluntary clean-up programme (Bech 1995). The adverse effects of lost pots are relatively easily averted by incorporating escape panels into pot design and by using biodegradable materials. These technical measures are cheap and simple to instigate and are extremely effective.

16.8 CONCLUSIONS

The study of the ecosystem effects of fishing is gathering momentum, and even in the brief period since our previous review (Jennings and Kaiser, 1998), there has been a book (Hall 1999) and four major symposia (Dorsey and Pederson 1998; Benaka 1999; Kaiser and de Groot 2000; Gislason et al. 2000) on this subject. The most rapid developments are now being made in understanding the impacts of trawling disturbance on habitat and integrating ecosystem concerns into fishery management practices. Habitat conservation is now a management objective in several fisheries. In the United States, for example, amendments to the Magnuson–Stevens Fishery Conservation and Management Act require fisheries managers to describe and identify essential fish habitat, to minimize to the extent practicable adverse effects on such habitat caused by fishing and to identify other actions to encourage the conservation and enhancement of such habitat (Kurland 1998). As the habitat requirements of a large number of species are described, and the potential impacts of gears are assessed, it is likely that the use of towed fishing gears will be controlled on a much wider scale than ever before.

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17 Recreational Fishing

I.G. COWX

17.1 INTRODUCTION

Definitions of recreational fishing vary depending on the origins and diversity of the activity. The FAO (1997), for the purposes of reporting catch statistics, defined recreational fisheries as: 'Fisheries conducted by individuals primarily for sport but with a possible secondary objective of capturing fish for domestic consumption but not for onward sale.' Thus recreational fisheries involve both subsistence fishing, where the catch is consumed, and leisure fishing, where the fish are returned live to the water. Both types of recreational fishing are not only extremely important activities, but also are valuable resources contributing significantly to national economies. Pitcher (1999), however, considered that recreational fishing should essentially be for 'fun', based on the premise that 'it costs far more to catch the fish than they can possibly be worth as marketed commodities'. Against this argument it seems perverse that anglers often endure torturous conditions to pursue their sport!

The true origins of recreational fishing (i.e. angling, like hunting) began as a means of obtaining food. It was not until 1496 that angling as a true sport or recreation can be interpreted from the literature. In that year, the *Treatyse of Fysshynge wyth an Angle*, attributed to Dame Juliana Berners, a sportswoman and nun, was published in the second *Book of St. Albans*, a treatise on hawking, hunting and heraldry. These were major interests of nobility and the publisher, Wynkyn de Worde, emphasized that the book was intended to be kept away from those who were not gentlemen and who, through immoderation in angling, might 'utterly destroye it'.

The importance of recreational fishing as a sport or leisure activity emanates from the 16th and 17th centuries, and coincides with the publication of Izaak Walton's *The Compleat Angler, or Contemplative Man's Recreation* in 1653. This volume fixed for all time the position of the angler who loves fishing for the sake of fishing; a position summarized by Carlton (1975) as: 'recreational fishing is the ritual pursuit of pleasure associated with the experience'. This definition has now been superseded, with a change in demand for leisure activities. The sport is now highly developed and pursued by large numbers of people around the world, primarily for pleasure, but also for income generation and to supplement food supply, as exemplified by the following statistics.

- Amongst 22 European countries there are an estimated 21.3 million anglers, with an estimated expenditure on recreational fishing in 10 of the countries in Western Europe where data were available, in excess of US$10 billion (Cowx 1998b).
- In 1996, 18% of the US population 16 years of age and older, i.e. 35 million persons, exerted 514 million angler-days in fresh waters, expending US$38.0 billion (US Fish and Wildlife Service 1997).
- In Canada in 1995, 4.2 million anglers exerted 55.5 million days and caught over 254 million fishes while spending US$5.1 billion of which US$3.4 billion was directly associated with the

sport. Of these fishes some 113 million were retained (Department of Fisheries and Oceans, Canada, 1998).

- It is estimated that total recreational catch worldwide is of the order of 2 million tonnes, and represents an important source of animal protein in many developing countries (Coates 1995).

This chapter examines the status of recreational fishing around the world, mechanisms for assessing the status of recreational fisheries, current management methods for recreational fisheries, some of the issues and problems facing recreational fisheries, and future needs for maintaining the status of the subsector.

17.2 TYPES OF RECREATIONAL FISHING

Exploitation of living aquatic resources for recreational and leisure purposes has a long tradition in temperate countries. However, recreational fishing is now becoming common in some tropical countries. Brazil, the Great Lakes of Africa and southeast Asia, for instance, have witnessed huge diversification of interest towards recreational fishing to satisfy the needs of the growing urban populations, but also as a result of expansion in ecotourism linked to diversification of sport fishing opportunities. Many people are now targeting the major rivers and lakes of the world for large-sized fish (e.g. Nile perch, *Lates niloticus*, in Lake Victoria), or those species that put up a good fight, e.g. mahseer (*Tor tor*) species in the Himalayan rivers of the Indian subcontinent or tiger fish (*Hydrocynus vittatus*) in East African lakes. Similarly, interest in coastal game fisheries targeting marlin (*Makaira* spp.), sailfish (*Istiophorus* spp.), and other large species has exploded with the growing affluence of the 20th century (e.g. McGrath et al. 1997). Recreational fishing, however, comprises a diverse array of approaches, which can be broken down into exploitation of natural and enhanced fisheries for pleasure, competition or supplementing domestic food supply, both in the marine and freshwater environments.

17.2.1 Fishing gears

Most recreational fishing is carried out using rod and line, or a variation on the theme (Wilson 1999). In the past 30 years, the gears used by recreational fishers have developed out of all recognition, from traditional cane and glass fibre rods, towards the use of modern materials, such as carbon fibre, and technology such as echosounding to detect and catch fish. The line used nowadays is almost exclusively monofilament nylon, and hooks are baited with a diverse range of foods, both natural and artificial. The natural baits include maggots, meal paste, fish, worms or shrimp, although the more sophisticated anglers use a concoction of ingredients to improve the chances of catching fish. They may also use artificial flies and lures, particularly in game fisheries for salmon and trout (*Salmo* and *Oncorhynchus* spp.) or sailfish and marlin. These materials and methods have allowed the practitioner to increase the possibility of encountering and capturing fish, and to some extent have removed some of the skill of the sport (Wilson 1999).

In fresh waters, fishing is carried out from the bank, from small boats or wading in rivers or shallow lakes. Sea fishing is carried out both from the shore, on beaches and off rocky coastline, and from inshore and offshore boats, depending on the species being targeted.

Recreational fishing in some countries (e.g. Canada, Finland, Sweden, Eastern Europe) is practised with gears that were predominantly designed for commercial purposes, such as gill-nets and traps. Although classified as recreational fishing by the host countries, there is some debate as to the validity of the claims because considerable harvests of fish are removed in these fisheries, and in some cases they have contributed towards the demise of the fish stocks (e.g. Müller 1990; Gautman and Hicks 1999). Furthermore, regulations over the fishing activities have more in common with commercial than recreational fishing practices. Access and catch restrictions, are being used to regulate the salmonid sport fisheries of Canada (Walters and Cox 1999), which suggest that this is the case.

17.2.2 Recreational fishing classified by objective

According to the FAO (1997) definition, participants in recreational fishing do not depend directly on the fishery for employment, treating fishing more as a pastime. Exponents come from all levels of society, from juveniles through to the old age groups, but the type of fishing they participate in often reflects their social status. Game fishing, either in fresh or marine waters, for example, is usually dominated by the wealthier sectors of society coming from professional backgrounds because of the high costs of participation. This is particularly true of the salmon fisheries of northern Europe and the offshore marlin and sailfish fisheries throughout the world. Conversely, freshwater fishing for cyprinids and fishing off the shore was, and still is, a major participatory sport of the middle and working classes. Recreational fishers can be categorized according to the way they exploit the main target fish species, although care must be taken not to compartmentalize persons, because they often pursue more than one type of recreational fishing activity.

Leisure fishing

Angling for leisure remains one of the primary reasons for participating in the activity. Numerous studies confirm this point and consistently cite that a high percentage of fishermen go fishing to be able to relax in pleasant surroundings and are not necessarily bothered as to the quantity of their catch (e.g. Wolos 1991; Steffens and Winkel 1999). The majority of these prefer natural fisheries in urban and rural environments with an emphasis on enjoyment of nature, good fellowship and simple pleasures. Considerable numbers of people, for example approximately 30% of persons fishing in the UK, fish off beaches and rocky shores in pursuit of marine species such as codling (*Gadus morhua*), whiting (*Merlangius merlangus*) or bass (*Dicentrarchus labrax*), which feed or breed in coastal waters. These fish are eaten. Leisure anglers are not necessarily interested in catching large numbers of fish or specimen fish, although this is considered a bonus from the experience. In recent years, however, there has been a trend towards wanting to catch large numbers of fish. This is coupled with the decline in many natural fisheries, and movement away from classical leisure fishing venues around rivers and coasts to intensively stocked fisheries where big catches are guaranteed (North 2002).

Match fishing

Match fishing is the competitive pursuit of angling to catch the biggest weight of fish or the largest fish in a defined period of time. Fishermen either perform individually or form groups that compete according to a specified set of rules, usually defining the gear and bait to be used, and the species to be caught. Such fishing, although mainly practised in Europe and North America, is highly organized and culminates in international competitions and world championships. A small number of highly successful participants are able to earn considerable sums of money by winning competitions, or make a living by endorsing angling products, fishing venues or writing popular articles for the media. However, the majority compete for the prestige gained through winning.

Match fishing takes place in all types of waters, both natural and stocked. Competitors are usually assigned a fixed fishing station or peg when based from the shore or bank, but when fishing off a boat this can be randomly positioned to pursue the best catch. The premise underwriting match competitions from fixed stations is that there is potentially an equity of catches between stations, thus the winner is the person showing the greatest skill. Unfortunately this remains an anathema because fish are rarely randomly distributed in water bodies and drawing the best fishing station can have a major influence on the outcome of the competition.

Game fishing

The origins of recreational fishing probably stem from game fishing. It can be considered a ritualistic pursuit of fish species which put up a good fight. Target species in fresh waters typically include salmon and trout in temperate rivers, mahseer or tiger fish in tropical rivers and lakes, and marlin and sailfish in the sea. Proponents usually prefer to fly fish for salmon and trout, although artificial lures and natural baits are also used. In fresh waters, these types of fisheries are usually highly regulated for access because they command high economic and social values. Thus the participants tend to be from the higher income bracket of the population. Similarly, in the seas, the cost of pursuing this type of fishing activity from dedicated boats makes it the domain of the wealthy. Nevertheless, the contribution game fishing can make to the local economy in terms of indirect expenditure is immense (see Chapter 6.3).

Specimen and specialist anglers

A small proportion of anglers fish exclusively for one species or specimen-sized individuals, meaning larger fish of that species. Specimen fishermen use rod and line, and target species that are long-lived and grow to a big size, for example carp (*Cyprinus carpio*) or pike (*Esox lucius*). Most specialist fisheries are privately owned by individuals and syndicates who manage them for the particular species in demand. They are particularly common in Western Europe, UK and France, and attract anglers from long distances with the prospect of catching large fishes. Because fishermen want to improve on the size of fish caught, all fish are carefully handled and returned to the water after capture. These fisheries are more and more being managed by stocking few, large fish in anticipation that they will grow to a specimen size quickly.

Domestic consumption

Although recreational fishing is considered a leisure activity, a significant proportion of the catch is removed for human consumption. This is particularly true of freshwater game fishing, where the catch is considered to have high organoleptic qualities, especially salmon and trout in North America and Scandinavia. However, in many countries of the world, recreational fisheries play an important role in supplementing diets. In Eastern Europe, for example, carp is a traditional Christmas meal and many larger specimens are retained towards the end of the year for this purpose. Similarly, in poorer countries the recreational catch supports domestic food supply. By contrast, recreational fishing for a variety of freshwater species in Nordic countries, with commercial gears such as gill-nets, is exclusively for consumption. Most fish caught from sea fisheries are also retained for consumption. The contribution to the landings from these fisheries is rarely accounted for in national statistics. However, the fishing effort exerted by recreational fisheries can be massive, and it can account for a significant component of the catch for a country. For example, Mike and Cowx (1996) estimated that the recreational boat catch of the Trinidadian inshore fishery was equivalent to 11% of the total commercial catch, whilst the contribution of recreational fishers to the total landings in the marine inshore fishery of South Africa was over 30% (Cockcroft et al. 2000). In these cases the fish are often sold in local markets and compete directly with the commercial fisheries.

17.2.3 Recreational fisheries classified by location

Natural freshwater fisheries

Natural fisheries are those in which the productivity of the fishery or water body is not enhanced in any way. The proliferation of the stocks, and hence availability of fish for capture, relies entirely on natural reproduction and feeding. Such fisheries are bound by the strict limits of the productivity of the water in which they are practised, and by the reproductive potential of the target stock. The productivity of the water is determined by geomorphological considerations, including the nature of the bedrock in the basin, the quantity and type of effluent discharges from human activities, the depth and shoreline development of a lake, the extent of flooding in rivers and the residence time in reservoirs. Reproductive potential is regulated by biotic factors such as abundance of the species, the degree to which the population is harvested, and competition and predation from other species (Fig. 17.1). It may also be influenced by physical characteristics of the environment, such as the abundance of spawning substrates, temperature, the rate of drawdown in reservoirs or the extent of flooding in rivers.

These fisheries were traditionally the main target of recreational anglers because they supported good stocks of catchable fish and provided condi-

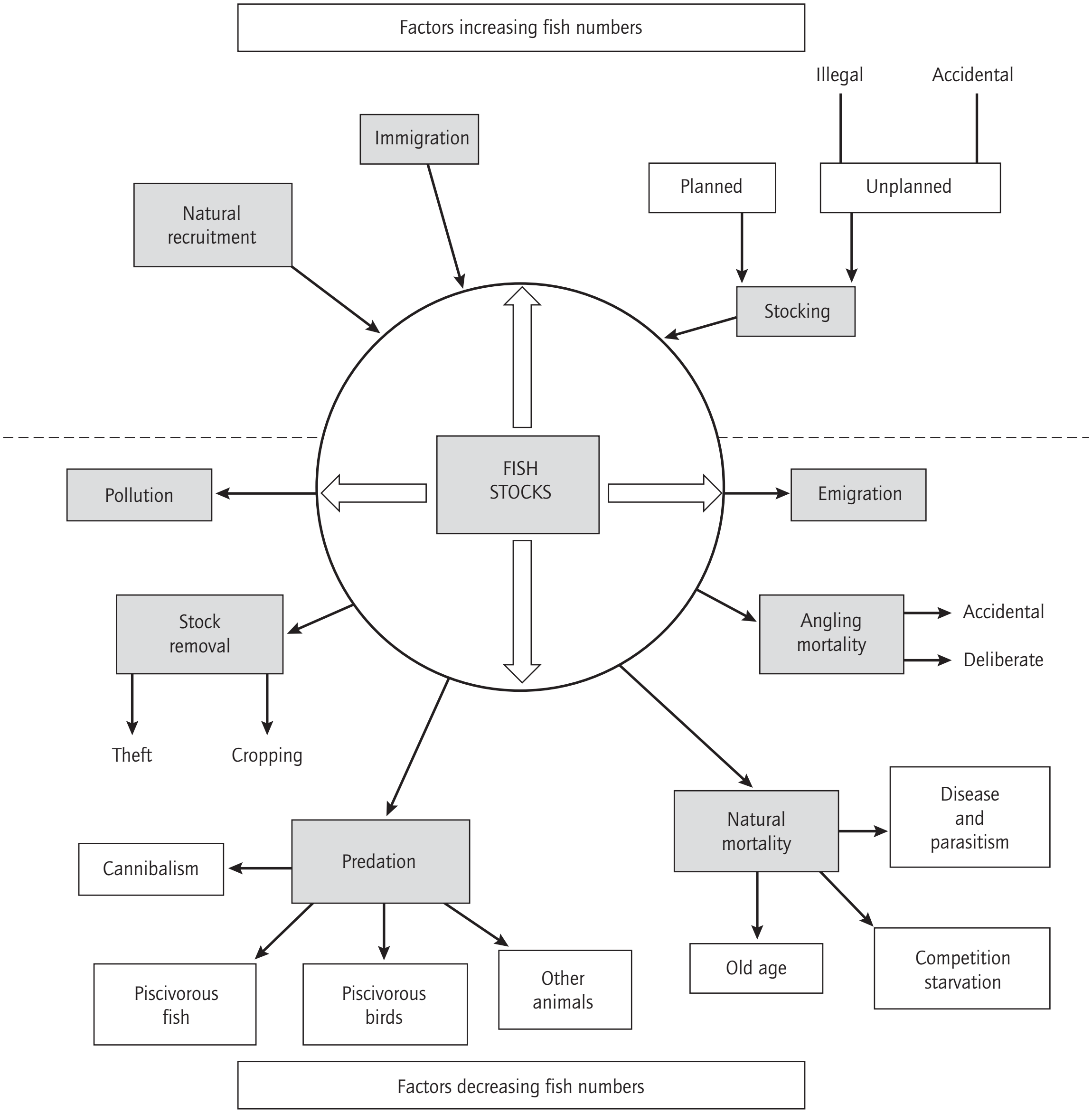

Fig. 17.1 Factors influencing the numbers and size of fish in a fishery. (Source: adapted from Cowx 2001.)

tions conducive to relaxation and enjoyment of nature, two of the main reasons why people go fishing (Wolos 1991; Roth et al. 2001). Unfortunately, in major industrial countries of Europe and North America, many of the waters supporting these fisheries have suffered from a legacy of pollution, habitat degradation, overfishing and flow manipulation (Cowx and Welcomme 1998), and they no longer satisfy the demands of anglers. Consequently, anglers have turned more and more to highly managed systems (see below and North 2002). Notwithstanding this, many good-quality natural fisheries still exist, especially game and coarse fisheries, but they are now considered less productive in terms of quality of catch and concerted action is needed to prevent further loss.

Natural fisheries are operated both on a catch-and-return basis, as in the coarse and centrachid fisheries of Western Europe and North America respectively, and on removal of part or all of the catch, for example game fisheries in North America and Europe and carp fisheries in Eastern Europe. In catch-and-return fisheries, emphasis is orientated towards the welfare of the fish, in order to minimize fishing mortality and ensure that fish survive to be caught again, and to support the reproductive processes. In Western Europe the catch-and-release strategy often involves keeping the fish in a keep-net for extended periods of time until the fishing experience is complete (see 17.5.1). This is particularly true for match and leisure fishing for coarse fish. The catch-and-remove fisheries are managed to ensure sufficient fish escape capture to replenish the stocks.

Stocked freshwater fisheries

When the quality of the fishing is below expectation or does not satisfy the demands of the anglers, fishery managers seek to intervene in the system to overcome the limiting factors. This problem arises principally because the fish stock is overexploited, the productivity of the water is naturally low, the habitat has been degraded or access to spawning areas has been compromised and recruitment is poor. The principal intervention used is the stocking of artificially reared fish to boost recruitment and production to overcome natural shortfalls. Stock enhancement can also be achieved through the transfer of fish from one water body, where the stock size is considered adequate or at too high a density, to another. The main types of fisheries operated on the basis of stocking are as follows.

1 *Put, grow and take*. The commonest type of stocked fishery is where juvenile fish are introduced to grow on natural foods. The adult fish are later captured and removed from the system by recreational fishermen for consumption. The extensive carp fisheries of Eastern Europe or the large-mouth bass (*Micropterus salmoides*) fisheries of North America fall into this category. These fisheries are usually established because reproductive success of the wild fish population(s) is impaired by there being too few mature fish or loss of spawning and nursery areas. This type of stocking is only possible if the natural productivity of the water body provides good potential for growth. Such fisheries are highly desirable to the managers and owners because the high cost of growing fish to table size in a fish farm is borne by the natural productivity of the water body.

2 *Put and take*. Put-and-take fisheries aim to provide the angler with a quality fishing experience by enhancing stocks on a regular basis. These fisheries are regularly stocked exclusively for the capture and removal of fish by anglers. They classically target rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus* spp.), although there is now considerable species diversification to meet the demands of anglers. Stocked fish are usually bred and grown on to a takeable size in a fish-farming facility and released for capture. Successful put-and-take fisheries monitor the catch rates of anglers and restock on a continuous basis, but in the best-run fisheries stocking occurs when the fishing success falls below an established threshold (North 1983). The time between release and capture is usually short, typically less than 4 weeks, although fishing pressure often increases around the time of stocking and many fish are removed within a few days of release. Put-and-take fisheries are practised in some natural waters, such as trout streams, but more normally are restricted to purpose-built ponds or reservoirs, often associated with a fish culture station (Templeton 1995; Flickinger et al. 1999). These types of fisheries are generally operated as commercial ventures, so are dependent on anglers fishing the water, and paying a fee for the fishing experience and removal of a number of fish for consumption. To prevent overfishing or to regulate successful anglers removing too many fish, most fisheries have a bag limit. In successful fisheries the density of fish stocked is usually high and scope for any natural production is limited.

3 *Put, catch and return*. There is an increasing trend in recreational catch-and-return fisheries in Europe and North America to enhance the fish stocks to increase angler satisfaction and demand (Kohler and Hubert 1999; North 2002). These types of fisheries either: manipulate the fish communities to provide specialist fisheries for a particular target species; stock specimen fish; or intensively stock water bodies of target species well above that sustainable by natural productivity. The fisheries are intensively managed to maintain the desired stocks and ensure angling success is high. However, there is now considerable debate over the general welfare of the fish in intensively stocked fisheries because the fish are living in highly stressed conditions and exposed to the further stresses from capture, handling and release (Section 17.5.1). Specialist and specimen fisheries are, by contrast, considered acceptable because they are usually stocked at low density and cater for anglers who seek to catch large individual fish or specific species. They are also highly managed and often have restricted access.

Sea fisheries

Recreational sea fishing almost exclusively targets wild stocks in usually one of three ways: rocky shore fishing or beach casting; inshore line fishing; and offshore sport/game fishing for oceanic species. In some Scandinavian countries, recreational fishermen also use commercial gears such as gill-nets to catch fish, although this, as in fresh waters (Section 17.2.1), is more akin to subsistence fishing than recreational angling. With the exception of game fishing, the catch is usually for domestic consumption, although some competitions are organized. Sea fishing is often highly seasonal, exploiting the migratory patterns of species as they move inshore to breed or feed. This is mainly an open-access and unregulated activity, with the exception of a few gear restrictions. However, in recent years access restrictions and closed seasons have been imposed on certain fisheries which exhibit signs of overfishing (Gautman and Hicks 1999).

17.3 RECREATIONAL FISHERY ASSESSMENT METHODS

An integral part of the management of recreational fisheries is an understanding of the status of the resources in terms of fish stock structure, the value of fishing to the anglers, and to the local and regional economies, and, perhaps most importantly, of end-user satisfaction. This information is required both to formulate management measures and to assess the impact of management policy on the fishery performance. For exploited natural stocks, annual assessment of the stock status through catch-and-effort sampling appears acceptable, whereas put-and-take fisheries need weekly monitoring for angler satisfaction and stock depletion, so that management can respond quickly to any measured deterioration in either characteristic. For unexploited stocks in catch-and-return fisheries, trends are usually the main requirement.

Surveys to collect this type of information are generally constrained by money and manpower, and the degree of precision required in the information collected to meet management objectives (Cowx 1996). Problems are also encountered in the assessment of the economic status because of the difficulty of putting value on non-tangible resources. Several methods have now been developed to overcome these problems and provide baseline information on which management policy can be formulated.

Two distinct strategies for obtaining the information from anglers are used (Malvestuto 1983; Pollock et al. 1994; Cowx 1996):

- off-site event recall methods such as log books, mail questionnaires and phone surveys, which require the angler to evaluate the fishing experience some time after the event (e.g. Axford 1991; Beaumont et al. 1991; Bunt 1991; Churchward and Hickley 1991; Cowx 1991; Gardiner 1991; Gerard and Timmermans 1991; O'Hara and Williams 1991; Small 1991).
- on-site intercept methods such as aerial count methods, access point methods and roving creel methods, which collect information at the time of the event or immediately following it (e.g. Cryer and MacLean 1991; Gerard and Timmermans 1991; Malvestuto 1991; Pawson 1991).

Information collected by either method can include total weight of catch, weight or number of each fish species caught, time of day spent fishing, duration of fishing experience in terms of number of man-hours or other unit of effort, location of fishing and method of fishing. These data are used to determine the catch per unit of effort, usually represented as g man-hr^{-1}, fish man-hr^{-1} or similar measure. In addition, the survey methods can be used to collect information to determine the value of the fishery, using contingent valuation methodologies or other similar techniques (Pollock et al. 1994; Gautam and Steinback 1998; Postle and Moore 1998). However, it should be recognized that each approach has distinct advantages and biases over the other (see Table 17.1).

Off-site event recall methods tend to make use of lists of names of anglers, perhaps those in receipt of a fishing licence or permit, or boat licence, from which a random sample is selected to provide the necessary information, or they make use of obligatory returns of information linked to the issuing of licences. Mail and telephone surveys tend to be low cost and can have a regional coverage, but suffer from biases associated with non-response, vagaries of recall and memory, angling prestige and enthusiasm (Bunt 1991; Churchward and Hickley 1991; Dekker 1991; Gardiner 1991; Löffler 1991; Small 1991).

Dependence on lists of names also has biases: for example, not all anglers may be required to have licences, especially when sea fishing. To obtain acceptable data, the recall time interval should be kept to a minimum (<2 months preferred) and the questions need to be simple. If at all possible, the participants should be encouraged to complete the questionnaires at the time of the fishing experience, i.e. set up a fishing diary or logbook, although these too can be biased. Licence returns overcome some of the problems of random sampling but, despite statutory obligations, still suffer from non-response and recall biases. The non-response can be minimized by sending out reminders, but rarely is a 100% return rate achieved.

Table 17.1 Advantages and disadvantages associated with event recall and on-site intercept approaches for recreational fishery assessment.

Approach	Advantages	Disadvantages
Event recall methods	Low cost Regional coverage Immediate response (phone surveys)	Non-response Recall bias Digit bias Prestige bias Avidity bias
On-site intercept methods	Minimization of response biases Visual assessment of information exchange	High cost Biases based on survey design Interruption of angling experience

On-site intercept methods minimize the biases associated with event recall methods because they have a high response rate, they allow direct information exchange which can be confirmed by the interviewer, and anglers are not required to recall catch information. Disadvantages are the high cost per angler interview, difficulties in contacting a representative sample of anglers in a large geographical area, and reliance on a random stratified survey design, similar to that used for commercial fisheries, which may introduce biases associated with the estimator used. With roving surveys, the interviewer contacts the anglers as he moves around the fishing area along a predetermined route. The primary weakness of roving survey methods is that catch-and-effort information is based on incomplete rather than complete fishing trips, because anglers are contacted while they are fishing. In access point surveys, the interviewer is stationed at a strategic site such as a car park, jetty or boat landing beach used by anglers, preferably at the end of the fishing trip. The surveyor then randomly selects a predetermined number of anglers for questioning. The access point survey is ideal where the anglers must leave via a small number of points or where anglers report their catches at a central location. Although the complexity of the questions in on-site methods can be increased it should not be so great as to interfere with the angler experience. On-site methods can also be combined with aerial surveys, boat counts or bank angler counts to determine the total fishing effort and assess the actual exploitation patterns.

To ensure accuracy of the data retrieval, several important aspects should be addressed (Cowx 2001).

- Event recall methods must be validated with respect to the accuracy of the responses. Calibration with on-site survey data is one option.
- On-site intercept methods must be evaluated with respect to field techniques and design efficiency. New design alternatives must be developed, particularly with respect to obtaining precise estimates of catch rate.
- Indices which truly reflect the quality of the fishery from the angler's point of view must be developed, and used for justification and evaluation of management programmes. Lorenz curves, which quantify the probability of catching a certain number or weight of fish (O'Hara and Williams 1991), or the utility-per-recruit concept of Die et al. (1988), which uses an objective measure of angler satisfaction in place of catch weight in the usual yield-per-recruit model (Shepherd and Pope, Chapter 8, this volume), are good examples of this approach.
- The use of catch per unit effort (CPUE) as an index of change in stock abundance for recreational resources must be evaluated, particularly for those fisheries where fluctuations in stock size and high rates of exploitation are critical factors related to efficient functioning and the economic value of the fishery (put-and-take systems).

Many of the methods introduced above traditionally focus on estimation of the biological parameters, i.e. catch, effort and CPUE related to fishery. However, in recent years there has been an increasing need for valuation of the economic and social benefits of recreational fisheries to justify their position in a wider multiple resource-user environment (Cowx 1998b). As already indicated, this is a complex problem because it is difficult to put value on non-tangible recreational resources. Nevertheless several approaches, which can be built into the traditional angler intercept and event recall methods, have been developed to overcome these problems (Table 17.2).

Reviews on how to use these approaches are given by Pollock et al. (1994) and Weithman (1999). However, in general terms, the gross economic value of a recreational fishery is composed of: (1) explicit costs of local, regional and national services which contribute directly to the angler; (2) total angler expenditures directed towards the fishery, derived from licence and permit fees, equipment and travel costs; (3) the value over and above the actual expenditures that anglers would be willing to spend to fish; and (4) the additional value based on non-users' willingness to pay to preserve the fishery (Malvestuto 1983; Weithman 1999). On-site intercept and event recall methods can be used to provide estimates of average expenditure per angler-trip or over a defined period, by asking the appropriate questions. The same surveys can be used to provide information on the net

Table 17.2 Methods of assessing fishery benefits. (Source: after Weithman 1999.)

Benefit measurement	Approach
Non-monetary	
Social well-being	Angler survey on changes in a fishery
Psychophysical measures	Angler survey on aesthetic appeal
Multi-attribute choice approach	Angler survey on a variety of fishery characteristics
Attitude measures	Angler survey of factors that affect the quality of fishing
Social impact assessment	Projection of changes that will likely result from a new policy
Monetary	
Economic impact assessment	Angler expenditure used as input for regional economic models
Economic value assessment	Angler expenditure used as input for travel cost or contingent valuation
Total economic valuation	Angler expenditure used as input for contingent valuation, plus non-consumptive user values
Combination	
Total value assessment	Comprehensive evaluation that combines non-monetary and monetary evaluations to determine social and economic values

willingness to pay, often defined as consumer surplus, using contingent valuation or travel cost methodologies (Pollock et al. 1994; Baker and Pierce 1997; Postle and Moore 1998). This will provide an economic value of angling to the region or the value individuals place on the fishery, and they can be used as persuasive arguments for the maintenance and improvement of the fishery.

17.4 MANAGEMENT OF RECREATIONAL FISHERIES

Recreational fisheries are underpinned by a complex interaction of physical, chemical and biological conditions, which need to be regulated in such a manner as to enhance the fishery output and maintain quality fishing (Fig. 17.1). Management of recreational fisheries is realized in three ways, targeting the fish, the fishery and the habitat (Table 17.3).

Table 17.3 Interventions used in the management of recreational fisheries.

Fish stock
Restocking to enhance stock
Introductions to increase species diversity
Culling to remove predators and pest species

Fishery
Closed seasons
Closed areas
Access rights
Gear restrictions
Harvesting size regulations

Habitat
Rehabilitation of habitat
Increasing fish habitat diversity
Improvement of water quality

17.4.1 Stock manipulation

Management of the fish population size or community structure is based on a variety of stock manipulation techniques (Fig. 17.1).

Stock enhancement

Stocking is probably the most widespread, and abused, management tool used in recreational inland fisheries today (Cowx 1998a). There is little evidence of successful enhancement of marine fish stocks through stocking (Howell et al. 1999), and thus it is a technique rarely considered for enhancing recreational marine fisheries. Most countries report stocking of freshwater fisheries as more conventional approaches to management have failed to control fisheries exploitation or reduction in stock biomass through environmental degradation. The importance of stocking to support recreational fisheries is demonstrated by the huge stocking programmes that take place each year (see Table 17.4), and the economic value of the activity was illustrated by Cowx and Godkin (2000), who estimated some US$90 million of fish were produced in aquaculture units in the European Union countries in 1997. This represents an estimated 7.6% of the value of inland fisheries and aquaculture production in these countries, and does not account for the value-added revenue generated by the fishing activity itself.

Unfortunately, this strategy to enhance the fish stocks is often used to respond to anglers' complaints that the fishing is poor or just to increase the fish stocks in general. Stocking in natural waters should aim to improve recruitment, bias fish assemblage structure to favoured species, or maintain productive species that would not breed naturally in the system (Cowx 1994a). However, all this should be carried out so that there is no impact on the indigenous fish populations (see Section 17.5.2). In man-made water bodies stocking is usually carried out to create fisheries which satisfy the general demand of the public, for example to create specialist fisheries for trout, carp or large-mouthed bass. Irrespective of the type of water body, the technique involves the injection of takeable-sized fish for easy capture in put-and-take fisheries, or a large number of juveniles which are intended to grow on to a large size and satisfy the demands of the angler.

There are a variety of strategies used to ensure the success of a stocking exercise in inland waters (Cowx 1994a). Explanation of these strategies is beyond the scope of this chapter, but issues that must be addressed are: sources of stocked fish; species to be stocked; stocking density; age and size of fish to be stocked; choice of season for stocking; acclimation of stocked fish; mechanism of stocking; potential interaction with wild fishes; transmission of parasites and disease; and genetic integrity of the wild stocks (see Cowx 1994a for details).

Increasing species diversity

One of the common complaints about recreational fisheries is poor diversity of species. To overcome this problem there has been considerable movement of fish from one water to another (translocations) or the introduction of exotic species throughout the world (Welcomme 1988, 1992, 1996; Cowx 1997, 1998a; also see Juanes et al., Chapter 12, Volume 1 and Section 17.5.2 for more discussion). The most commonly introduced or translocated species involve cyprinids, with 57 species put into European fresh waters, of which common carp is the most frequently involved; salmonids with rainbow trout, brook trout and

Table 17.4 Numbers of fish (millions) of different species stocked in fresh waters in North America and the European Union countries in 1998.

	Eggs	Fry	Fingerlings	Sub-adults	Total
United States and Canada					
Salmonidae	34 999	24 691	149 363	67 188	276 241
Warm-water sport fishes		24 581	112 523	4 030	141 134
Cool-water sport fishes (Percidae and Esocidae)	4 502	1 193 705	71 028	169	1 269 404
European Community					
Atlantic salmon	3 124	13 732	2 559	1 077	20 492
Salmonidae (all)					214 372
Non-salmonidae (coarse fishes)				210 675	210 675

brown trout being the most common and, finally, largemouth bass (*Micropterus salmoides*). All these species groups are to enhance sport fishing. Although the movement of fish is highly regulated in most countries, indiscriminate actions are commonplace and lead to introduction of diseases, loss of genetic integrity and species extinctions in the worst possible case (Cowx 1997, 1998a; Cowx and Godkin 2000). Introductions have also arisen because of release or escape of fish used as live bait for predatory species such as pike (Welcomme 1988; Cowx and Godkin 2000). Such releases form more than 1% of cases.

Elimination of unwanted species

Elimination of unwanted species that either compete with, or prey upon, target species is another tool often used in recreational inland fisheries. Cropping can either target excessive numbers of fish of a species or species group to allow the remainder to grow to a larger size, or can target predators, which are considered undesirable because they prey on the fish targeted by anglers. Cropping is a useful tool in fisheries that have a high stock density or biomass and the growth of the fish is poor. The culling of predators has been used with some success on fisheries where new species of predators have been introduced deliberately or accidentally and have caused the demise of the indigenous stocks. An example is the control of pike perch (*Stizostedion lucioperca*) in the Midlands of England (Smith et al. 1998). However, there is considerable debate over whether the method is inappropriate for controlling indigenous predator populations (see next section).

Predator control

Predator control is perhaps one of the most controversial methods of fishery management. It involves regulating the numbers of predators, usually fish or avian, to reduce predation pressure. The culling of piscivorous fish is a typical example of this approach, with many fisheries having a policy to kill major predators if they are caught. This technique has rarely proved successful as it can create an imbalance in the fishery, which becomes dominated by large numbers of small, often planktivorous, fish (Templeton 1995; Persson, Chapter 15, Volume 1; Kaiser and Jennings, Chapter 16, this volume). The removal of the predators can also reduce predation pressure on the faster growing and prolific breeding species, which in many cases may not be the target of the anglers, and can ultimately be a nuisance. Furthermore, fish predators often control their own numbers through cannibalism, and the removal of larger individuals from a population can leave many smaller conspecifics which have a great impact in terms of reduction in prey density. In marine ecosystems, there is evidence of mixed effects of reductions in predatory fishes (Kaiser and Jennings, Chapter 16, this volume).

Of more concern at present is the control of fish-eating birds, particularly cormorants (*Phalacrocorax* sp.) and herons (*Ardea* sp.). In recent years, their numbers have increased dramatically at a rate of around 16% p.a. to about 150 000 pairs between 1978 and 1993 around inland waters in Europe and North America (Russell et al. 1996). They are perceived to cause considerable damage to fish stocks. Whilst there is no doubt they can cause damage to intensively stocked still-water fisheries, there is still debate over the damage to other natural freshwater fisheries (Feltham et al. 1999). For example, at least 57% of carp stocked into a still-water fishery near London were consumed over a period of 4 weeks (Feltham et al. 1999) and up to 75% of stocks can be removed from fish farms by cormorants (Russell et al. 1996). Consequently, there are calls for control of birds, especially cormorants, by fisheries managers and anglers, but this is hotly contested by conservationists (Russell et al. 1996). Notwithstanding, control measures for cormorants, such as using scaring noise or visual methods or shooting small numbers of birds, have proved rather ineffective, and the creation of refuge habitats and stocking with larger fish at times when the birds are foraging off the coast are recommended to minimize the impact (McKay et al. 1999).

17.4.2 Fishery regulations

In addition to direct intervention on the fish populations/communities, recreational fisheries also require the introduction and enforcement of various regulatory constraints to prevent overexploitation of the fishery and maintenance of a suitable stock structure. The various measures that are commonly operated in recreational fisheries through Europe (Hickley et al. 1995) and North America (Noble and Jones 1999), and their expected outcome, are summarized in Table 17.5. These regulations are similar to those imposed on major commercial fisheries but the scale and intensity are usually less draconian. Elsewhere in the world, regulations are mainly restricted to the gear that can be used.

Closed seasons are imposed to protect the fish mainly during the breeding season or the early development stages. This includes protection of migratory fish as they move towards spawning or feeding grounds, especially at places where they will be particularly vulnerable to heavy exploitation, and provides a respite for fish to spawn unimpeded (Noble and Jones 1999). In practice this action has been extended to protect stocks which are heavily exploited and thus restrict catch, for example chinook salmon (*Oncorhynchus tshawytscha*) off the west coast of Canada (Walters and Cox 1999). This restriction has often come under heavy criticism because closed seasons are wrongly timed and do not protect the fish when they are most vulnerable, because the season does not always coincide with the reproductive period, as is typically observed in the UK (Hickley et al. 1995). Furthermore, there is no evidence that closed seasons lead to better recruitment within the fish populations, as other biotic and abiotic factors appear to have a stronger influence on this process (Mills and Mann 1985).

Closed areas are designed to protect stocks directly by denying access to the angler. These can range from sanctuary areas, where fishing is prohibited to protect vulnerable life stages or species of fish (e.g. Polunin, Chapter 14, this volume), to restrictions on fishing in areas where the fish are particularly vulnerable to exploitation, such as the aggregation of salmon below weirs and waterfalls during their upstream migration. For example, Ontario, Canada, has used seasonal sanctuaries to restrict anglers from large-mouth bass spawning areas for over 60 years (Noble and Jones 1999). Management of put-and-take fisheries may include closed areas where stocking takes place to prevent anglers removing fish when they are highly vulnerable immediately after they have been stocked.

Where the catch is removed for consumption, limits are frequently placed on total catch to prevent overexploitation and conserve the spawning stock. Such restrictions allow for the sharing of the catch when stocks are low or under intense fishing pressure. Bag limits are commonly applied in migratory game and put-and-take fisheries to ensure equity of catch. An alternative to the bag limit is catch and release (see Section 18.2.3) where restric-

Table 17.5 Techniques for regulating angling effort and the ecological requirements of the fish stocks that are addressed.

Regulatory technique	Population size	Broodstock protection	Undisturbed spawning	Free passage	Fish welfare
Closed areas	*	*		*	
Closed season		*	*	*	*
Catch limit	*				
Fishing pressure	*	*			
Type of gear					*
Size of fish	*	*			*

tions are placed on catch and all fish must be released back to the water. However, for this action to be successful it is important that proper procedures are followed with regard to playing, handling and releasing of fish. A combination of both catch restrictions and release is often employed so that the angler can still enjoy the experience if fishing is good but he has reached the bag limit.

Gear restrictions are used to reduce exploitation of populations by influencing the efficiency of the fishing method, the species caught or the size of fish caught (Misund et al., Chapter 2, this volume). There is also the requirement to protect individual fish by reducing any stress and physical damage associated with being caught and held in keep-nets, if the intention is to return them alive. In some cases, angling may still impose physiological costs on the fish, even if the fish are released (Forsgren et al., Chapter 10, Volume 1). It is necessary to base the regulations on sound information on the life histories and effectiveness of different angling techniques, but this information is rarely available. In recreational fisheries, angling is often restricted to hook-and-line fishing practices. Commercial gears, such as nets and traps, are rarely used except in countries where recreational fishing has more in common with subsistence fishing and provides food for consumption.

The final regulatory mechanism commonly used is limitation on the size of fish that can be taken. Restrictions of the size of fish that can be removed for consumption are commonplace in commercial fisheries and are equally applicable to recreational fisheries. The restriction is designed to ensure all immature fish are returned to the water to allow a self-sustaining population to persist. This is sometimes supported by restricting retention of larger mature individuals to allow spawning escapement, thus creating what is termed a ‘slot size’ for fish that may be retained. These restrictions generally refer to salmonid fisheries in Europe (Templeton 1995) and North America, and work especially well where harvest is high and recruitment low (Noble and Jones 1999). For size limitations to work, they must be based on sound information about population size structure, size at sexual maturity and natural mortality rates. In addition, problems may arise because too little is known about post-release mortality (e.g. Bettoli and Osborne 1998; Cooke et al. 2000; also see Section 17.5.1).

17.4.3 Habitat management

Fisheries managers use habitat management techniques to improve access to, and quality of, fishing, improve degraded habitats and increase the production potential of the fishery. The following are some of the main actions used: construction of groynes and fishing platforms; creation of fishing pools; raising of water level using small dams, cutting off access to spawning streams to control recruitment; blocking of outflows (usually with some kind of screen) to prevent stocked fish escaping; removal of natural barriers to fish migration such as waterfalls; provision of fish ladders; addition of fertilizers; liming; clearance of aquatic weeds by herbicides or the use of grass carp; and cutting of bankside vegetation including trees (see Cowx and Welcomme 1998 for details). All these are designed to improve the fishing experience and if carried out in a sympathetic manner will enhance the status of the fishery.

Engineering of the environment to improve levels of reproduction, shelter, food resources and vital habitat is a tool which deserves considerably more attention. It is a long-term solution to improving fish stocks, but is expensive, and unless carried out correctly can cause further degradation of the habitat (Cowx and Welcomme 1998). It is recommended that full consultation with water resource managers and environmental experts is made before any action is taken, to avoid undesirable responses.

17.5 ISSUES RELATING TO THE DEVELOPMENT OF RECREATIONAL FISHERIES

Despite the importance of recreational fisheries worldwide, there is a general perception that natural fisheries have undergone major, often adverse, changes in recent years. If recreational fisheries are to be sustained and developed for future generations, there are a number of issues that need resolution. These can be divided into three main categories relating to: (1) angling practises *per se*; (2) stock enhancement activities, which are potentially damaging to the aquatic ecosystem (Maitland 1995); and (3) cross-sectoral interactions.

17.5.1 Angling practices

Disturbance and damage. Angling, although essentially a quiet and often solitary activity, can result in disturbance to wildlife. Commonly, waterfowl, and coastal and wetland birds, many of which are now rare, are liable to disturbance if access of anglers to waters or shoreline is uncontrolled (Cryer et al. 1987b). Most damage is done at the nesting time, when birds are disrupted on their nests or prevented from gaining access to their nests (Maitland and Lyle 1992). There are also many mammals commonly found associated with the rivers and lakes, most of which are shy, such as the otter (*Lutra lutra*), and sensitive to disturbance. In addition they prefer secure places to rear their young (Jefferies 1987). Closed seasons or protected areas are designed to minimize these impacts, but problems still persist.

Disturbance is also caused by noise and pollution, such as oil leaks from boat engines where fishing takes place from a boat. Boat wakes can also cause erosion of river banks, especially where movements are excessive and uncontrolled (Pygott et al. 1990; Ellis 1998). This leads to collapse of banks, loss of riparian vegetation, and, on a more subtle level, change of littoral water temperatures, which directly affects juvenile fish growth and recruitment (Hodgson and Eaton 2000).

Habitat management. Anglers also cause physical damage to the habitat, especially riparian vegetation, to gain access to the water. This can lead to loss of sensitive wetland flora and fauna if left uncontrolled and can damage the integrity of the fishery (Swales and O'Hara 1983; Cowx 1994b). Other management practices, as described in Section 17.4.2, can also be damaging; therefore to minimize any problems they should be carefully planned, taking into account wider environmental considerations (Cowx and Welcomme 1998).

Litter. Angling, like other human activities, creates litter, including everyday items such as drink cans, polythene bags and paper cartons. Angling litter is, however, characterized by the inclusion of items such as discarded bait containers, lead shot, nylon line and fish hooks (Cryer et al. 1987a). The latter, which are either discarded unintentionally or lost inadvertently during angling, are particularly damaging, because birds and other animal life become entangled. Lead shot has been implicated in the decline of bird species such as swans (*Cygnus olor*), because they inadvertently ingest discarded items when feeding. This problem has largely been addressed through the introduction of non-lead alternatives in angling.

Groundbaiting. The practice of groundbaiting with cereals, maggots or other bait is commonly practised in Europe and North America to attract fish to the hook. When used excessively, it can lead to a deterioration in water quality (Cryer and Edwards 1987; Edwards 1990), increase phosphorus loading (Edwards and Fouracre 1983), and lead to a substantial reduction in benthic fauna (Cryer and Edwards 1987). In many places this practice is now discouraged to minimize the problems.

There is a surprising lack of information on the ways in which stocked systems function. The few data sets that exist (see Cowx 1998a for examples) show interplay of two main variables: area of the stocked system and stocking rates. They indicate that the output of stocking is highly variable and that in the majority of cases stocking does not achieve any major increase in fish production or yield (Cowx 1998a). Indeed, anecdotal evidence suggests that the majority of stocking in rivers to enhance fish populations is of marginal value. The notable exceptions are the stocking of migratory salmonids, especially where the river has been heavily degraded, such as in Sweden, or the polluted rivers of Western Europe, such as the Rhine and the Thames, once water quality had been improved. Improvements in catches of non-migratory salmonids have been achieved by stocking rainbow trout or brown trout, but these results tend to be short term because the recruitment bottleneck has not been removed or, as in the case of rainbow trout, the species does not breed successfully in European conditions.

The stocking of rivers with cyprinids has achieved little success, considering the large numbers that have been introduced. For example, after reviewing over 50 years of stocking activity in the lower Welsh Dee, Pearce (1983) concluded that 'stocking on the Dee would not appear to have been successful, only extremely limited short-term and scarcely any long-term benefits to angling or stock recruitment have resulted'. This is despite there having been some 76 stocking events over the study period, involving approximately 400 000 fish with, typically, two or three species being used on each occasion.

The stocking of still waters exhibits the opposite outcome, especially when stocked with robust species like rainbow trout and carp. These have been highly successful and constitute fishery enhancement in a greater proportion of cases. For example, the numerous put-and-take and catch-and-return fisheries found throughout Europe are based on this premise, and they have proved highly successful. Intensive carp fisheries and numerous other cyprinid and specialist fisheries are supported in the same way. However, stocking is not always successful, and the few reported examples of where attempts have been made to support commercial fisheries based on stocking suggest these are not worthwhile (Salojärvi and Mutenia 1994; Löffler 1998).

Animal welfare. There is growing concern that the holding of fish at high density in keep-nets, coupled with the hooking, playing and handling of the captured fish, causes unnecessary distress (Berg and Rösch 1998). Although the impact of catch and return on fish behaviour and populations is not well understood, there is evidence that fish do suffer from being caught and handled, procedures which have reduced recruitment success (e.g. Bettoli and Osborne 1998; Cooke et al. 2000). By contrast, recent studies on holding fish in keep-nets suggest that the fish are not unduly stressed until the density held is high (Pottinger 1997; Raat et al. 1997). Another argument being presented by environmental lobby groups is that fish may sustain damage, especially from barbed hooks, which increases their proneness to disease and feeding difficulties. As a consequence, some regions of Europe have now banned put-and-take fisheries, and the use of live bait and keep-nets (e.g. Norway, Netherlands and several Länder in Germany), and others are looking carefully at the issue (Wortley 1995). Whatever the outcome, anglers must be aware of animal welfare issues and continue to do everything possible to minimize the impact of the activity on fisheries and wildlife.

17.5.2 Stock enhancement

As previously indicated, stocking, which is used extensively to enhance fisheries, is frequently carried out with no due regard for the environmental or ecological consequences. Stocking can be damaging to the native stocks through competition, predation, loss of genetic integrity, or the spread of disease and parasites (Cowx 1994a, 1998a; Cowx and Godkin 2000). Unfortunately there is a relatively little information about the effects, including successes, of various stocking practices (Cowx 1998a). If the species is being released in high numbers then changes in the ecosystem are likely to occur via fish species interactions and food web dynamics (see Persson, Chapter 15, Volume 1, and Pauly and Christensen, Chapter 10, this volume, for commentary on ecosystem responses to perturbation). Vulnerable fish species, and aquatic flora and fauna, can be eliminated through predation, and the stocking, intended to enhance the fishery, can result in the opposite effect, including elimination of species (Cowx 1997). The loss of genetic integrity of the native stock, which is thought to have adapted to local environmental conditions over many years, is a major issue and is considered to be responsible for a decline of many fisheries, especially salmon stocks (Carvalho and Cross 1998).

The introduction of new species to promote angling diversity was common practice worldwide in the 1960s and 1970s (Welcomme 1988), but concerns over the impact of this activity and the implementation of tough regulations has restricted the practice in industrialized countries in recent years. Introductions, for example rainbow trout and largemouth bass, have proved successful in a number of cases but this has usually been at great cost, most often expressed through the demise of indigenous species or the spread of diseases (Cowx 1997, 1998a). Other introductions have been disastrous, with wholesale ecosystem change and elimination of species (Cowx 1997). With the recent decline in the status of many fisheries, there is renewed interest in species introductions. This should be prevented at all costs, and the causes of the deterioration in extant fisheries should be identified and where possible addressed. If a species is to be considered for introduction, it should be carried out under the auspices of the appropriate governmental organization and following guidelines such as those promoted by the United Nations Food and Agriculture Organization (FAO 1996), the International Council for the Exploration of the Seas (ICES 1988) or the European Inland Fisheries Advisory Committee (EIFAC, see Coates 1998).

In reality, stock enhancement practices are often carried out in response to angling pressure and do not address the underlying problems within the fishery, such as recruitment bottlenecks or overfishing. In this respect stocking exercises are just short-term fixes and maintenance of stock size will require continuous intervention. It is thus not necessarily a desirable solution and alternative mechanisms should always be sought in the first instance. In addition, there are many examples where fish species have been illegally or accidentally introduced to increase the diversity of the target species of anglers. Finally, there are many cases of fish introductions stemming from the use of live bait for catching predators (Cowx 1998a). All these practices are potentially damaging to fisheries and have rarely proved successful (Cowx 1997). Indeed, they usually lead to the demise of the resident fish populations and further deterioration of the stocks. Anglers and managers alike need to be educated in the problems and consequences associated with stocking and introduction of fish, whether deliberate or accidental, and all efforts should be made to minimize this management practice.

17.5.3 Subsector interactions

One of the major constraints on the future development of recreational fisheries is from other users and occupiers of the water body. Such activity can be classified as cross-sectoral interactions and mostly arise from conflicts of interest. Within the development of any activity there is a need to consider the overall framework within which the activity exists (Fig. 17.2). There is no value in attempting to improve recreational fishing in a multi-user situation if cross-sectoral issues are not addressed. These issues arise from interactions: (1) between commercial and recreational fishing; (2) within recreation fishing groups; and (3) with other aquatic resource users. Furthermore, recreational

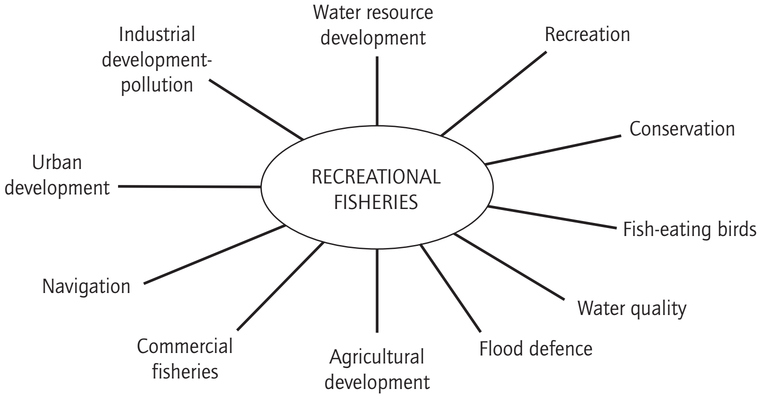

Fig. 17.2 Factors affecting recreational fisheries development.

fishing cannot be treated as an open-access activity because it is usually governed by considerable legislative and administrative protocols. This is often tied up with rights to fish, and regulations governing such issues at closed seasons, gear and catch restrictions, and licensing, most of which are set up to protect the fishing, but others to protect the environment. Access is also further complicated by social issues such as traditional-use rights and family obligations.

Commercial and recreation fishing interactions. Direct conflicts exist between commercial and recreational angling because they exploit the same resource base. The arguments usually relate to commercial fisheries depleting stocks through overfishing, and demands from the recreation sector to restrict commercial exploitation, although many studies indicate that commercial and recreational fisheries can coexist (see Hickley and Tompkins 1998 for examples), supplementing each other, creating an overall larger output than would have resulted from sport fishing only. When the commercial and recreational fisheries interfere with each other, the allocation of the harvest generally falls in favour of recreational fishing, as it is perceived to have an overall greater benefit to society (Cowx 2001).

Interactions between recreation fishing groups. There is also increasing conflict between groups of recreational fishermen, for instance between residents and non-residents (e.g. Morgan 1999). Reasons for this include: the loss of access to fishing waters resulting in crowding problems and overexploitation on the remaining waters; increased specialization among anglers, which puts pressure on attractive waters; and increased focus on tourist fishing in many areas, so introducing new angler groups to many districts, which may cause different conflicts of interest related to social and allocation controversies (Hickley and Tompkins 1998).

Cross-sectoral interactions. Perhaps the greatest threats to recreational fisheries come from outside the fisheries sector. Aquatic resources are subject to numerous anthropogenic perturbations, such as pollution discharge from agricultural, domestic and industrial sources, eutrophication, acidification, afforestation, mineral extraction, damming for power generation and water supply, flood alleviation works, weirs, intakes, bridges and similar structures (Fig. 17.2; Petts 1984; Cowx and Welcomme 1998; Kohler and Hubert 1999). All of these activities have resulted in a shift in the status of the fisheries and a general decline in the yield. In these circumstances fisheries are not considered of sufficiently high priority or value, and thus suffer in the face of economically and socially higher priorities, for example agriculture, hydroelectric power production or flood prevention.

Problems relating to pollution are in the main being addressed in Western industrial countries, and waters that were once fishless or supported poor stocks are now recovering. Such water quality improvements are, however, rare in Third World countries, where the scenario remains one of continued environmental degradation and consequent demise of the fisheries. Notwithstanding, water quality improvements do not always lead to a desirable outcome in terms of fishery status. The cleaning up of water bodies often results in reduced nutrient input and the loss of productivity, which has a knock-on effect on the fish community structure and stock size. This results in a change in the catch composition and reduction in catches, which is quickly followed by complaints from anglers (Cowx 1991).

Abstraction of surface or ground water, or the impoundment of rivers, may also damage fisheries through reduced flows downstream of reservoirs, the interruption of migratory pathways and the isolation and drowning of spawning and rearing areas. Conversely, reservoirs may provide attractive fishing opportunities, especially when intensively managed. Resolution of the conflicts caused by the structures is difficult and costly because of the high social and economic value of water resource schemes.

Interactions between other recreational uses of water, as well as recreation in the vicinity of water bodies, are also sources of conflict. The following pursuits can impact on recreational fisheries: bird watching, cycling, motor boating, canoeing, cruising, rowing, sailing, diving, swimming and bathing, water-skiing, wind surfing, water bikes and wild fowling. The problems arise from disturbance of fish, noise, litter, the loss of access to the water body and general disruption of the angling experience (for examples see Pygott et al. 1990; Ellis 1998; and Gerard 1999).

17.6 VALUE

From the previous section, it should be recognized that recreational fishing activities and development in a multiple-user environment are fraught with problems. Fisheries are often considered marginal activities because the value of the resource is usually ill defined and poorly represented from an economic and social perspective. Fisheries are traditionally managed based on the quality of the fishing experience, whereby the managers use simple techniques such as stocking to maintain fishery quality. However, few recreational fisheries are managed from an economic perspective, and this is borne out by the paucity of information on the economic value of such fisheries (e.g. Radford 1984; Whelan and Whelan 1986; Kennedy and Crozier 1997; Peirson et al. 2001). Consequently, fisheries are given low priority in any consultation process and it is difficult to attract investment or credit for development of a fishery.

To overcome this problem there is an urgent need to provide accurate social and economic valuation of recreational fishing (Aas and Ditton 1998) for justification of its position in conflicts between several users. There are various direct methods of valuing a fishery, such as financial and cost–benefit analysis (e.g. Kennedy and Crozier 1997). Alternative indirect methods such as contingency valuation analysis have also been used (e.g. Baker and Pierce 1997; Postle and Moore 1998; Gautam and Steinback 1998). However, in most cases these methods rarely give a true economic value to the fishery because they are based on the willingness of the end-user to pay for the fishing experience and do not account for the value of fishing rights and access rights. If recreational fisheries are to be preserved in the future, it is essential that more appropriate techniques are developed to provide sound economic valuation of the fisheries.

Furthermore, increasing pressures on aquatic resources dictate that fisheries can no longer be treated in isolation, and an integrated approach to aquatic resource management is required (Cowx 1998b). Consequently, the way forward for the management of recreational fisheries must be as a stakeholder in the wider resource-user domain. It is essential that the fisheries are well represented in any decision making and that their true value is promoted to the full.

17.7 CONCLUSIONS

Increasing pressures on aquatic resources dictate that fisheries can no longer be treated in isolation that and an integrated approach to aquatic resource management is required (Cowx 1998b). As shown in this chapter, the well-being of any recreational fishery is being constantly eroded, not only by exploitation of the fish directly but also through degradation of their habitat. Inland waters in heavily populated areas have to serve the needs of water supply, waste water and sewerage disposal, canoeists, sailors, bird watchers, recreational fishers and those who just like to walk along canals, rivers and lakes. In addition, the demands for sustainable use of the environment that grew out of the Rio conference of 1992 have put emphasis on the need not only to manage exploited resources but also to promote biodiversity. How the conflicts of interest between these various interests are resolved must depend on involving all stakeholders in the management process. In Britain, the Environment Agency consults widely over conservation and management plans. In the US similar stakeholder involvement exists, but in many parts of the world there is still little integration between the different demands placed on waters exploited by recreational fishers. Integration and cooperation will be essential for their sustainable development.

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