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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

INTERACTIONS BETWEEN FISHES AND ZOOPLANKTON, WITH EMPHASIS ON AN EXOTIC CLADOCERAN, *DAPHNIA LUMHOLTZI*, IN LAKE TEXOMA, OKLAHOMA-TEXAS.

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

PHILIP W. LIENESCH

Norman, Oklahoma

1997

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300 North Zeeb Road
Ann Arbor, MI 48103

INTERACTIONS BETWEEN FISHES AND ZOOPLANKTON, WITH EMPHASIS ON AN EXOTIC CLADOCERAN, *DAPHNIA LUMHOLTZI*, IN LAKE TEXOMA, OKLAHOMA-TEXAS.

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

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PREFACE

This dissertation has been prepared as three separate chapters which will be submitted to refereed journals. The first two chapters have been prepared for the Canadian Journal of Fisheries and Aquatic Sciences. The last chapter has been prepared for the journal Environmental Biology of Fishes.

Acknowledgments

I would like to thank Moshe Gophen and Bill Matthews, both of whom have served as my major professor during some portion of my doctoral program. They both played integral roles in my development as limnologist and ichthyologist. My committee members, Bill Shelton, Jim Thompson, and Linda Wallace have helped guide me through my doctoral program and I have benefited greatly from their diverse perspectives. They have given their time generously, often when it was the one thing they could least afford to give.

Kirsten Work has played an integral role in my studies of *Menidia beryllina* predation on *Daphnia lumholtzi*. She was involved in the both field collections and performing the laboratory experiments. Chapters one and two have benefited greatly from her input.

I thank the University of Oklahoma Biological Station for awarding to me a Centennial Research Fellowship for four years and the OU Department of Zoology for providing a teaching assistantship for another two years. The OU Biological Station and the Loren G. Hill Fund provided additional financial support for my dissertation research.

I wish to thank my fellow graduate students for their support and camaraderie during the past six years. I need to give special thanks to Chris Taylor, for all of his advise and assistance in various projects. I feel very lucky to have had the pleasure of working with such an enthusiastic group of ecologists, aquatic and otherwise.

Finally, I need to thank my family for supporting me. They have never faltered in their encouragement of my continuing education.

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Abstract

In the early 1990's, *Daphnia lumholtzi,* an exotic cladoceran, invaded Lake Texoma, OK-TX. This species is large and has a large helmet which has been proposed to defend the animal from fish predation. The introduction of a species into an ecosystem can either benefit, harm, or not affect other organisms in the system. I was interested in what affect this invading *Daphnia* would have on the most abundant planktivorous fish in the littoral zone of Lake Texoma. I examined the diet of *Menidia beryllina*, a zooplanktivorous atherinid fish, throughout one year and compared it to the available zooplankton to determine the fish's selectivity for different species of zooplankton (Chapter 1). Next I examined size specific differences in the selectivity of *Menidia beryllina* with a laboratory experiment and tested the results with data collected from Lake Texoma (Chapter 2). I also examined the effects of daily environmental variability on the abundance of fishes and zooplankton in the littoral zone of Lake Texoma (Chapter 3).

Menidia beryllina do utilize the invading cladoceran, *Daphnia lumholtzi*, as an additional food source. The increase in *D. lumholtzi* abundance during the middle of the summer, a period when native zooplankton are scarce, makes it an important food source for *M. beryllina* during this time. This also corresponds to the period when young-of-the-year *M. beryllina* are abundant. The large spines on *D. lumholtzi* have been shown to afford the animal protection from predation by small fishes. Although large *M. beryllina* are size selective planktivores, small *Menidia beryllina* selectively feed on the smaller size classes of *D. lumholtzi.*

The interaction of fishes and zooplankton is dependent on the spatial distribution of the animals in the environment. I measured the daily abundances of fish and zooplantkon in the littoral zone of Lake Texoma and tried to correlate them with daily abiotic variables. None of the variables measure explained much of the variation observed in daily zooplantkon abundances. Fish responded most strongly to changes in wind related variables, especially wave height. specific responses to the wave height were probably related to availability to food and avoidance of turbulence and predators.

Utilization of an Exotic Cladoceran, *Daphnia lumholtzi*, and Native Zooplankton by *Menidia beryllina* in Lake Texoma, Oklahoma-Texas.

Philip W. Lienesch and Moshe Gophen

Abstract

In the early 1990's, Lake Texoma was invaded by *Daphnia lumholtzi*, a large, spiny, exotic cladoceran. We examined the utilization of *D. lumholtzi* by inland silversides, *Menidia beryllina*, the dominant zooplanktivorous fish in the reservoir. We examined *M. beryllina* stomach contents and zooplankton availability at three shoreline sites on 17 dates from April 1994 to April 1995. *Daphnia lumholtzi* was most abundant after the native population of zooplankton declined in early summer. *Menidia beryllina* selected the largest zooplankton taxa available. *Menidia beryllina* selectively preyed on *D. lumholtzi* but appeared to prefer the large native zooplankton when they were present. *Daphnia lumholtzi* was an important prey item for *M. beryllina* in early to mid-summer when large native zooplankton were scarce. We conclude that the addition of *Daphnia lumholtzi* to the Lake Texoma zooplankton assemblage will benefit zooplanktivorous fishes by increasing foraging opportunities during a time of low prey availability.

Introduction

North America has been invaded by many non-native aquatic plants and animals (Mills et al. 1994; Mooney and Drake 1986). Although many organisms, such as plants and fish, are intentionally introduced, others are released accidentally and their arrival often goes unnoticed (Welcomme 1986; Mills et al. 1994). Invertebrate introductions usually have occurred unintentionally, but their effects on ecosystems may be extreme (Lasenby et al. 1986; Mills et al. 1994; Ram and McMahon 1996). For example, the zebra mussel (*Dreissena polymorpha*), which was first found in the Great Lakes in the late 1980's, is expected to have severe impacts on native mussels as it expands its range (Williams et al. 1993; Schloesser et al. 1996). Jennings (1996) found that zebra mussel densities above 3000 m^{-2} could adversely affect survival and growth of fathead minnows, *Pimephales promelas*. Zebra mussel densities in nature can far exceed this level (MacIsaac 1996).

All introduced species have an effect on the systems they invade because they use resources that otherwise would be available to native species (Lehman 1991; Mills et al. 1994). When the zooplanktivorous spiny water flea (*Bythotrephes cederstroemi*) invaded Lake Michigan, it caused a decline of *Leptodora kindtii*, a native zooplanktivorous cladoceran (Lehman 1991). An invading species also can affect the species it eats (Brooks and Dodson, 1965; Rieman and Falter 1981; Baskin 1992). The introduction of the piscivorous Nile perch (*Lates nilotica*) in Lake Victoria, Africa, caused drastic declines of the native haplochromine fishes (Baskin 1992; Gophen et al. 1995). It is estimated that more than half of the lake's endemic species may have been driven to extinction since the introduction of the Nile Perch. Many invertebrate predators have caused changes in the zooplankton assemblage of the systems they invaded (Rieman and Falter 1981; Lehman and Caceres 1993).

Some organisms will have little effect on the ecosystems they invade. This may occur if the organism never attains large population sizes or utilizes habitats and food sources less used by the pre-existing members of the ecosystem. The introduction of the striped bass (*Morone saxatilis*) into Lake Texoma, Oklahoma-Texas, had minimal effects on the pre-existing population of black bass (*Micropterus spp.*) (Harper and Namminga 1986). Matthews et al. (1992) found that interaction (competition and predation) was minimal between the two groups due to habitat segregation.

Invading species not only affect competitors and prey, but also the species that may utilize it, or its competitors, as a food source. The influence of invading species on higher trophic levels has received much less attention than their effects on lower levels. We examined the effects of a large, exotic zooplankter, *Daphnia lumholtzi*, on a zooplanktivorous atherinid fish, the inland silverside (*Menidia beryllina*), in Lake Texoma, Oklahoma-Texas.

Daphnia lumholtzi (Sars) is a zooplankton species that is rapidly invading waters in North America (Havel et al. 1995). *Daphnia lumholtzi* (Anomopoda, Daphniidae) (Dodson and Frey 1991) is a large cladoceran, native to northeast Africa to southern Asia, and Australia (Benzie 1988; Havel and Hebert 1993). It was first identified in the U. S. from Fairfield Lake, Texas, in 1991 (Sorenson and Sterner 1992) and appears to be spreading throughout the southeast. It is now found from Arizona to Florida and has been reported as far north as Chicago (J. Havel, SW Missouri State University, Springfield, MO, U.S.A., personal communication).

Daphnia lumholtzi is a relatively large species with an elongate helmet and large tail spine. In Lake Texoma, its length can exceed 5 mm from the tip of the helmet to the tip of the tail spine but the body of the animal is usually less than 1.5 mm (Work, 1997). *Daphnia lumholtzi* is also characterized by a pair of lateral fornices from the base of the helmet and prominent denticles along the posterior edge of the carapace and along the tail spine (Sars 1885). The helmet and spines exhibit cyclomorphosis (Sorenson and Sterner 1992) and have been shown to be induced by the presence of fish (Tollrian 1994). Green (1967) noted that *D. lumholtzi* in areas of Lake Albert, Africa, with more planktivorous fish had larger spines than those in areas where plankivorous fish were rare. When brought into the laboratory, the helmet and tail spine are reduced after a few molts (Work and Gophen 1995). Sorenson and Sterner (1992) cultured *D. lumholtzi* for several generations and while the helmet was reduced, it was never lost.

Daphnia lumholtzi was first collected from Lake Texoma, Texas-Oklahoma, in 1991 (Work and Gophen 1995). It can reach very high densities (> 100 $\cdot$ liter^{-1}) during the summer, and is a major component of the zooplankton community during that time. Work and Gophen (1995) also found that the distribution of *D. lumholtzi* was primarily restricted to the upper portion of the Red River arm of Lake Texoma except in the summer months. Lake Texoma experiences an annual zooplankton decline in early summer (Matthews 1984). The density of zooplankton then remains low until the end of the summer when water temperatures decrease. *Daphnia lumholtzi* reaches its peak density in late June or early July as the densities of other zooplankton species are declining (Work and Gophen 1995) and, therefore, may be an important food source for zooplanktivorous fish, especially the young-of-the-year, during this period.

The inland silverside (*Menidia beryllina*) is a slender atherinid fish native to the Gulf and Atlantic coasts of the U.S. It was introduced into Lake Texoma in 1953 and quickly replaced the native atherinid, the brook silverside (*Labidesthes sicculus*) (Dowell and Riggs 1958). *Menidia beryllina* is abundant in surface waters of the littoral zone in Lake Texoma. It feeds primarily on zooplankton and dipterans (Saunders 1959; Elston and Bachen 1976) and is a size selective particulate feeder (McComas and Drenner 1982).

We investigated the interaction of *M. beryllina* and the zooplankton assemblage in Lake Texoma from April 1994 to April 1995. We wanted to determine whether *D. lumholtzi* would be eaten by *M. beryllina* and if it would be selectively preyed upon relative to other zooplankton in Lake Texoma. We monitored the diet of adult *M. beryllina* and the abundance of larval fish and zooplankton at three sites in the reservoir, with emphasis on predation by *M. beryllina* on *D. lumholtzi*.

Methods

Study site

Lake Texoma is a 36,000 hectare impoundment of the Red and Washita Rivers on the Texas-Oklahoma border. It was constructed in 1944 by the U.S. Army Corps of Engineers as a flood control reservoir. At normal pool level (188 m above mean sea level), the reservoir has 933 km of shoreline, a storage capacity of 3.36 X 10^9 m^3, and a shoreline development index of 13.9 (Vaughn 1979). The average depth is 9.3 m and the maximum depth is 34 m (Vaughn 1979). The littoral zone is typically gently sloping with soft mud to hard mud-sand substrate (Matthews et al. 1992). Because it is used for flood control the reservoir experiences high fluctuations in water level.

Three sampling sites were selected on the upper Red River arm of the lake (Fig. 1). All of these site were characterized by a sandy substrate, and extensive, gently sloping beaches which would allow sampling regardless of water level. The upper and middle sites were exposed to prevailing southerly winds and were adjacent to the main channel of the reservoir. The lower site was on the northeastern shore of an island and faced a shallow (3 m maximum depth at normal pool level) basin. Because *D. lumholtzi* is found throughout the reservoir during the summer (Work and Gophen 1995), we sampled four additional sites (two in the Washita River arm and two in the main basin of the reservoir) on two dates to examine the reservoir-wide pattern of predation.

Sampling

Samples were collected every other week from 28 April to 31 August 1994, and monthly thereafter until 20 April 1995. Reservoir-wide sampling was on 8 July and 17 August 1994. Fish and zooplankton were collected at each site and water temperature and secchi depth were recorded. Collections were made between 1200 and 1700.

Adult and juvenile fish were collected from the littoral zone with a 9 X 1.5-m, 3-mm mesh bag seine. Capture depth was approximately 1 m and never more than 1.5 m. Three 20-m seine hauls were taken and, if necessary, additional hauls were taken until at least 10 adult *Menidia* ($\geq$ 50 mm Standard Length, i.e. length from tip of snout to base of tail) were captured. Fish were preserved in 15% formalin and returned to the lab for weight and length determination and for stomach content analysis. After at least one week in formalin, fish were washed and then transferred to 50% isopropyl alcohol.

The standard length (SL) of each *Menidia* was measured to the nearest 1 mm. These data were used to construct a size distribution for the population on each sampling date. Each fish was weighed to the nearest 0.01 g with a Mettler PE 3600 scale. The weight and length of each fish was used to calculate the condition factor (K). The formula $K = W \cdot 10^5 \cdot L^{-3}$ (Carlander 1977), where W is the weight in grams and L is the standard length in millimeters, was used. The average condition factor of small adults (SL = 50 to 70 mm) was compared for each date during the summer of 1994. The size distribution and condition factor data were used to examine the growth of the young-of-the-year throughout the summer.

The stomach contents of 10 adult *M. beryllina* from each sample, selected to represent the available sizes present, were examined. The stomach was defined as the section of the gut anterior to the first turn. The stomach was removed from the fish and the contents diluted in a known volume of distilled water. Dipteran larvae, terrestrial insects, larval fish, and amphipods were identified and enumerated with a Nikon SMZ-10 stereoscopic microscope. The remaining organisms were further diluted and a subsample of at least 10% of the total volume taken. Organisms in the subsample were identified and enumerated with the stereoscopic microscope. Organisms in the subsample were classified as copepodite and adult cyclopoid copepods, copepodite and adult calanoid copepods, copepod nauplii, *Daphnia lumholtzi*, other *Daphnia* spp., *Bosmina* sp., *Ceriodaphnia* sp., *Diaphanasoma* sp., other cladocera, rotifers, fish eggs, insect eggs, and ostracodes.

A zooplankton sample was taken offshore with a one liter LeMotte water sampler at a depth of 1 m immediately after the fish were collected. The sample was filtered (80-um) and preserved in 5% sucrose formalin. Samples were enumerated using the same categories as in the stomach content analysis.

Larval fish were collected with a 50-cm diameter, 500-um mesh net towed at the surface for 5 minutes. The distance covered by the tow was approximately 250 m. The organisms collected in the net were preserved in 15% formalin and returned to the lab for identification and enumeration. Fish in the *M. beryllina* stomachs could rarely be identified beyond class so all larval and juvenile fish were lumped together for the analysis.

The Linear Index of Food Selection (L) (Strauss 1979) was calculated for the larger taxa of zooplankton food items (*D. lumholtzi*, cyclopoid copepods, calanoid copepods, *Daphnia* spp., *Bosmina* spp., *Ceriodaphnia* spp., *Diaphanosoma* spp.). Smaller zooplankton (rotifers, copepod nauplii, ostrocodes) were not included in this analysis because overall they accounted for a small proportion of the diet yet a large proportion of the zooplankton assemblage. Insect data were not included because we did not sample for them in the environment.

Strauss' Linear Index of Food Section (L) is calculated by r_i-p_i where r_i is the proportion of food item $_i$ in the gut, and p_i is the proportion of the food item $_i$ in the habitat (Strauss, 1979). Strauss' L was used because it does not give extreme selectivity ratings to rare taxa. Some other indices (such as Ivlev's E, for example) give the highest possible selectivity score to a species in which one individual is found in the stomach of a predator and none are collected in the habitat regardless of the number of items ingested. This condition was a frequent occurrence because our study spanned the entire year, and thus included periods of low or no abundance for each taxon. During these periods a taxon scored a low L unless it comprised a large portion of the diet of *M. beryllina*. Values of L near 0 should not be necessarily be interpreted as an indicator of no selection. Only when the taxon is present in the environment and relatively abundant can any determination of selectivity be made.

Results

Menidia beryllina abundance and condition

Menidia beryllina young-of-the-year (YOY) appeared in seine samples in late May 1994 (Fig. 2). Most of the adult population, the 1993 year class, had apparently died by late June. Obtaining adults for diet analysis subsequently was difficult until August, when the largest YOY reached adult size. The YOY grew quickly and the largest individuals had attained a standard length of 45 mm by 24 June. Little growth occurred from then until the end of the summer (Fig. 2).

The average condition factor of small *M. beryllina* adults (SL 50 to 70 mm) was >0.87 until the end of June (Fig. 3). At this point the 1993 year class died off and the first recruitment of YOY into the 50-70 mm size class occurred (Fig. 3). By mid-July the adult population was primarily YOY and average condition factor of small adults remained <0.80 until the end of the summer (Fig. 3).

Zooplankton in the environment

The three sites had similar trends in abundance of large zooplankton (Fig. 4). The abundance of zooplankton decreased in early summer as calanoid copepods, cyclopoid copepods and *Daphnia* spp. (*D. galeata, D. parvula*) declined. As other zooplankton taxa declined in June, *Daphnia lumholtzi* appeared in the assemblage and peaked in abundance. Abundance of zooplankton was low all summer with the exception of occasional increases in *Diaphanosoma* (grouped with "Other Cladocerans" in fig. 4) and cyclopoid copepods. Calanoid copepods and the other species of *Daphnia* increased in the fall and were present until spring. There was no difference between the abundance of *D. lumholtzi* in the habitat at the three sites throughout the year (Fig. 4) although peak abundance at the lower site was less pronounced and occurred later. *Daphnia lumholtzi* was only abundant at the middle site on one sample day (23 June 1994).

Menidia beryllina diet

Daphnia lumholtzi was eaten by *Menidia beryllina* (Table 1, Fig. 4). The prey most frequently eaten by *M. beryllina* were the other species of *Daphnia* (23% by number) followed by the cyclopoid copepods (22%), calanoid copepods (17%), and *D. lumholtzi* (10%) (Table 1). After the zooplankton population declined, *M. beryllina* ate more small zooplankton such as *Diaphanosoma* sp., copepod nauplii, and rotifers (Table 1).

Because of their large size, dipteran larvae and terrestrial insects were an important portion of the diet although this was not reflected in the frequency of ingestion (Table 1). They were especially important late in the summer after the zooplankton population declined (Table 1, Fig. 5). During late summer the number of fish with sand grains in their stomachs also increased. This indicated that *Menidia* were picking dipteran larvae from the substrate rather than foraging higher in the water column. While *M. beryllina* did not prey heavily on the larval fish as larval fish abundance peaked, *Menidia* did eat some after the zooplankton population declined (Fig. 6). Larval fish were abundant from the beginning of the study until early June (Fig. 6). Of the larval fish collected at the three sites, *M. beryllina* and *Dorosoma* sp. accounted for 3.5 and 92.2 %, respectively. The Upper site had the highest density of *Dorosoma* sp. larvae but the Middle and Lower sites had more *M. beryllina* larvae.

The *M. beryllina* stomach content data showed large differences between consumption of *D. lumholtzi* at the three sites (Fig. 4). *Daphnia lumholtzi* was a major part of the *M. beryllina* diet from June until August at the Upper site. The *M. beryllina* at the Middle (with the exception of 23 June 1994) and Lower sites did not feed heavily on *Daphnia lumholtzi*. *Menidia beryllina* fed heavily on calanoid copepods and the other *Daphnia* species when they were present (fall, winter, spring). During the summer, *M. beryllina* fed on *D. lumholtzi*, cyclopoid copepods and *Diaphanosoma*. There was a decrease in the number of prey eaten during the summer at all sites.

Menidia beryllina prey selectivity

The Linear Index of Food Selection (L) (Strauss, 1979) for *M. beryllina* eating *D. lumholtzi* was highest at the Upper site followed by the Middle site and was negative at the Lower site (Fig. 7). The other species of *Daphnia* were more highly selected than the other zooplankton types. *Menidia beryllina* at the Upper site showed a lower selectivity for the other *Daphnia* spp. than at the other sites, whereas fish at the Lower site had the highest selectivity. The L for the other *Daphnia* spp. declined at the Upper and Middle sites as the L for *D. lumholtzi* increased. The *M. beryllina* at the Lower site, where there never was positive selection for *D. lumholtzi*, had a positive L for the other species of *Daphnia* even after their population had declined (Fig. 4). Calanoid copepods were selectively eaten in the spring but were unavailable from early summer until fall. Cyclopoid copepods were available all year, but were not positively selected until the large zooplankton (calanoid copepods, *Daphnia* spp., *D. lumholtzi*) disappeared in early July (Fig. 4). *Diaphanosoma*, *Ceriodaphnia* and *Bosmina* all were selected against when they were present at the three sites. Although it was not positively selected, *Diaphanosoma* was a major food source for *M. beryllina* during July (Table 1).

The *M. beryllina* at the supplemental sites had food selectivities similar to those seen at the permanent sites (Fig. 7). Notable exceptions are a positive selection for *Diaphanosoma* at one site and a negative selection for calanoid copepods at two sites on 8 July.

Discussion

Menidia beryllina grew little in summer in Lake Texoma. Young-of-the-year *M. beryllina* grew quickly in the spring but after the zooplankton declined, growth decreased and condition factor remained low through the end of summer. During July and August, there were few large zooplankters in the lake and *M. beryllina* ate more small prey types such as copepod nauplii, rotifers, and ostracodes and also ate more terrestrial insects and dipteran larvae. Some *M. beryllina* started to feed on larval fish and YOY fishes although few adults had been piscivorous earlier in summer. It appears that when faced with decreased food supplies, *M. beryllina* become less zooplanktivorous and utilize other sources of food. This pattern follows the predictions of optimal foraging theory that predators in prey poor environments should feed on a wider breadth of prey types (Werner and Hall 1974; Charnov 1976). The Linear Index of Food Selection data showed that *M. beryllina* were selectively feeding on the largest available zooplankton (*Daphnia* spp., *D. lumholtzi*, calanoid copepods). Cyclopoid copepods, which were present throughout the year, were most highly selected during periods when larger zooplankton were absent or in low abundances.

The decline of the native zooplankton in early summer in Lake Texoma occurred historically, before the invasion of *D. lumholtzi* (Matthews 1984; Dirnberger and Threlkeld 1986; Threlkeld 1986). The date of the decline has varied between years (mid-July, Threlkeld 1986; mid-June, present study). We found that in 1994 the native zooplankton decreased dramatically before *D. lumholtzi* became abundant. It appears that *D. lumholtzi* reaches peak densities after the decline of the native assemblage and is not the cause of the decline. The timing of the decline of native zooplankton is probably controlled by factors such as temperature and resource availability (Threlkeld 1986). The increase in *D. lumholtzi* is probably the result of increased reproductive output at higher temperatures (Work 1997). Although *D. lumholtzi* can become abundant in up-reservoir areas during the winter (Work and Gophen 1995), it is most abundant in summer.

Because *Daphnia lumholtzi* becomes abundant at the time of year when other species of large zooplankton are declining, it can be an important additional food source for fish in Lake Texoma. The fish at the Upper site fed heavily on *D. lumholtzi* throughout the summer. *Daphnia lumholtzi* was only abundant at the Middle site on one sampling day but it was preyed upon heavily by the *M. beryllina*. More zooplankton were eaten at this site on this day than any other from 27 May through 10 December. *Daphnia lumholtzi* was never a large part of the diet of *M. beryllina* at the Lower site where the native zooplankton were available well into summer. Because *D. lumholtzi* is not evenly distributed throughout Lake Texoma (Work and Gophen 1995; Work 1997), the availability of *D. lumholtzi* to *M. beryllina* will depend on where the fish lives in the reservoir.

The timing of the *D. lumholtzi* increase in abundance is important in that it occurs during the spawning season for *M. beryllina* (from late March to mid-July; Mense 1967). Spawning ceases when temperature exceeds 30 C (Hubbs and Bailey 1977). Young-of-the-year can reproduce in their first summer if their growth rate is high and water temperature remains below 30 C (Hubbs and Dean 1979). Females spawn 5.6 to 7.5% of their body weight in eggs every morning (Hubbs 1976) in early summer. Hubbs (1976) estimated that *M. beryllina* can produce over 5 times its body mass in eggs each spawning season. With such a large amount of energy used in production of gametes it is not surprising that adult *M. beryllina* do not increase in length or condition during the early summer (Fig. 2 and 3) even though zooplankton are abundant. Early to midsummer is also a period of high mortality for *M. beryllina* in Lake Texoma (Mense 1967). The condition factor for adults does not indicate any gradual decrease throughout the spawning season. This suggests that the fish are not using stored resources for gamete production. The precipitous decline of adult *M. beryllina* in early summer may result from a combination of increased metabolic demands due to higher temperatures, high reproductive demands, and low availability of food.

The timing of the increase in the abundance of *Daphnia lumholtzi* may also be important for YOY *M. beryllina*. Predation often is highest on the smaller size classes of juvenile fishes. Gleason and Bengtson (1996) found that juvenile striped bass (*Morone saxatilis*) selected the smallest *M. beryllina* available in laboratory experiments. Similarly, young largemouth bass (*Micropterus salmoides*) in ponds with *M. beryllina* preyed most heavily on the smallest individuals (Stoeckel and Heidinger 1992). Lake Texoma supports a large striped bass fishery and juvenile striped bass were often caught in the same seine haul as *M. beryllina*. Moreover, white bass (*Morone chrysops*) and black bass (*Micropterus spp.*) also occur in the littoral zone of Lake Texoma. As the young-of-year of these species switch from zooplanktivory to piscivory, they are gape-limited (Timmons et al. 1980; Hambright 1991). By growing rapidly, a juvenile fish can reduce its risk of being eaten by remaining too large for the juvenile predators to consume. The presence of *D. lumholtzi* may delay the summer period of low zooplankton availability, thus allowing YOY *M. beryllina* to attain a larger size before growth decreases.

Lengthening the spring-summer growing season will also result in larger individuals entering winter. Larger young-of-the-year have a higher probability of surviving through the winter (Quinn and Peterson 1996) and larger fish emerge from winter in better energetic condition (Cargnelli and Gross 1997).

Daphnia lumholtzi was positively selected by *M. beryllina* at most sites and dates but it was not preferred when other large zooplankton were available. Although *Daphnia lumholtzi* was present at the Lower site on many dates, it was never selected for by the *M. beryllina,* which preyed upon the other large zooplankton that remained available. *Daphnia lumholtzi* was positively selected for by *Menidia beryllina* when the other species of *Daphnia* were absent. *Menidia beryllina* showed the most preference for the other species of *Daphnia* in Lake Texoma. The only time these species were selected against was when the abundance of *Daphnia lumholtzi* was at its peak at the Upper site. Threlkeld found (1986) that as the annual zooplankton crash progressed, the size distribution of cladocerans was shifted toward smaller individuals. This may explain why *M. beryllina* did not select for the native species of *Daphnia* at the Upper site even though some *Daphnia* spp. were present in small abundances. *Menidia beryllina* at the Lower site showed the highest selectivity for the other *Daphnia* species even when *D. lumholtzi* was more abundant. Apparently *M. beryllina* preferred the native *Daphnia spp.* but selected *D. lumholtzi* when no other large zooplankton were available.

Although introduced invertebrates have been used as food by fishes in the systems they invaded, they may have a negative impact on the fish by decreasing native zooplankton abundance (Rieman and Falter 1981; Lehman and Caceres 1993). *Daphnia lumholtzi* appears not to compete with the native zooplankton but becomes abundant during a time of year when the native zooplankton are absent or declining. In this way, *D. lumholtzi* is an additional food source for the zooplanktivorous fish and is not replacing the food sources available prior to its invasion. We predict that the invasion of *D. lumholtzi* will have a positive effect on zooplanktivorous fishes in Lake Texoma. Because *D. lumholtzi* is most abundant in the upper portions of the reservoir (Work and Gophen 1995; Work 1997) it will have a greater effect on fishes in this area.

Acknowledgments

PWL was supported by a Centennial Research Fellowship from the University of Oklahoma. We thank K. Work, M. Craig, and J. Stewart for help with field work and Coral McCallister for help preparing the figures. The University of Oklahoma Biological Station provided laboratory space and field vehicles.

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Table 1. Numbers of prey items in *Menidia beryllina* stomachs (n=30) from each date. The percentage of diet is in parenthesis.

DATE\TAXA	Cyclopoida	Calanoida	*D. lumholtzi*	Other *Daphnia sp.*	*Bosmina sp.*	*Ceriodaphnia sp.*
28-Apr-94	1958 (7)	7751 (29)	11 (<1)	9244 (35)	6504 (25)	526 (2)
12-May-94	1097 (5)	14305 (62)	7 (<1)	6885 (30)	282 (1)	327 (1)
27-May-94	1625 (9)	1586 (9)	25 (<1)	14877 (80)	169 (<1)	60 (<1)
10-Jun-94	1218 (20)	708 (12)	1683 (30)	2274 (37)	16 (<1)	- -
23-Jun-94	119 (1)	34 (<1)	7754 (91)	304 (4)	8 (<1)	39 (<1)
7-Jul-94	1387 (14)	883 (9)	1796 (18)	1552 (15)	5 (<1)	6 (<1)
21-Jul-94	1933 (24)	208 (3)	489 (6)	468 (6)	404 (5)	63 (<1)
3-Aug-94	1877 (22)	193 (2)	246 (3)	28 (<1)	179 (2)	17 (<1)
15-Aug-94	2614 (34)	7 (<1)	769 (10)	24 (<1)	803 (10)	1 (<1)
31-Aug-94	1847 (33)	189 (3)	131 (2)	42 (<1)	1837 (33)	35 (<1)
20-Sep-94	6140 (47)	1433 (11)	94 (1)	32 (<1)	334 (3)	68 (<1)
19-Oct-94	6218 (37)	816 (5)	78 (<1)	3272 (19)	3420 (20)	399 (2)
7-Nov-94	3728 (25)	2067 (14)	301 (2)	3885 (26)	4202 (28)	154 (1)
10-Dec-94	1967 (8)	2300 (9)	20 (<1)	20285 (81)	318 (1)	60 (<1)
21-Jan-95	3223 (24)	4578 (34)	145 (1)	4034 (30)	1438 (11)	17 (<1)
16-Mar-95	3240 (25)	8020 (61)	137 (1)	614 (5)	634 (5)	107 (<1)
20-Apr-95	9688 (39)	8333 (34)	10 (<1)	4740 (19)	1047 (4)	482 (2)
TOTALS	49879 (22)	53411 (18)	13696 (10)	72560 (23)	21600 (9)	2361 (<1)

Table 1. Continued.

DATE\TAXA	*Diaphanosoma*		Other Clado.		Ostracodes		Nauplii		Rotifers	
28-Apr-94	25	(<1)	-	-	-	-	-	-	-	-
12-May-94	8	(<1)	7	(<1)	-	-	8	(<1)	-	-
27-May-94	81	(<1)	12	(<1)	-	-	-	-	-	-
10-Jun-94	6	(<1)	7	(<1)	-	-	11	(<1)	-	-
23-Jun-94	85	(1)	19	(<1)	-	-	-	-	-	-
7-Jul-94	4294	(42)	-	-	54	(<1)	106	(1)	18	(<1)
21-Jul-94	2542	(32)	-	-	6	(<1)	152	(2)	1612	(20)
3-Aug-94	113	(1)	-	-	147	(2)	4730	(55)	959	(11)
15-Aug-94	51	(<1)	-	-	65	(<1)	161	(2)	3050	(40)
31-Aug-94	152	(3)	-	-	13	(<1)	332	(6)	777	(14)
20-Sep-94	512	(4)	4	(<1)	5	(<1)	1227	(9)	2462	(19)
19-Oct-94	660	(4)	7	(<1)	8	(<1)	792	(5)	816	(5)
7-Nov-94	287	(2)	7	(<1)	-	-	65	(<1)	135	(<1)
10-Dec-94	210	(<1)	6	(<1)	-	-	17	(<1)	-	-
21-Jan-95	10	(<1)	6	(<1)	-	-	6	(<1)	-	-
16-Mar-95	-	-	100	(<1)	17	(<1)	-	-	137	(1)
20-Apr-95	-	-	-	-	54	(<1)	-	-	-	-
TOTALS	9036	(5)	175	(<1)	369	(<1)	7607	(5)	9966	(7)

Table 1. Continued.

DATE\TAXA	Dipt. Larvae		Ter. Insect		Insect Eggs		Amphipods		Fish		Fish Eggs	
28-Apr-94	47	(<1)	133	(<1)	153	(<1)	-	-	-	-	27	(<1)
12-May-94	8	(<1)	53	(<1)	-	-	-	-	-	-	135	(<1)
27-May-94	13	(<1)	44	(<1)	-	-	-	-	11	(<1)	8	(<1)
10-Jun-94	13	(<1)	36	(<1)	-	-	-	-	5	(<1)	88	(1)
23-Jun-94	9	(<1)	93	(1)	-	-	-	-	8	(<1)	12	(<1)
7-Jul-94	125	(1)	8	(<1)	-	-	-	-	-	-	9	(<1)
21-Jul-94	46	(<1)	63	(<1)	-	-	-	-	10	(<1)	-	-
3-Aug-94	105	(1)	28	(<1)	7	(<1)	13	(<1)	-	-	1	(<1)
15-Aug-94	124	(2)	21	(<1)	21	(<1)	-	-	5	(<1)	-	-
31-Aug-94	68	(1)	89	(2)	-	-	1	(<1)	2	(<1)	-	-
20-Sep-94	653	(5)	23	(<1)	23	(<1)	-	-	-	-	-	-
19-Oct-94	208	(1)	249	(1)	-	-	3	(<1)	-	-	-	-
7-Nov-94	9	(<1)	187	(1)	-	-	-	-	-	-	-	-
10-Dec-94	6	(<1)	4	(<1)	-	-	-	-	-	-	-	-
21-Jan-95	40	(<1)	-	-	-	-	-	-	-	-	4	(<1)
16-Mar-95	84	(<1)	44	(<1)	-	-	-	-	-	-	49	(<1)
20-Apr-95	139	(<1)	80	(<1)	-	-	-	-	-	-	55	(<1)
TOTALS	1697	(<1)	1155	(<1)	204	(<1)	17	(<1)	41	(<1)	388	(<1)

List of Figures

Figure 1. Map of the three sampling sites (Upper, Middle, Lower) on the Red River arm of Lake Texoma, Oklahoma-Texas, U.S.A.

Figure 2. Size distribution (standard lengths) of *Menidia beryllina* collected from all three sampling sites on each sampling date from 28 April 1994 to 20 April 1995.

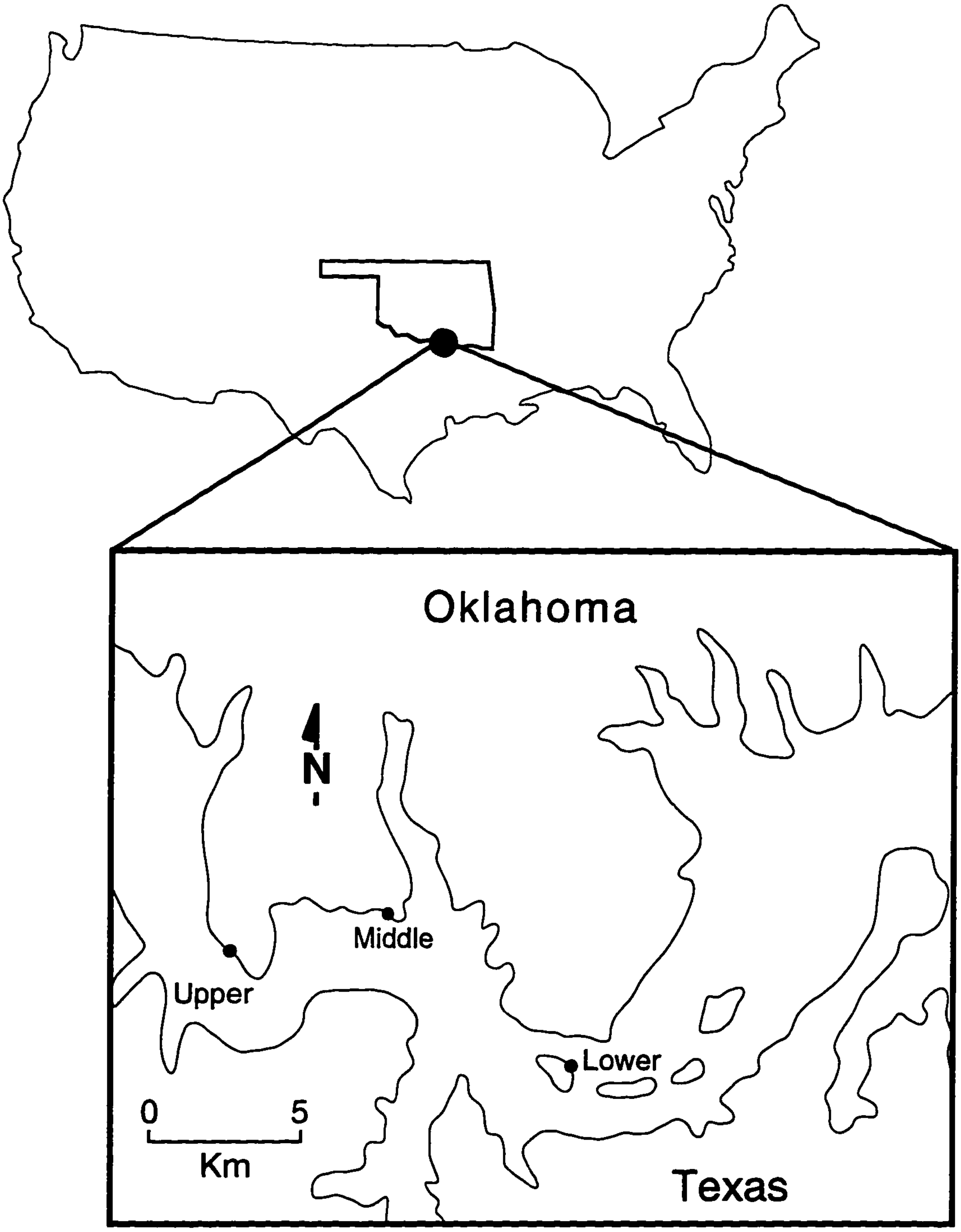
Figure 3. Average condition factor (K) (± 1 SE) for small adult (50 to 70 mm standard length) *Menidia beryllina* from all sites from 28 April to 31 August, 1994.

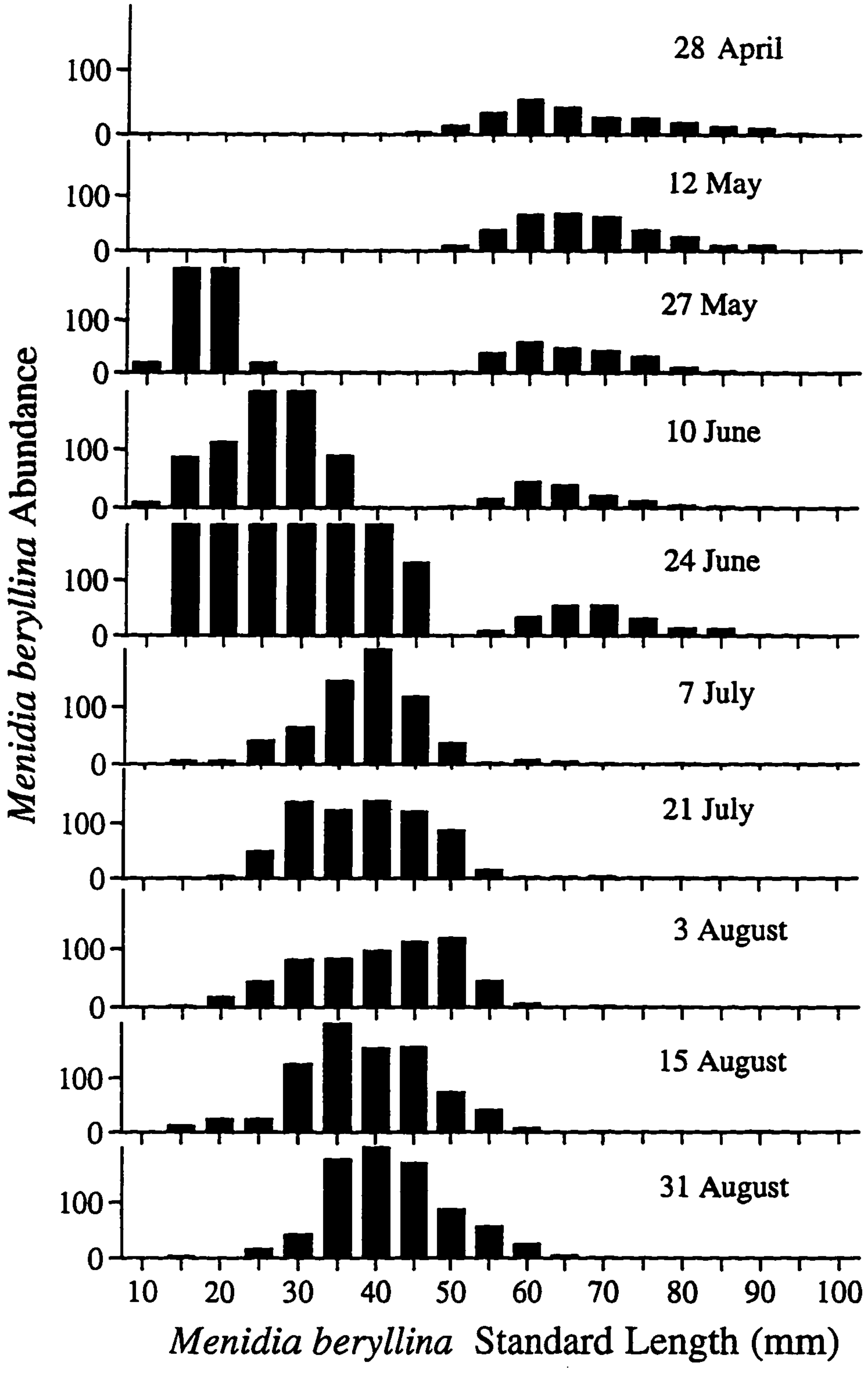
Figure 4. Density of cladoceran and copepod zooplankton at the Upper (A), Middle (C), and Lower (E) sites on each sampling date. The average number of cladoceran and copepod zooplankton in the stomachs of adult *Menidia beryllina* (n = 10) at the Upper (B), Middle (D), and Lower (F) site on each sampling date.

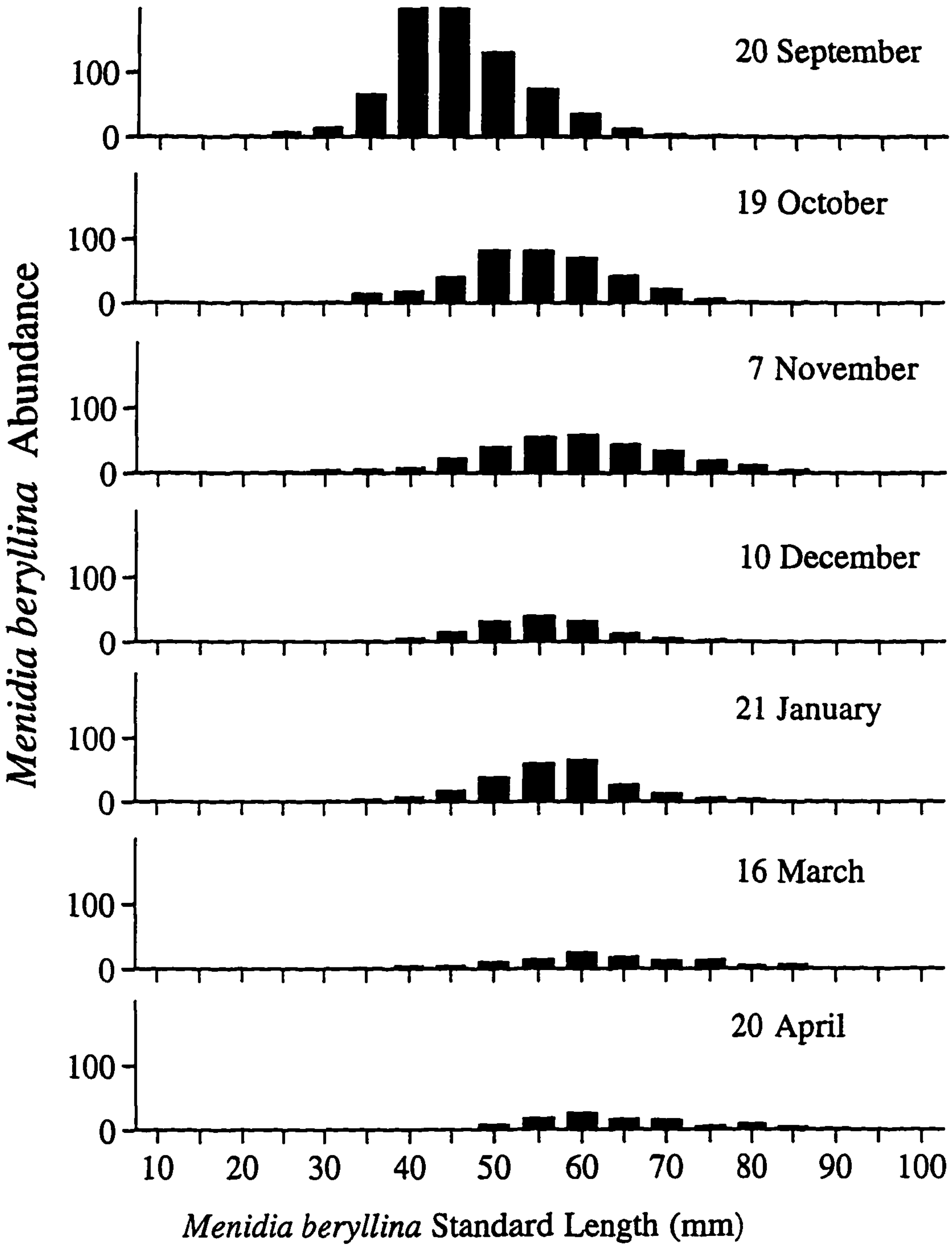
Figure 5. Average abundance of Dipteran larvae and terrestrial insects in the stomachs of adult *Menidia beryllina* (n =30) on each date (top panel). The percentage of fish with sand in their stomachs or empty stomachs (lower panel).

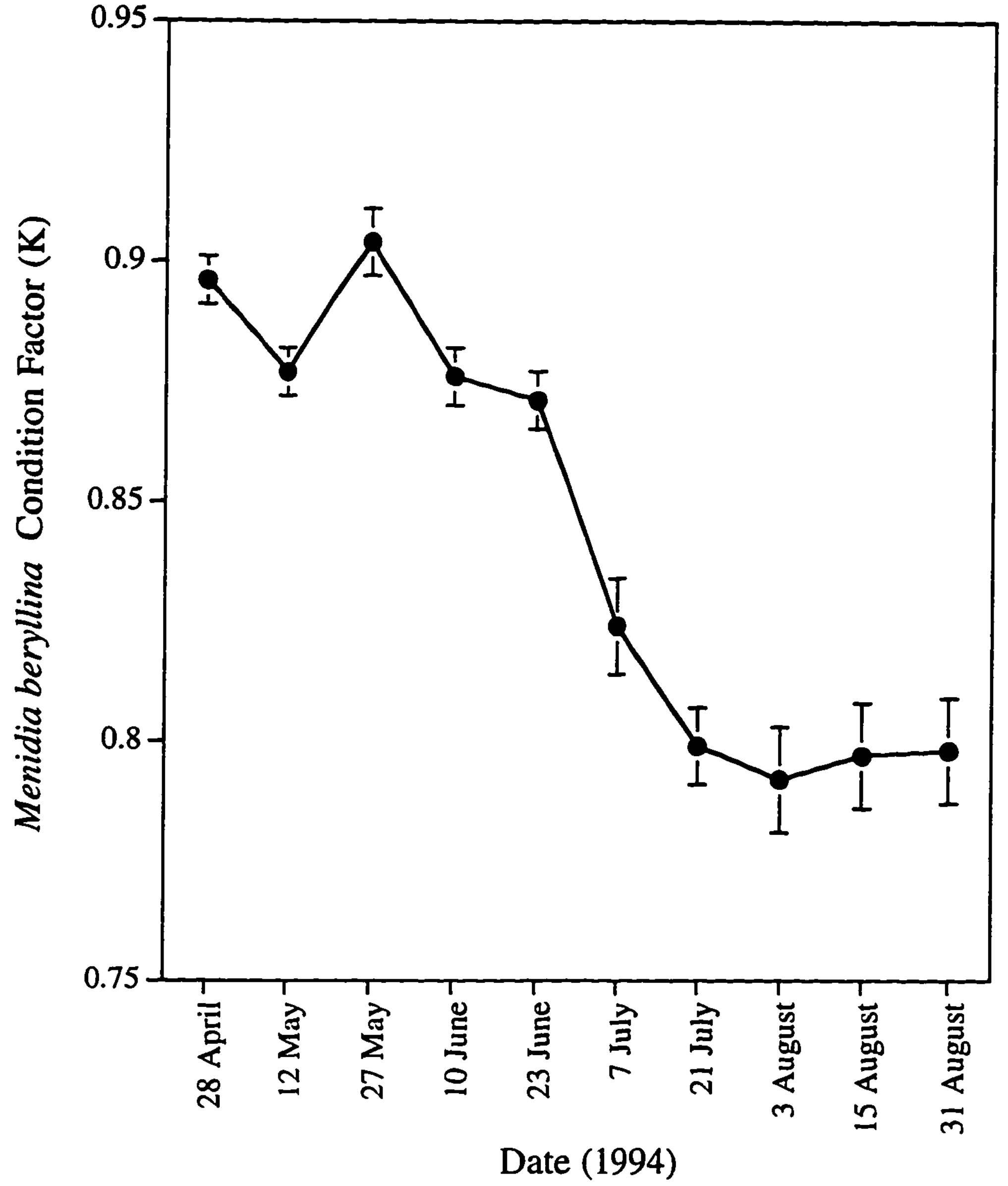
Figure 6. Average abundance of larval fish and zooplankton in the habitat of the three sites on each date (top panel). Average number of larval and juvenile fish in the stomachs of adult *Menidia beryllina* (n =30) on each date (lower panel).

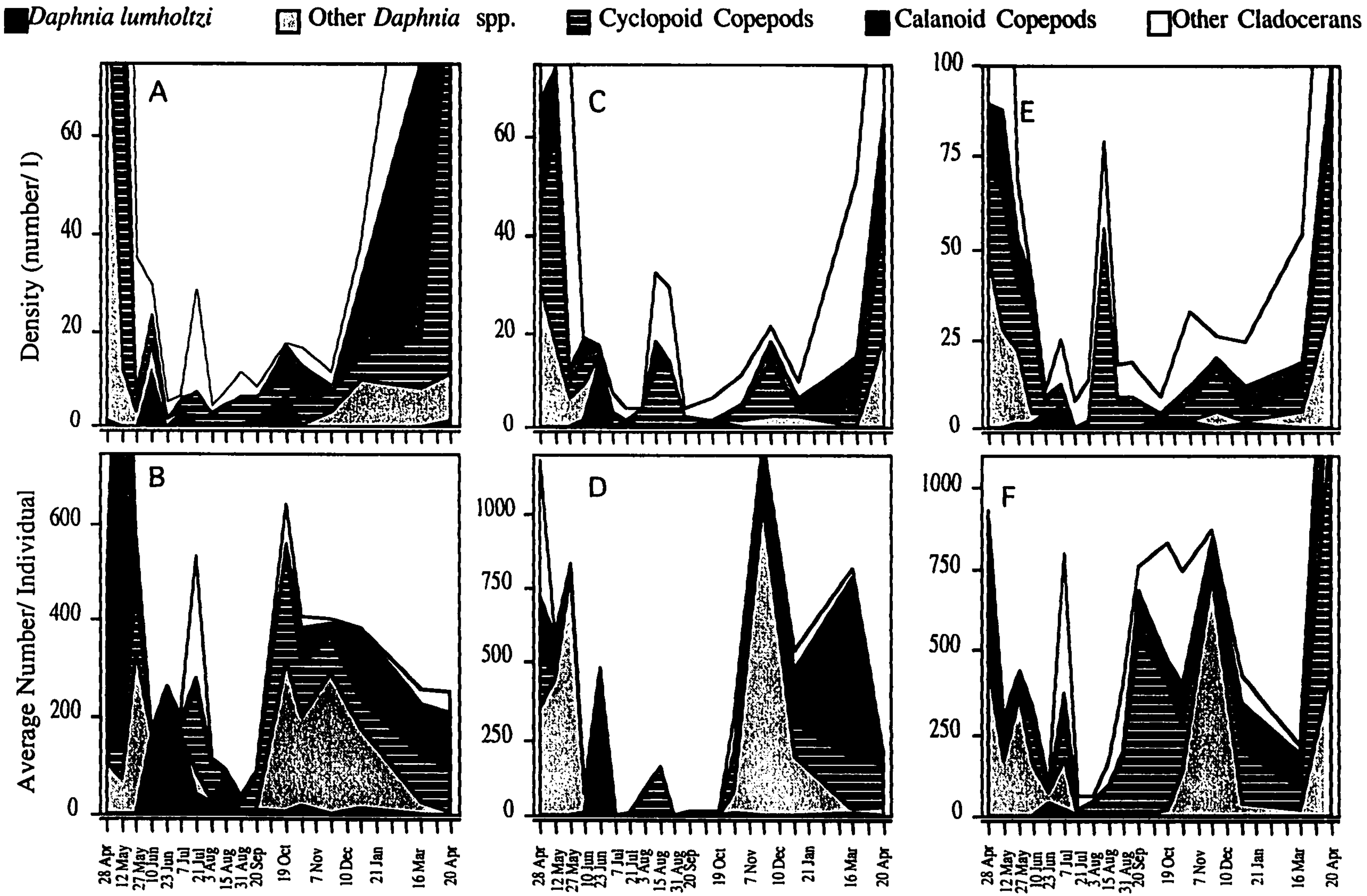
Figure 7. Average Linear Index of Food Selection (L) (Strauss, 1979) for *Menidia beryllina* (n =10) feeding on *Daphnia lumholtzi*, *Daphnia* spp., Calanoid copepods, Cyclopoid copepods, *Bosmina* sp., *Ceriodaphnia* sp., and *Diaphanosoma* sp. at each site and date.


Oklahoma
N
Middle
Upper
Lower
0
5
Km
Texas


28 April
12 May
27 May
10 June
24 June
7 July
21 July
3 August
15 August
31 August
100
0
10
20
30
40
50
60
70
80
90
100
Menidia beryllina Abundance
Menidia beryllina Standard Length (mm)


20 September
19 October
7 November
10 December
21 January
16 March
20 April
100
0
10
20
30
40
50
60
70
80
90
100
Menidia beryllina Abundance
Menidia beryllina Standard Length (mm)


Menidia beryllina Condition Factor (K)
0.95
0.9
0.85
0.8
0.75
28 April
12 May
27 May
10 June
23 June
7 July
21 July
3 August
15 August
31 August
Date (1994)


Daphnia lumholtzi
Other Daphnia spp.
Cyclopoid Copepods
Calanoid Copepods
Other Cladocerans
Density (number/ l)
Average Number/ Individual
A
B
C
D
E
F
0
20
40
60
0
200
400
600
0
250
500
750
1000
0
25
50
75
100
28 Apr
12 May
27 May
10 Jun
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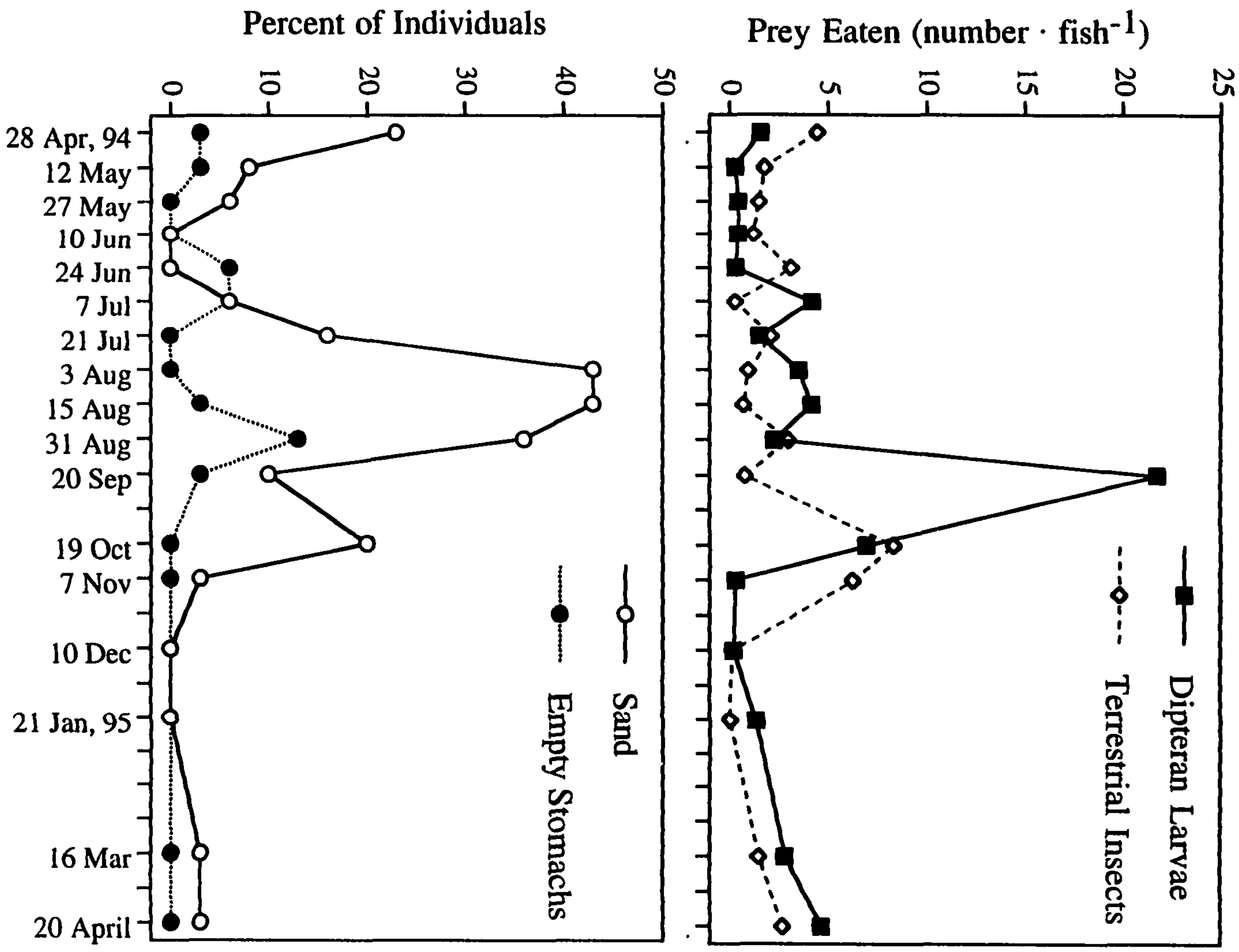
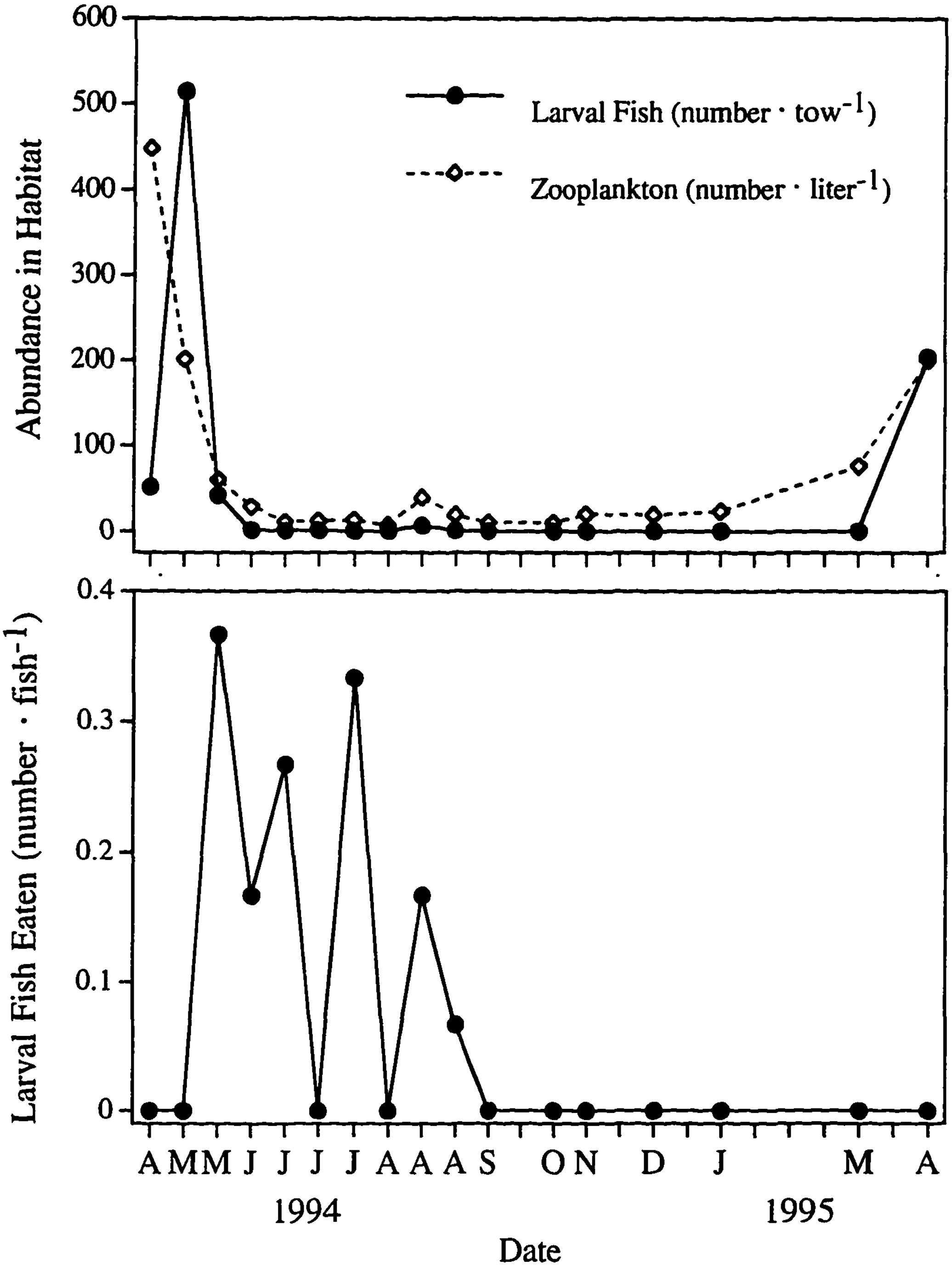
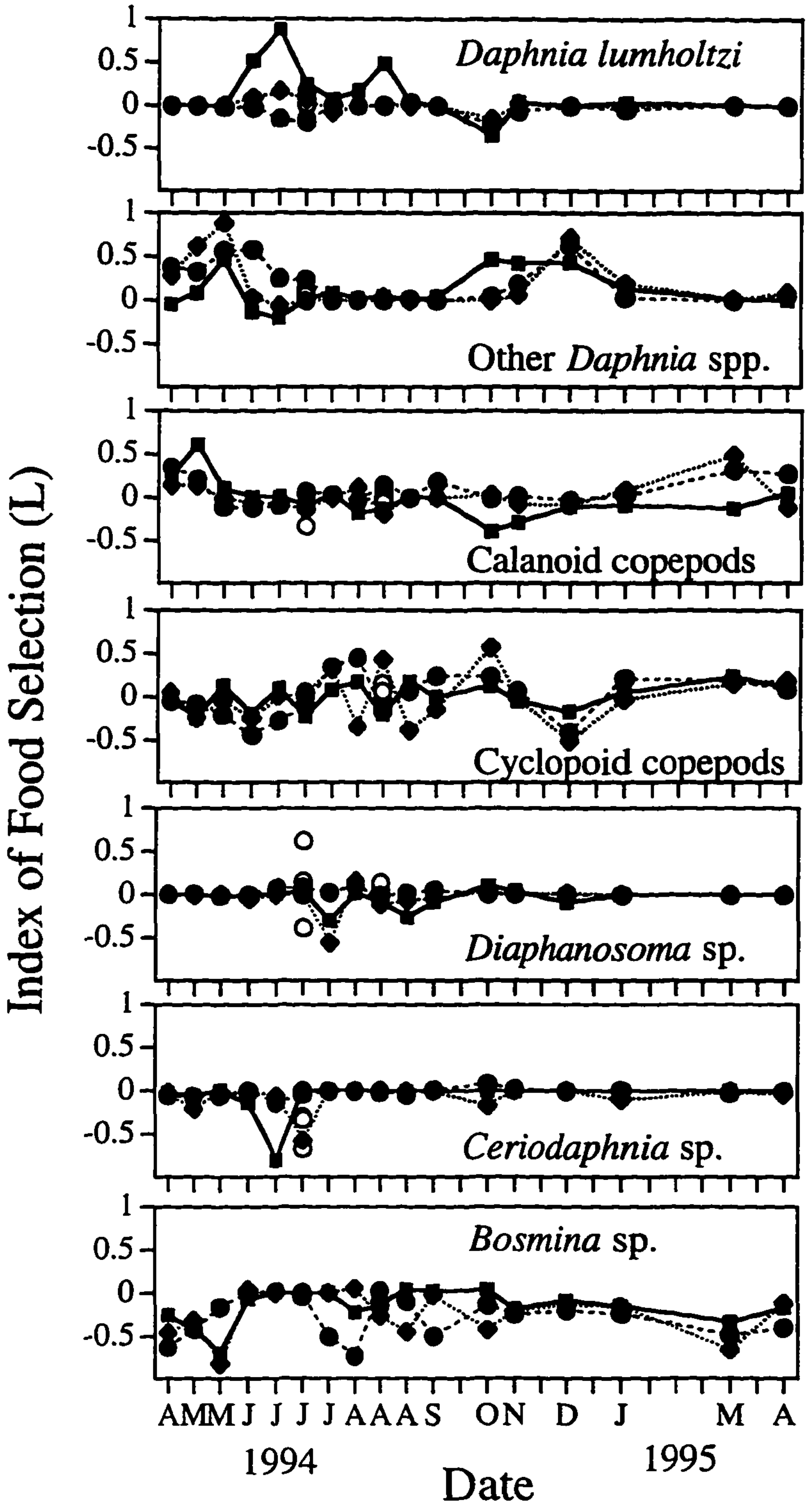
7 Nov
10 Dec
21 Jan
16 Mar
20 Apr


Prey Eaten (number · fish^{-1})
0
5
10
15
20
25
Dipteran Larvae
Terrestrial Insects
Percent of Individuals
0
10
20
30
40
50
Sand
Empty Stomachs
28 Apr, 94
12 May
27 May
10 Jun
24 Jun
7 Jul
21 Jul
3 Aug
15 Aug
31 Aug
20 Sep
19 Oct
7 Nov
10 Dec
21 Jan, 95
16 Mar
20 April
Date


600
500
400
300
200
100
0
Abundance in Habitat
Larval Fish (number · tow^{-1})
Zooplankton (number · liter^{-1})
0.4
0.3
0.2
0.1
0
Larval Fish Eaten (number · fish^{-1})
A M M J J J J A A A S O N D J M A
1994
1995
Date


Index of Food Selection (L)
1
0.5
0
-0.5
Daphnia lumholtzi
Other Daphnia spp.
Calanoid copepods
Cyclopoid copepods
Diaphanosoma sp.
Ceriodaphnia sp.
Bosmina sp.
A M M J J J J A A A S O N D J M A
1994
1995
Date

Size Selective Predation by *Menidia beryllina* on an Exotic, Long-spined Cladoceran, *Daphnia lumholtzi*.

Philip W. Lienesch and Moshe Gophen

Abstract

Large spines on zooplankton have been shown to inhibit predation by small fishes. *Daphnia lumholtzi* is a long-spined, cladoceran which has recently invaded the North America. We conducted laboratory feeding experiments to determine if the size of *Menidia beryllina* affected the size *D. lumholtzi* they ate. Three size classes of *M. beryllina* were allowed to feed on *D. lumholtzi* of various sizes. Large *M. beryllina* ate more large *D. lumholtzi* and small *M. beryllina* ate more small *D. lumholtzi*. All sizes of fish tested could ingest the largest *D. lumholtzi*. We also examined the lengths of *D. lumholtzi* and the native *Daphnia* species eaten by large and small *M. beryllina* in Lake Texoma, Oklahoma-Texas, USA. The *Daphnia* sizes selected by *M. beryllina* in the field agreed with the results of the experiments. In addition, small *M. beryllina* appear to select smaller *D. lumholtzi* than native *Daphnia* spp. Because *D. lumholtzi* reaches peak abundances during a period of low zooplankton abundance in Lake Texoma, it may be an important food source for young-of-the-year *M. beryllina.*

Introduction

Due to recent invasions of *Bythotrephes cederstroemi* (Lehman 1987) and *Daphnia lumholtzi* (Sorenson and Sterner 1992), some zooplanktivorous fishes in North America are encountering prey types with large spines that may provide defense against fish predation. *Bythotrephes cederstroemi*, native to Europe, invaded the Great Lakes in the mid-1980's (Bur et al. 1986; Lange and Cap 1986) and has slowly invaded inland waters (Yan et al. 1992). *Bythotrephes cederstroemi* has a large caudal spine that increases with body size and can be 3-4 times the body length (2 mm) of adults (Barnhisel 1991a). *Daphnia lumholtzi* was first found in Texas in 1990 (Sorenson and Sterner 1992) and has spread quickly throughout the southeastern U.S. (Havel et al. 1995). It is characterized by a large helmet, long tail spine, lateral fornices on the neck, and small spines along the carapace and tail spine (Havel and Hebert 1993). As in the case of *B. cederstroemi*, the spines of *Daphnia lumholtzi* can account for over 75% of the total length of the animal (personal observation). Although these zooplankton are eaten by fishes in the systems they have invaded (Bur and Klarer 1991; Barnhisel and Harvey 1995; Lienesch 1997), laboratory studies have shown that their spines can hinder fish predation (Barnhisel 1991a, 1991b; Swaffar and O'Brien 1996).

Barnhisel (1991a) performed laboratory experiments that showed that the spine of *B. cederstroemi* greatly increased handling time for young rainbow trout (*Onchorhynchus mykiss*). As the fish became experienced with *B. cederstroemi*, they developed an aversion to feeding on it (Barnhisel 1991a). Similarly, juvenile yellow perch (*Perca flavescens*) developed an aversion to feeding on *B. cederstroemi* (Barnhisel 1991b). Experienced yellow perch were less likely to attack *B. cederstroemi*, more likely to reject it if they captured it, and less likely to eventually ingest the animal (Barnhisel 1991b). When its spines were experimentally removed or reduced, the perch showed less aversion to *B. cederstroemi* (Barnhisel 1991b).

Fish size also affected the ability of the fish to handle spiny prey. Small fish encountered more difficulty feeding on *B. cederstroemi* than did large fish (Barnhisel, 1991a; Barnhisel and Harvey 1995). Barnhisel and Harvey (1995) found that *B. cederstroemi* in Lake Superior were not selected by juvenile fishes and were protected from predation by fishes under 7 cm. Small rainbow trout feeding on *B. cederstroemi* had longer handling times and higher rejection rates than larger fish (Barnhisel 1991a). When the spine was removed, the handling times for small and large fish were not significantly different (Barnhisel 1991a). Swaffar and O'Brien (1996) found that small bluegills (*Lepomis macrochirus*) had a higher rejection rate for *D. lumholtzi* than did larger bluegills.

A year-long field investigation in Lake Texoma, Oklahoma-Texas, showed that adult (SL> 50 mm) inland silversides (*Menidia beryllina*) preyed heavily on *Daphnia lumholtzi* during the summer (Lienesch 1997). Due to food limitation during this period, *D. lumholtzi* was an important food source and was selected by adult *M. beryllina* in Lake Texoma. Although Lienesch (1997) examined the diet of only adult *M. beryllina*, *D.*

lumholtzi also may be important in the diet of juveniles. The zooplankton assemblage in Lake Texoma experiences an annual peak in late spring and then declines drastically by mid-summer (Matthews 1984; Threlkeld 1986). *Daphnia lumholtzi* reaches peak abundances as the native zooplankton assemblage is declining (Work and Gophen 1995; Lienesch 1997; Work 1997) and the abundance of juvenile *M. beryllina* is increasing (Lienesch 1997).

Because *D. lumholtzi* is an abundant food source during the peak abundance of juvenile *M. beryllina* in Lake Texoma, we tested whether the size of *M. beryllina* has an influence on their size selection of *D. lumholtzi*. We conducted a laboratory experiment to determine the size selectivity of three size classes of fish feeding on a population of *D. lumholtzi*. We wanted to determine if *M. beryllina* of different sizes would feed on the same range of sizes of *D. lumholtzi* and would they apply the same amount of predation pressure on each size class of *D. lumholtzi*.

We also examined the size distribution of *D. lumholtzi* from the stomachs of large and small *M. beryllina* from Lake Texoma to test whether *M. beryllina* prey selectivity in the field would agree with predictions from the experiment. These fish were collected on a day when *D. lumholtzi* dominated the diet of *M. beryllina*. We also examined the size distribution of native *Daphnia* eaten by large and small *M. beryllina* in Lake Texoma on a day when native *Daphnia*, which do not have the extensive spination of *D. lumholtzi*, were the dominant prey. We wanted to determine if they would also follow the size selective predictions of the experiment.

Methods

Laboratory experiment

Menidia beryllina was collected from the shore at the University of Oklahoma Biological Station on Lake Texoma with a 7.6 X 1.5-m bag seine (3-mm mesh) and transported to the biological station's laboratory. Fish for the experiment were selected by size (small, medium, large; Table 1) and placed into holding tanks containing lake water. Fish were acclimatized to the laboratory for at least 1 week before the experiments began, during which they were fed commercially prepared flake fish food supplemented with live zooplankton from Lake Texoma.

Because *Daphnia lumholtzi* had already declined in Lake Texoma, it was collected on the day of each trial from Lake Hugo, a reservoir in Choctaw County, southeastern Oklahoma. The *Daphnia* were collected by surface tows of a 0.5-m larval fish net (500-um mesh) and a 0.25-m Wisconsin plankton net (353-um mesh). Zooplankton were transported to the laboratory and used in the experiment within 5 hours of collection. Although *D. lumholtzi* was not the only species of zooplankton collected, they accounted for over 95% of the assemblage.

The two trials were conducted on 25 and 27 July, 1995. For each trial, two large, five medium, or eight small *M. beryllina* (Table 1) were placed into 38-liter aquaria, each containing 30 liters of aerated lake water. There were four aquaria (n=4) for each *M. beryllina* size class. The fish densities were based on the results of pilot studies to equalize the overall predation pressure in each tank. One aquarium served as a fishless control. Fish were placed into the tanks 24 hours before the experiment to allow for acclimatization. Fish were not fed during the acclimatization period to standardize hunger and gut fullness.

At the beginning of the trial, 1-liter aliquots of zooplankton were introduced into each experimental tank and in the fishless control. Fish were allowed to feed for 80 min., after which a zooplankton sample was collected from each tank. Three samples were taken from the control tank (after 20, 40, and 80 min.) to determine densities of *D. lumholtzi* without predation. Each sample consisted of three tube samples (Drenner and McComas 1980). After gently stirring the water, a 3.4-mm diameter PVC tube was dropped onto a rubber stopper randomly placed on the aquarium floor thereby enclosing a column of water. The water from the three tube samples was combined, the total volume measured, and the zooplankton concentrated by filtering the sample through 80-um mesh. The densities of *D. lumholtzi* (all size classes combined) in the fishless control tank and the experimental tanks were compared to determine whether the *M. beryllina* had fed.

Daphnia lumholtzi in the samples were counted and the total lengths of 50 individuals measured. Total length was measured from the tip of the helmet to the tip of the tail spine (Fig. 1). From these data, the densities of four size classes (Table 1) of *D. lumholtzi* in each tank were estimated. Density of *D. lumholtzi* in the control tank was estimated from the average of the three samples. Tanks in which less than 20 % of the *D. lumholtzi* were consumed were omitted from the analysis. One tank containing large fish from each trial was omitted from the analysis due to lack of feeding. For each size class, the change in the density of *D. lumholtzi* (number $\cdot$ liter^{-1}) was estimated by subtracting the density of *D. lumholtzi* remaining in each tank from the density in the fishless control tank. The reduction in the density of *D. lumholtzi* was used as a measure of *M. beryllina* predation.

Statistical analysis

To determine if predation pressure was equal among fish size treatments, the reduction of *D. lumholtzi* density in different treatments (all size classes of *Daphnia* combined) were compared with a two-way ANOVA. This test was performed to ensure that tanks with a given size class of *M. beryllina* did not have higher overall predation than the other treatments. The trial term (Day of experiment) was included in the model because the beginning total densities of *Daphnia* differed on the two days.

To test for differences in size selective predation among fish size treatments, a two-way Multivariate Analysis of Variance test (MANOVA) (Scheiner 1993) was performed. This test used the data from all four size classes of *D. lumholtzi* to determine if the fish of different sizes had the same pattern of predation. The trial term (Day, Table 2) was included in the analysis due to different beginning densities of *D. lumholtzi*. MANOVA is similar to ANOVA except that MANOVA compares the variances of the centroids of multiple variables (Scheiner 1993) whereas ANOVA examines the variances of a single variable (ex. reduction of the density of large *D. lumholtzi*). The reduction of the density of each *D. lumholtzi* size class was used as a separate response variable. Each tank could then be characterized by the reduction in the density of the four *D. lumholtzi* size classes and overall difference between fish treatments determined. Based on the results of the MANOVA, individual ANOVAs were performed for the reduction of density of each *D. lumholtzi* size class. These tests indicated whether the size of *M. beryllina* had an effect on the amount of *D. lumholtzi* eaten within each of the four size classes of *D. lumholtzi*. Sheffe's Multiple Comparison Procedure was performed to determine differences between individual fish size treatments.

Field data

The gut contents of 10 large and 10 small *M. beryllina* from two dates were examined to test for differences in size selectivity for *D. lumholtzi* and the native *Daphnia* spp. (*D. galeata* and *D. parvula*). The fish were collected from Lake Texoma with a 7.6 X 1.5 m bag seine (3 mm mesh) and preserved in 15% formalin. A more detailed description of the field methods is in Lienesch (1997). The selectivity for the native species of *Daphnia* was examined for *M. beryllina* collected on 17 June 1994, when native species of *Daphnia* dominated the diet. The selectivity for *D. lumholtzi* was examined on 30 June 1994, when *D. lumholtzi* dominated the *M. beryllina* diet. Up to 50 individual *Daphnia* from each fish gut were measured. Only individuals which showed minimal mastication and digestion were used in the analysis. Measurements for the native species of *Daphnia* were from the top of the helmet to the base of the tail spine (Fig. 1). For this analysis, measurements of *D. lumholtzi* were taken from the base of the spine of the helmet to the base of the tail spine (Fig. 1). The number of *Daphnia* in each size class taken by each size of *M. beryllina* on each date were combined to create histograms.

Size-frequency distributions of *Daphnia* consumed by large and small *M. beryllina* on each date were compared by Kolmogorov-Smirnov analysis (Sokal and Rohlf 1981). Although we do not know the size distribution of *D. lumholtzi* available on 30 June, we knew the large and small fish were collected in the same area and therefore, we assume they were exposed to the same population of *D. lumholtzi*. The same assumption is made for the *M. beryllina* feeding on the native *Daphnia* spp. on 17 June. We used a regression of the total length to body size for *D. lumholtzi* used in the experiment to assign the *D. lumholtzi* from the *M. beryllina* stomachs to the four size classes based on body size.

We also compared the size-frequency distribution of *D. lumholtzi* eaten by small fish on 30 June to that of the native *Daphnia* spp. taken by small fish on 17 June. There were approximately twice as many size categories of the native *Daphnia* because they had a larger body size range. We adjusted the ranges of the *Daphnia* size categories of the two taxa so that they had the same number of size classes to correct for the effect of the number of categories on size frequency data. A similar comparison (with adjusted body size categories) was made for the *Daphnia* consumed by large *M. beryllina* on each date. No statistical tests are reported for these comparisons because the size distribution of *Daphnia* available on the two dates is unknown and cannot be assumed to be similar.

Results

Although the number of fish in each aquarium was different for the three fish size treatments (Table 1), the reduction of the density of *D. lumholtzi* was not significantly different between treatments (ANOVA, $p = 0.9831$). There also was a significant difference between the predation rate in the two trials ($p < 0.0001$) but there was no significant interaction between the Day and Fish Size ($p= 0.7342$). This indicated that although more prey were consumed in the second trial, it did not affect the pattern of predation. This analysis showed that the predation pressure did not differ in the three treatments but did not address the issue of size selection.

The MANOVA showed a difference in the size selective predation of the different sizes of *M. beryllina* (Table 2). There was a difference between the three treatments (Fish Size) and also between the two trials of the experiment (Day). The interaction between the treatment and trial was not significant (p=0.8559). This indicated that although there were differences in the reduction of the density of each *D. lumholtzi* size class on each day, it did not affect the pattern of predation by the three size classes of *M. beryllina*. Based on the significant results of the MANOVA, we ran individual ANOVA's on the reduction in the density of each *D. lumholtzi* size class.

There were significant differences in the reduction of densities of small, large, and huge *D. lumholtzi* in each fish treatment (Table 3). Although there were significant differences between trials for the three largest *D. lumholtzi* size classes, the interaction terms were not significant for any of the *D. lumholtzi* size classes. Small *M. beryllina* reduced the density of small *D. lumholtzi* more than the large or medium *M. beryllina* (Fig. 2). There was no significant difference in the reduction of density for medium *D. lumholtzi* in the three treatments (Fig. 2). Large *M. beryllina* reduced the density of large *D. lumholtzi* significantly more than did the small *M. beryllina* (Fig. 2). The reduction of the density of large *D. lumholtzi* in the medium *M. beryllina* treatment was intermediate between the large and small fish (Fig. 2). The large *M. beryllina* reduced the density of huge *D. lumholtzi* more than the other fish treatments although only the large and medium treatments were significantly different (Fig. 2). All three size classes of *M. beryllina* consumed at least some huge *D. lumholtzi*.

Field comparison

The size distributions selected by large and small *M. beryllina* were significantly different (Kolmogorov-Smirnov, $X^2 = 259.3, p<0.0001$) (Fig. 3A). The size distribution for the large and small *M. beryllina* consists of 332 and 318 *D. lumholtzi*, respectively. Although there was a difference in the body sizes of *D. lumholtzi* selected by the two size classes of fish, they both fed on a similar range of animals (Fig. 3A). The sizes of *D. lumholtzi* selected by large and small *M. beryllina* agree with the results of the experiment. Small *M. beryllina* fed on more small *D. lumholtzi* than did the large *M. beryllina* (Fig. 3A; Table 4). Both fish sizes fed about equally on the medium *D. lumholtzi*, and the large *M. beryllina* fed most heavily on the large *D. lumholtzi* (Fig. 3A;

Table 4). Neither size class of fish fed heavily on the huge *D. lumholtzi* (Fig. 3A; Table 4), but this may have been an artifact of low abundance in the environment rather than selection against the size class.

The comparison of the body sizes of native *Daphnia* spp. selected by large and small *M. beryllina* was similar to that for *D. lumholtzi* (Fig. 3A, B). The size distributions of *Daphnia* spp. selected by the two sizes of *M. beryllina* were significantly different (Kolmogorov-Smirnov, $X^2 = 128.5$, $p<0.0001$) (Fig. 3B). The size distribution for native *Daphnia* from the large and small *M. beryllina* consists of 282 and 238 native *Daphnia*, respectively. Small *M. beryllina* preyed most heavily on the smaller bodied native *Daphnia*, but also consumed some individuals of the largest size classes. The size selective predation observed in the experiment does not appear to be unique to the case of *M. beryllina* feeding on *D. lumholtzi*.

Small *M. beryllina* selected the smaller bodied individuals whether it was feeding on *D. lumholtzi* or the native *Daphnia* (Fig. 4A). The distribution of body sizes selected was much more skewed toward smaller sizes for *D. lumholtzi* than for the native *Daphnia* spp., even though native daphnids have larger bodies. Half of the *D. lumholtzi* selected by small *M. beryllina* had a body size 0.35 to 0.52 mm (Fig. 4A; Table 4). When feeding on the native *Daphnia*, 53 % of the prey selected by small *M. beryllina* were larger than 0.76 mm (Fig. 4A). Only 6.5 % of the *D. lumholtzi* were larger than 0.76 mm, even though large *D. lumholtzi* were present in the environment (Fig. 4A; Table 4). Over 50 % of the *D. lumholtzi* eaten by large *M. beryllina* were larger than 0.76 mm (Fig. 4B; Table

4). Although large *M. beryllina* ate larger bodied native *Daphnia* than *D. lumholtzi* (Fig. 4B) the patterns of the two distributions are similar.

Discussion

Optimal foraging theory predicts that an animals will feed in such a way as to maximize its net energy gain and thereby maximize its fitness. Optimal foraging theory also predicts that when prey are abundant and handling time is not related to prey size, predators should select the largest sized prey available (Werner and Hall 1974). Size selective predation has been described for many species of fish (Brooks and Dodson 1965; Werner and Hall 1974; Eggers 1982; Unger and Lewis 1983), including *M. beryllina* (Drenner and McComas 1980; Lienesch 1997). In laboratory experiments, Drenner and McComas (1980) found that *M. beryllina* selectively fed on larger species of zooplankton. Lienesch (1997) found that adult *M. beryllina* (SL ≥ 50 mm) selectively ate the largest zooplankton species available in Lake Texoma. Optimal foraging theory also can be used to predict which size classes of a zooplankton species will be selected (Werner and Hall 1974). Werner and Hall (1974) found that bluegills, *Lepomis macrochirus*, selected the largest size classes of *Daphnia magna* when prey densities were high. The results of our experiment showed that large *M. beryllina* prey more heavily on the larger size classes of *D. lumholtzi* than do small *M. beryllina*. The field study showed that large *M. beryllina* exhibited size selective predation when feeding on *D. lumholtzi* or the native species of *Daphnia* (*D. galeata and D. parvula*).

Optimal foraging theory predicts that when prey densities are high, the range of prey sizes selected (diet breadth) will decrease (Werner and Hall 1974; Charnov 1976). At high densities the animal will encounter enough favored prey that it does not need to utilize less favored prey to maximize energy input. Therefore, when prey densities are high, the smaller sized prey decrease in the animal's diet (Charnov 1976). Unger and Lewis (1983) found that the diet breadth of *Xenomelaniris venezualae* (Atherinidae) was inversely related to fish body size. They proposed that larger fish had decreased diet breadth due to their higher encounter rate and capture efficiency (Unger and Lewis 1983). In our experiment, we used high densities of *D. lumholtzi* but found that all size classes of fish fed on all size classes of *Daphnia.* This pattern could have been a result of the 24-hr starvation period the before the experiment. Hunger level has been shown to increase the diet breadth of planktivorous fishes (Bence and Murdoch 1986; Confer and O'Bryan 1989). Our field comparisons also showed that large and small *M. beryllina* fed on a similar range of *Daphnia* sizes regardless of whether they are feeding on native daphnids or *D. lumholtzi.* The native *Daphnia* and *D. lumholtzi* were moderately abundant (>5 · liter^{-1}) on 17 and 30 of June, respectively. In fact, these two samples were selected because *M. beryllina* had fed extensively on the available *Daphnia.* Therefore, it appears that both large and small *M. beryllina* feed on the full range daphnids available, even when *Daphnia* are abundant.

We found that, unlike large *M. beryllina*, small *M. beryllina* selected the smaller size classes of native *Daphnia* and *D. lumholtzi.* Both the experimental and field portions of this study showed that small *M. beryllina* are capable of feeding on large *Daphnia*, yet small fish fed disproportionately on the smaller size class. The selection of small *Daphnia* by small fish has previously been reported for other species of fish (Hansen and Wahl 1981; Mills et al. 1984;Bence and Murdoch 1986; Parrish and Margraf 1991). Hansen and Wahl (1981) found that young yellow perch, *Perca flavescens*, selected smaller sized *Daphnia pulex* than they were capable of ingesting. They hypothesized young yellow perch selected smaller *Daphnia pulex* due to differences in handling time. Mills et al. (1984) tested this hypothesis and found no difference in handling time for young yellow perch feeding on large or small *Daphnia pulex*. They hypothesized that the digestive abilities of small perch favored the selection of mid-sized over larger *D. pulex* (Mills et al. 1984).

Handling time may play a larger role in determining the predator-prey relationship between small planktivores and spiny zooplankton. Barnhisel (1991a) found that small *Onchorhynchus mykiss* had significantly higher handling times than larger fish when feeding on *Bythotrephes cederstroemi*. When Barnhisel (1991a) removed the spine from the prey the difference in handling time between the two fish sizes disappeared. Although Barnhisel (1991a) did not address the issue of whether the size of the prey has an effect on the handling time, her results indicated that there is an effect of fish size on the handling time for spiny prey. Swaffar and O'Brien (1996) found that small bluegills (*Lepomis macrochirus*) rejected more *D. lumholtzi* than larger bluegills. They also found that bluegills eating *D. lumholtzi* exhibited a higher rejection rate than when they were feeding on *Daphnia magna* (Swaffar and O'Brien 1996).

Small *M. beryllina* appear to have difficulty handling *D. lumholtzi*. Small *M. beryllina* may capture and reject a *D. lumholtzi* many times before finally ingesting it (PWL, personal observation). Spines are common in North American species of zooplankton but they are most pronounced in smaller individuals. Dodson (1974) hypothesized that these spines protect small zooplankters from invertebrate predation. The spines are less pronounced in larger individuals because they are ineffective against vertebrate predators. *Daphnia lumholtzi* has larger spines than any *Daphnia* native to North America and the spines of *D. lumholtzi* are a larger proportion of total body length in larger individuals (Sorenson and Sterner 1992). Sorenson and Sterner (1992) noted that this contradicts predictions by the invertebrate predation hypothesis (Dodson 1974). Work and Gophen (1995) found that the size of the helmet and tail spine relative to body size of *D. lumholtzi* increased from winter to summer. Summer is a period of extensive zooplanktivory due to high abundances of larval and juvenile fishes. Furthermore, Tollrian (1994) was able to induce cyclomorphosis in *D. lumholtzi* by culturing it in medium in which fish had been kept. These studies indicated that the spines of *D. lumholtzi* may function in protecting the animal from fish predation.

During summer in Lake Texoma, native zooplankton were scarce, juvenile *M. beryllina* abundances were high, and predation on *D. lumholtzi* by adult *M. beryllina* was most intense (Lienesch 1997). This was also the time when *D. lumholtzi* spines were the largest (Work and Gophen 1995). Like *Bythotrephes cederstroemi*, *D. lumholtzi* may gain some protection from the spines if they increase the handling time for vertebrate predators, thereby lowering the value of *D. lumholtzi* compared to other large prey. Even though the value of *D. lumholtzi* may have been lower than that of a native *Daphnia* of similar body size, *D. lumholtzi* occurred when the other large zooplankton in the lake were scarce, and therefore, *D. lumholtzi* may have been the prey that optimized foraging efficiency during that period.

Daphnia lumholtzi has invaded reservoirs and lakes throughout the southeastern U.S. and is now found west to Arizona and north to Chicago (J. Havel, S.W. Missouri State University, Springfield, MO U.S.A., personal communication). Havel et al. (1995) reported that in Missouri, *D. lumholtzi* became abundant late in the summer after the period of high planktivory by larval fish, and therefore, had had no discernible impact on planktivorous fish. In Lake Texoma, *D. lumholtzi* was abundant earlier in the summer (Work and Gophen 1995; Work 1997) while juvenile fish were still abundant (Lienesch 1997). Lienesch (1997) found that *D. lumholtzi* was an additional food source for adult *M. beryllina* in Lake Texoma. The peak abundances of *D. lumholtzi* occurred in midsummer after the native species of *Daphnia* declined and therefore, the presence of *D. lumholtzi* in Lake Texoma was probably beneficial to zooplanktivorous fish (Lienesch 1997). This study showed that small *M. beryllina* also can eat *D. lumholtzi* and therefore, may have also benefited from the invasion of *D. lumholtzi.*

Acknowledgments

PWL was supported by a Centennial Research Fellowship from the University of Oklahoma. We thank K. Work for help in the field and in performing the laboratory experiments. The University of Oklahoma Biological Station provided field vehicles and laboratory space.

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Table 1. Sizes of *Menidia beryllina* and *Daphnia lumholtzi* used in the selectivity experiment. SL = standard length (i.e. tip of snout to base of tail). *Daphnia lumholtzi* were measured from the tip of the tail spine to the tip of the helmet (TL = total length; Fig. 1).

	Menidia beryllina (SL)		*Daphnia lumholtzi* (TL)
Size Class	Mean Length (mm)	Range (mm)	Range (mm)
Small	29.1	22-35	0.99 - 1.75
Medium	52.4	46-60	1.80 - 2.57
Large	74.2	67-80	2.62 - 3.44
Huge	-	-	3.50 - 5.25

Table 2. Results of Multivariate Analysis of Variance on the reduction in the density of *Daphnia lumholtzi* of four size classes by fish (*Menidia beryllina)* of three size classes. The decrease in the densities (number $\cdot$ liter^{-1}) of each of the four size classes of *D. lumholtzi* was used as the response variables in the analysis.

	F- Value	DF numerator	DF denominator	*p*-value
Fish Size	6.9644	8	28	<0.0001
Day	12.1082	4	13	0.0003
Fish Size*Day	0.4856	8	28	0.8559

Table 3. Results from Analysis of Variance tests on the reduction in the density of each size class of *Daphnia lumholtzi* during an 80 min. feeding bout by fish (*Menidia beryllina*) of three size classes.

Small *D. lumholtzi*	DF	F- Value	*p*-value
Fish Size	2	16.33	0.0001
Day	1	0.435	0.5187
Fish Size*Day	2	0.574	0.5747

Medium *D. lumholtzi*	DF	F- Value	*p*-value
Fish Size	2	0.744	0.4911
Day	1	38.06	0.0001
Fish Size*Day	2	0.087	0.9168

Large *D. lumholtzi*	DF	F- Value	*p*-value
Fish Size	2	6.799	0.0073
Day	1	5.887	0.0274
Fish Size*Day	2	0.325	0.7270

Huge *D. lumholtzi*	DF	F- Value	*p*-value
Fish Size	2	5.030	0.0202
Day	1	34.18	0.0001
Fish Size*Day	2	0.408	0.6719

Table 4. Estimated body sizes of *Daphnia lumholtzi* in the four size classes used in the experiment and percentage of *D. lumholtzi* from the stomachs of large (n=10) and small (n=10) *Menidia beryllina* collected from Lake Texoma. Percentages of *D. lumholtzi* are from 332 and 318 individuals in large and small *M. beryllina*, respectively.

Daphnia lumholtzi		Percent of *D. lumholtzi* in stomach	
Size Class	Body Size (mm)	Small *M. beryllina*	Large *M. beryllina*
Small	0.35 - 0.52	75.2	16.3
Medium	0.58 - 0.76	18.2	30.7
Large	0.82 - 1.05	6.6	52.7
Huge	1.11 - 1.46	0	0.3

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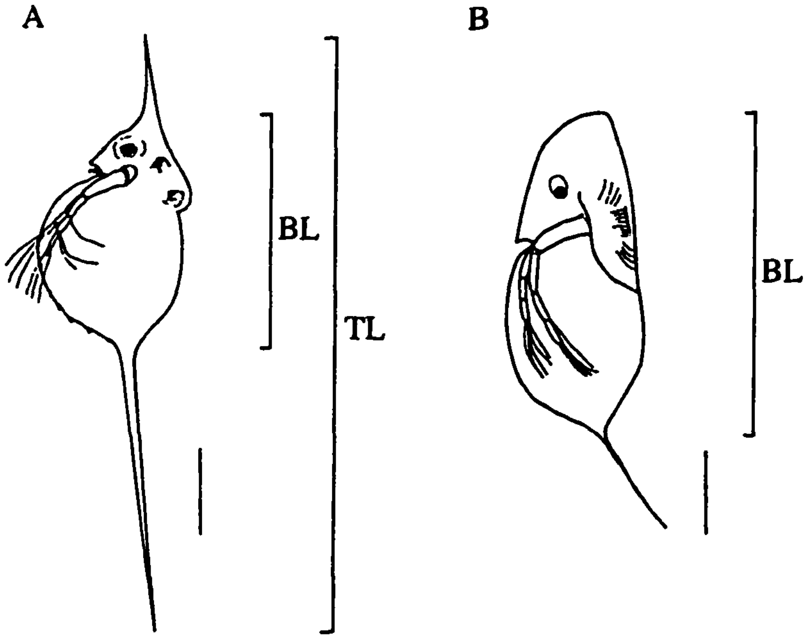
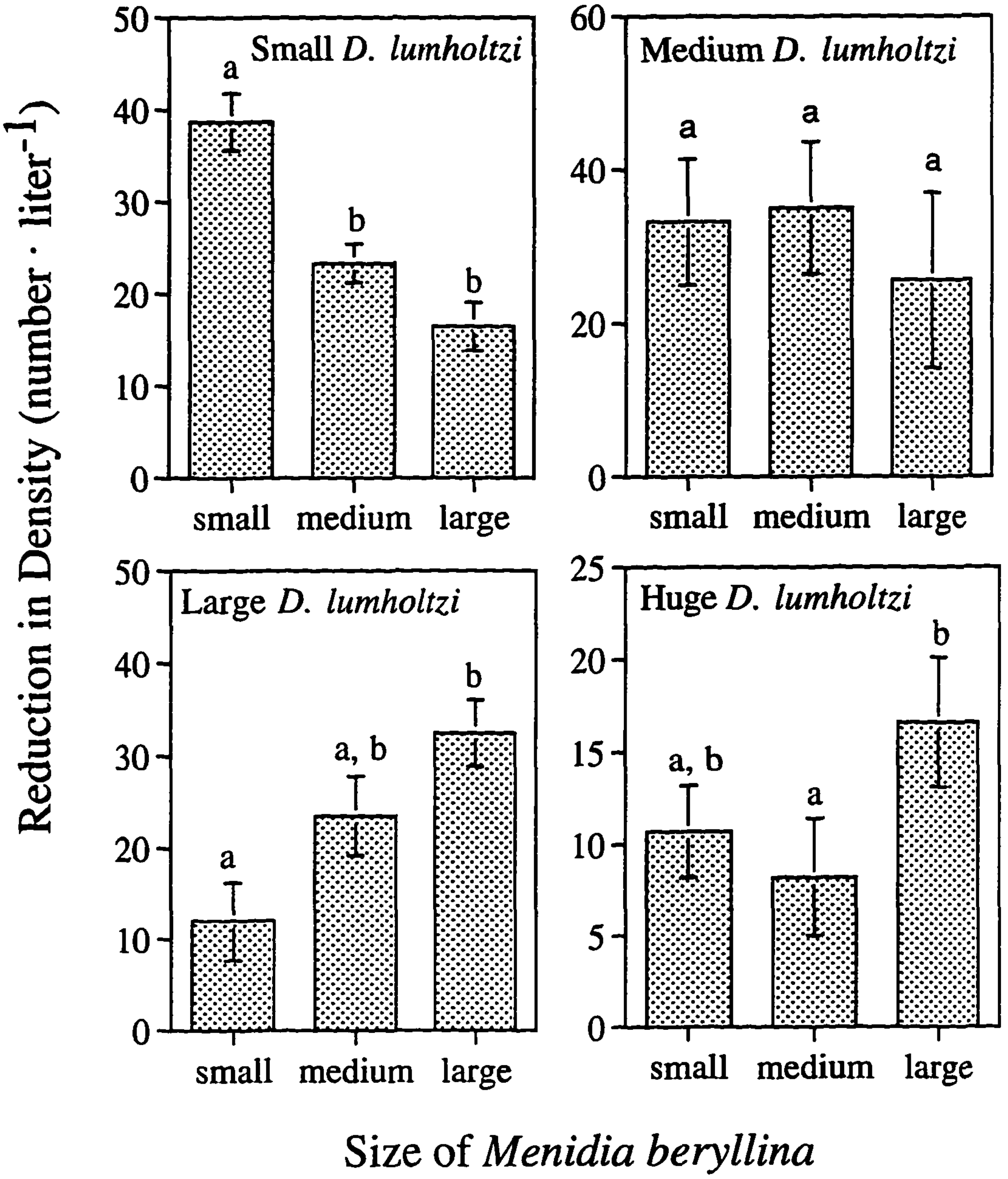
Figure 1. Points of measurement for the total length (TL) and body length (BL) of *Daphnia lumholtzi* (A), and the body length (BL) of native species of *Daphnia* (B, *Daphnia galeata* shown) (modified from Havel et al. 1995).

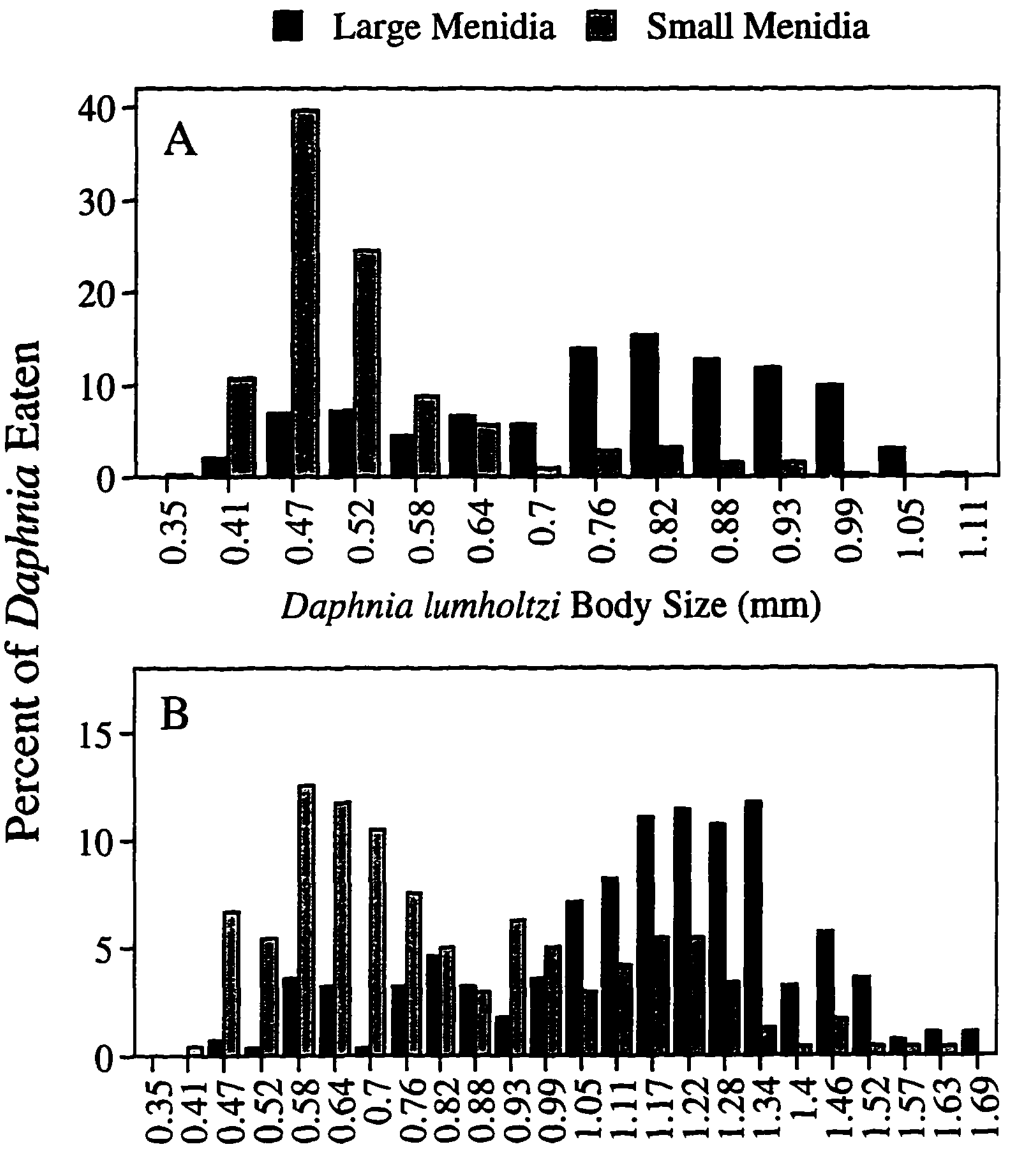
Figure 2. Reduction in density (± 1 SE) of *Daphnia lumholtzi* of four size classes by small (n=8), medium (n=8), and large (n=6) *Menidia beryllina*. Fish treatments with the same letter are not significantly different (*p*>0.05) from each other (Sheffe's multiple comparison procedure).

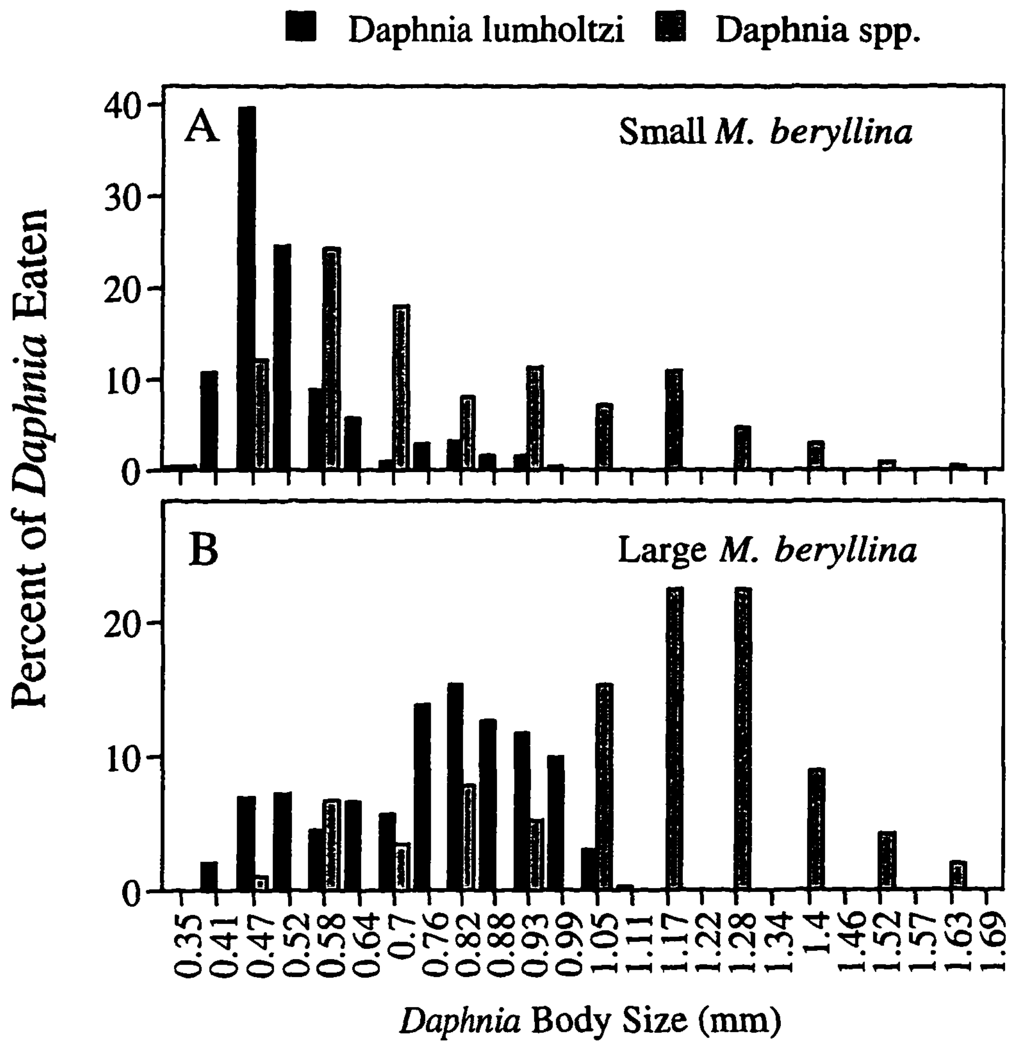
Figure 3. Size distributions of *Daphnia lumholtzi* (A) and *Daphnia spp.* (*D. galeata* and *D. parvula*) (B) ingested by large (n=10) and small (n=10) *Menidia beryllina* from Lake Texoma, Oklahoma-Texas.

Figure 4. Size distributions of *Daphnia lumholtzi* and native *Daphnia* spp. (*D. galeata* and *D. parvula*) ingested by 10 small *Menidia beryllina* on 30 and 17 June 1994, respectively (A). Size distributions of *D. lumholtzi* and native *Daphnia* spp. eaten by 10 large *M. beryllina* on 30 and 17 June 1994, respectively (B).


A
BL
TL
B
BL


Small D. lumholtzi
Medium D. lumholtzi
Large D. lumholtzi
Huge D. lumholtzi
a
b
b
a
a
a
a
a, b
b
a, b
a
b
0
10
20
30
40
50
0
20
40
60
0
10
20
30
40
50
0
5
10
15
20
25
small
medium
large
Reduction in Density (number · liter^{-1})
Size of Menidia beryllina


■ Large Menidia ▨ Small Menidia
Percent of *Daphnia* Eaten
A
0
10
20
30
40
0.35
0.41
0.47
0.52
0.58
0.64
0.7
0.76
0.82
0.88
0.93
0.99
1.05
1.11
Daphnia lumholtzi Body Size (mm)
B
0
5
10
15
0.35
0.41
0.47
0.52
0.58
0.64
0.7
0.76
0.82
0.88
0.93
0.99
1.05
1.11
1.17
1.22
1.28
1.34
1.4
1.46
1.52
1.57
1.63
1.69
Daphnia spp. Body Size (mm)



■ Daphnia lumholtzi
▨ Daphnia spp.
Percent of *Daphnia* Eaten
A
Small *M. beryllina*
40
30
20
10
0
B
Large *M. beryllina*
20
10
0
0.35
0.41
0.47
0.52
0.58
0.64
0.7
0.76
0.82
0.88
0.93
0.99
1.05
1.11
1.17
1.22
1.28
1.34
1.4
1.46
1.52
1.57
1.63
1.69
Daphnia Body Size (mm)

Prepared for Environmental Biology of Fishes

Daily fish and zooplankton abundances in the littoral zone of Lake Texoma, OK-TX, in relation to abiotic variables.

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Keywords: assemblage structure, meteorological, environmental, multivariate, canonical ordination, redundancy analysis, wind, wave height

Synopsis

Many studies have shown the effects of yearly or monthly environmental conditions on the structure of fish and zooplankton assemblages. Environmental conditions can also vary greatly on much shorter time scales. We tested the affect of abiotic conditions on the daily abundance of fish and zooplankton in the littoral zone of Lake Texoma, OK-TX. Fish and zooplankton were collected, and environmental variables were measured, from a site on Lake Texoma on 52 mornings from 7 June to 11 August 1993. We used partial redundancy analysis to examine the changes in fish and zooplankton assemblage in relation to changes in the abiotic conditions. After time of year was removed statistically from the analysis, no environmental variables were particularly important in determining the daily abundance of zooplankton, whereas, fish in the littoral zone appeared to respond to changes in wind velocity and wave height. Regressions of daily fish abundance against wave height showed that the response differed among species and among life-history stages within species.

Introduction

Meteorological events can have large impacts on ecosystems (Barber & Chavez 1983, 1986, Roemmich & McGowan 1995). The decreased winds and increased surface water temperatures associated with the El Nino Southern Oscillation phenomenon affect the productivity in the Pacific Ocean (Barber & Chavez 1983, 1986). Wind-induced currents are also important for the dispersal of young-of-the-year fishes in large bodies of water (Fechhelm & Fissel 1988, Fechhelm et al. 1994). Wind effects on the thermal structure of the water column can also affect fish abundances in near shore areas. When wind-induced advection increases the inshore temperature of northern Gulf of St. Lawrence, Atlantic mackerel (*Scomber scombrus*) migrate near shore (Catonguay et al. 1992) and Atlantic cod (*Gadus morhua*) migrate offshore (Rose & Leggett 1988). These studies examined environmental conditions on large temporal (monthly, annual) and spatial ($>10^5$ X km^2) scales. At smaller spatial scales (e.g., lakes and reservoirs), meteorological conditions can change on temporal scales of minutes to hours, and this may lead to large variation in the distribution of fishes in the littoral zone.

The effects of daily meteorological conditions on the horizontal and vertical distributions of fish in lakes or reservoirs has received little attention (Aggus 1979). Much of the research has concentrated on the negative effects of wind and temperature fluctuations on spawning success and recruitment (Kramer & Smith 1962, Goff 1985, Aalto & Newsome 1993). Wind has an especially strong influence on nest spawners such as smallmouth bass (*Micropterus dolomieiu*) (Goff 1985, 1986) and largemouth bass (*Micropterus salmoides*) (Kramer & Smith 1962). High winds and associated wave action and currents can damage eggs by agitation and siltation, carry larvae away from the nest, or destroy the nest (Kramer & Smith 1962, Goff 1985, 1986). High winds and subsequent high wave action can also affect the abundances of fishes in the littoral zone.

Massmann and Ladd (1952) noticed a change in the abundance of fishes along the shore of the Rappahannock River, Virginia, in less than an hour after a storm created large waves. These changes in the density of fishes could affect spatial or temporal patterns in the flow of energy and nutrients through the ecosystem.

We were interested in the effects of daily abiotic conditions, including meteorological variables, on the abundances of fishes and zooplankton in Lake Texoma, Oklahoma-Texas. Using multivariate analyses, we tested the null hypothesis that changes in abiotic conditions were unrelated to changes in littoral fish or zooplankton assemblages. Based on the results of the multivariate analyses, we also tested the null hypothesis that wave height had no effect on the daily abundances of individual species of fish in the littoral zone of Lake Texoma.

Study Site

Lake Texoma is a 36,000 hectare reservoir at the confluence of the Red and Washita Rivers (Figure 1). The reservoir was built for flood control but is also used for hydropower generation and supports an important sport fishery (Harper & Namminga 1986, Schorr et al. 1995). Our sampling site was at the University of Oklahoma Biological Station on the north shore of the Red River arm of the reservoir (Figure 1). The littoral zone is characterized by gently sloping beaches of sand or hard mud with patches of imbedded gravel. There were no aquatic macrophytes and scant accumulation of attached algae on rocks. South winds traveling toward the study site have a long fetch due to the position of a large cove on the southern shore of the reservoir (Figure 1).

Methods

We collected fish and zooplankton, and measured environmental variables from the study area on 55 mornings from 6 June to 11 August 1993. Samples were collected between 0700 - 0800 for the fish and 0800-1000 for zooplankton. Zooplankton collections were not taken on two dates due to equipment failure. Environmental variables were measured at the time of the fish collections.

On each day, fish were collected in three adjacent 20m seine hauls along the study area at the University of Oklahoma Biological Station (Figure 1). Seine hauls were parallel to and closing to shore and were taken out to a depth of approximately 1 m, with a 6.9 m X 1.3 m, 4.3 mm mesh seine with a 1.3 X 1.3 X 1.3 m bag. Fish from each haul were preserved separately in 15% formalin and transferred to 50% isopropyl alcohol for storage. Fish from each haul were identified, classified to life stage, and enumerated in the laboratory. All three samples on each date were pooled. Small fish that could not be positively identified to species (*Dorosoma petenense, D. cepedianum*; *Morone chrysops, M. saxatilis*) were lumped into generic taxa (Table 1). All other fish were identified to species and life-history stage (juvenile or adult). Abundances were log-transformed for the multivariate analyses. These species - life-history stage categories (Table 1) served as taxa in the multivariate analyses.

Zooplankton samples were collected approximately 20 m and 100 m offshore, with a 1-liter LeMotte water sampler, at 0.5 and 1.5 m depth. Four samples on each date were preserved separately with 5% sucrose formalin and returned to the laboratory. Zooplankton were concentrated by suction filtration (0.45um filters) and sorted with a Nikon SMZ-10 stereoscopic microscope (8-40X). Individuals were classified into broad taxonomic groupings but were identified to life history stage (Table 2). Each taxonomic group - life-history stage category was used as a taxon in the multivariate analyses.

Abundances of zooplankton in the four samples were combined for each date to characterize the zooplankton assemblage present at the site. The abundances of the taxa in each sample were log-transformed for multivariate analyses.

Environmental variables were measured at the site of the fish collections. We measured water temperature, wave height (crest to trough) and took a water sample for analysis with a Hach turbidometer. The wind direction and cloud cover were estimated and the wind velocity measured. Wind direction was transformed by taking the cosine of the angle from due south. This resulted in values between -1 and 1, with a value of 1 for wind from the south, 0 for wind from the east or west, and -1 for a north wind. We choose south as our orientation point because it was the prevailing wind direction, had the longest fetch across the lake, and produced waves traveling perpendicular to shore. Categorical variables, such as cloud cover, were entered into the data set using a series of dummy variables. There were three dummy variables for cloud cover (cloudy, partly cloudy, or clear), each with a value of 1 if the description was true or 0 for not true. Wind velocity was measured with an anemometer held into the prevailing wind for one minute. Lake level was taken from U. S. Army Corps of Engineers records for Denison Dam, Lake Texoma. We compared the lake level on the day of the sample to the level when the last sample was taken to determine if the lake level had risen or dropped. We created 2 dummy variables, water drop and water rise, to code for these changes. We recorded the time at which sampling began on each day and entered it rounded to the quarter hour in the data set. Day of study was recorded as the numbers of days since 6 June 1993 to indicate the temporal position of samples throughout the summer (e.g., on 12 June day of study = 6).

The same environmental variables were used in the analysis of the fish and zooplankton data with one exception. In the fish environmental data set, we included the log abundance of zooplankton as an additional variable. In the zooplankton environmental data set, we included the log abundance of fish as an extra variable.

Statistical Analysis

All multivariate analyses were performed using Canoco version 3.12 (ter Braak 1991). We performed Detrended Correspondence Analysis (DCA) separately on the fish and zooplankton abundance data sets to determine if the data were unimodal or linear (ter Braak & Prentice 1988, ter Braak 1995). We eliminated the first three samples in both data sets because they were outliers and repeated the analysis using Redundancy Analysis (RDA). Redundancy analysis uses both a sample by taxa abundance matrix and a sample by environmental variable matrix to ordinate the samples and taxa. Redundancy Analysis is similar to Principal Components Analysis (PCA) except that each axis is constrained to be a linear combination of the environmental variables. Because of this, the axis shows more of the variation in sample scores that can be explained by the environmental variables than a PCA axis created with only taxa data and then compared to the environmental data. We also ran Canonical Correspondence Analysis (CCA) and PCA on the data sets. The ordinations of the samples and taxa by all ordination techniques were similar, therefore, only the results of the RDA were reported.

We performed separate RDAs on the fish taxa abundance (52 samples) with the environmental variables (including zooplankton abundance), and on the zooplankton taxa abundance (51 samples) with the environmental variables (including fish abundance). We then performed partial RDAs including the environmental variable 'day of study' as a covariable. The partial RDA eliminated the variance in taxon abundances which was explainable by 'day of study', and performed RDA on the residual variance using the environmental variables other than 'day of study'.

Based on the results of the RDA and partial RDA, we examined the specific effect of wave height on the daily abundances of fishes. To examine how the assemblage responded to wave height, we regressed the sample scores for partial RDA Axis 1 and Axis 2 against the wave height (Sokal & Rohlf 1981). We also tested change in abundance of each taxon with wave height. To eliminate changes in the abundance of the taxa caused by temporal processes in the reservoir, we performed a polynomial regression of the log abundance of each species of fish with the environmental variable 'day of study'. The residual abundance from the regression was then regressed against wave height.

Results

Zooplankton Data

Copepod nauplii dominated the zooplankton assemblage, accounting for > 70% of the individuals (Table 1). *Diaphanosoma* sp. (5.4%), *Bosmina* sp. (6.6%) and the exotic *Daphnia lumholtzi* (6%) were the most abundant large zooplankters. Daily densities ranged from 7.5 to 359.5 individuals liter^{-1}.

The DCA sample scores for zooplankton data ranged 1.52 standard deviations (SD) with 51 of the 54 samples occurring within 1.35 SD. This indicated that the zooplankton taxa responded monotonically along the ordinated samples, and therefore, linear methods were more appropriate (ter Braak & Prentice 1988, ter Braak 1995).

The RDA showed the first axis to be associated with variables that changed relatively constantly throughout the study (day of study, temperature, turbidity, lake level; Figures 2c, d, e) whereas Axis 2 was correlated with wind related variables (wind, wind direction, wave height) that showed no discernible trend in time. There was a high water event just before the study began, which influenced the observed changes in turbidity and lake level

(Figure 2). As the study progressed, the water level dropped (Figure 2e) due to release of water from the dam and turbidity decreased (Figure 2d) as the inflow of clay and sediments from the Red River decreased. Temperature steadily increased from 7 June to 11 August (Figure 2c). All three variables were highly correlated with the variable 'day of study', which was included as a measure of the position of the samples through time. Temporal changes in the abundances of zooplankton and fish throughout summer in Lake Texoma are well known (Threlkeld 1986, Gelwick & Matthews 1990, Work 1997). After a peak in zooplankton abundance in early summer, Lake Texoma experiences an annual decline in zooplankton abundance (Matthews 1984, Threlkeld 1986, Lienesch 1997, Work 1997). Gelwick and Matthews (1990) found seasonal changes in the fish assemblage in the littoral zone of Lake Texoma. Many species of fish spawn in the spring and early summer, resulting in increasing abundances of juveniles during this period (Mense 1967, Lienesch 1997). Later in the summer, the abundance of adults may increase as the young-of-the-year reach adult size classes.

We were interested in how daily environmental variables affected fish and zooplankton abundances, so we wanted to eliminate the effects of seasonal changes in population abundance from the anlysis. To eliminate the influence of the temporal positioning of samples on the analysis, we performed partial redundancy analysis using the environmental variable 'day of study' as a covariable.

'Day of study' accounted for 27.7% of the variance in zooplankton abundance in the initial RDA. After 'day of study' was included as a covariable, the first two axes explained 35.2 percent of residual variance in the zooplankton assemblage data (Table 3). The sum of the constrained axes was much lower than the sum of unconstrained axes. This indicated that the environmental variables did a poor job of explaining the residual variance present in the zooplankton abundance data. Whereas little of this residual variance was explainable by the environmental data, the first two axes represented much of that variance which was explainable (75.1%, Table 3). Monte Carlo randomized permutation tests (Canoco, ter Braak 1987) were significant on the first axis and the overall ordination (first axis F-ratio = 11.48, $p < 0.01$; overall F-ratio = 2.44, $p < 0.01$).

The biplot generated by RDA shows the correlation of taxa and environmental variables with each other and with the biplot axes (Figure 3). The continuous environmental variables are represented by arrows in the RDA biplots. The direction the arrow points shows the direction of the gradient and the length of the arrow shows the strength of the gradient. Arrows which point in opposing directions indicate variables that are negatively correlated. Categorical variables (dummy variables), such as cloudy, partly cloudy and clear, are represented by points. The point represents the centroid of the variable. The taxa are also represented by arrows in the biplot. The direction of the arrow shows the direction of increased taxon abundance and the length of the arrow indicates the strength of the abundance gradient. Short arrows, either for environmental variables or taxa, indicate that the variable is not correlated with either axis of the biplot. The proximity of species arrows and environmental variable arrows indicates the strength of the correlation between the two.

After the influence of 'day of study' was removed from the data set, changes in water level, fish abundance, and wave height were important in explaining the residual variance in zooplankton abundance on the first axis (Figure 3). Temperature and turbidity were negatively correlated with each other ($r = -0.751$) but highly correlated with the second axis($r = -0.847, 0.707$; respectively) (Figure 3). None of the environmental variables accounted for more than 9% of the residual variance. Seven of the nine taxa comprising native zooplankton responded similarly throughout the study. They all were correlated positively with Axis 1 and negatively with Axis 2 (Figure 3). The native zooplankton were negatively correlated with temperature, fish abundance, and rising water but showed no correlation with wind, wave height, or wind direction. The two size classes of *Daphnia lumholtzi* (Large *D. lumholtzi* and Small *D. lumholtzi*) an exotic species which recently invaded Lake Texoma, correlated negatively with axis one and axis two but was positively correlated with wave height and wind velocity (Figure 3).

Fish Data

Nineteen species of fish comprising thirty-three taxa (species life history stages) were collected during the study (Table 3). The community was dominated by *Menidia beryllina* and *Dorosoma petenense*, but six other species were common (>90 individuals taken). All 33 fish taxa were included in the ordination by redundancy analysis, but only common taxa were well represented on the first two axes, thus, rare taxa were not included in the ordination diagrams (Figure 4a).

The sample scores on the first DCA axis had a range of 2.35 standard deviations (SD) with 52 of the 55 samples occurring within 1.05 SD. Like the zooplankton analysis, we eliminated the first three samples as outliers and repeated the analysis using linear techniques (RDA).

The initial redundancy analysis showed that 'day of study' accounted for 16.7 % of the total variance in the fish assemblage data. When 'day of study' was included as a covariable, 26.7% of the remaining variance was accounted for on the first two axes (Table 3). Like the zooplankton analysis, the sum of the constrained eigenvalues was much lower than the sum of the unconstrained eigenvalues (Table 3). The first two axes of the partial RDA explained 68.6 % of the residual variance that could be explained by the environmental variables. This indicated that the ordination diagram (Figure 4a) summarized the relationships between the fish assemblage and the environmental variables well. Randomized permutation tests on the first axis and the overall ordination were significant (first axis F-ratio = 7.97, $p < 0.01$; overall F-ratio = 2.01, $p < 0.01$).

Wind and wave height were the two most important environmental variables in the partial RDA (Figure 4a). They were highly correlated with each other (r = 0.9126) (Figure 4a) and positively correlated with both Axis 1 and Axis 2 (Figure 4a). Because the variance accounted for by 'day of study' was eliminated from the analysis, turbidity, temperature, and water level were relatively unimportant in explaining the residual variation. Unlike in the zooplankton analysis, the fish taxa did not respond similarly to the environmental variables. The abundances of juvenile *Dorosoma cepedianum* and *D. petenense* were highly correlated with axis one and wind from the south (Figure 4a). Juvenile *Notropis atherinoides* was highly correlated with rising water, wind, and wave height (Figure 4a). Juvenile *Morone chrysops* abundance was highly correlated with cloudy skies, wind, and wave height (Figure 4a). The abundance of adult *Cyprinella lutrensis* was negatively correlated with wind and wave height. The four taxa that showed the strongest change in abundance with the environment (i.e., the longest arrows) all increased with Axis 1 and either increased on or showed no correlation with Axis 2 (Figure 4a). The distribution of samples on the first two partial RDA axes even distribution of samples along axis 1 and clumped distribution on axis 2 (Figure 4b). At our study site, wave height is a function of wind velocity and wind direction and therefore, the three variables are not independent. Because wave height is the more biologically meaningful variable to aquatic organisms, we used it to examine the response of fish to the suite of wind related variables

Wave Height Regressions

The sample scores on partial RDA Axis 1 and Axis 2 were positively correlated with wave height (Figures 5, 3a, b). The relationship was much stronger on Axis 1 (p <0.0001), on which, wave height accounted for 28.8% of the variance in sample scores

(Figure 5). Partial RDA Axis 2 was weakly related to wave height ($p = 0.0300$) with only 9.1% of the variance explained (Figure 5).

There was a significant relationship between wave height and daily abundance of four of the eleven most abundant fish taxa (Figure 6). Regressions of the residual adundance of each taxon (after the effects of 'day of study' were removed) on wave height were non-significant for seven of the eleven taxa examined (Figure 6). The residual abundance of juvenile *Morone chrysops*, juvenile *Notropis atherinoides*, and adult *Dorosoma petenense* all showed positive correlations ($p < 0.0001$, $p = 0.0012$, $p = 0.048$, respectively) with wave height (Figure 6). Juvenile *Menidia beryllina* showed a significant negative relationship to wave height ($p = 0.022$) (Figure 6). Although there was a significant correlation between the residual abundance of these species and wave height, the amount of variance explained by wave height was always < 35 % (Figure 6). Whereas both juvenile *N. atherinoides* and juvenile *M. chrysops* exhibit a positive correlation with wave height in the RDA biplot, both adult *D. petenense* and juvenile *M beryllina* were not well represented on the first two axes (Figure 4, see caption).

Discussion

Although the environmental variables in the two partial RDAs explained little of the variation in the daily abundance of fish and zooplankton, the ordinations were significantly different than random (Monte Carlo permutation tests). After removal of the variation that could be explained by the temporal spacing of the samples, the wind related variables were the most informative in explaining the remaining variation in fish abundance. Although the overall explanatory power of the environmental variables included in the analysis was weak, trends were detected in the daily abundance of fish relative to wave height.

Unlike the fish assemblage, the wind related variables were not the most informative variables in explaining zooplankton abundance. Even after 'day of study' was included as a covariable, the remaining variables which had been highly correlated with 'day of study' on axis one (temperature, turbidity, lake level) still retained about as much explanatory power as did wind. This shows that wind and wave height were not particularly important in determining the daily abundance of zooplankton. Although zooplankton have limited swimming abilities (Kerfoot et al. 1980), changes in daily abundance at our site are probably more dependent on water currents from inputs of the Red River (Threlkeld 1982, Dirnberger & Threlkeld 1986) and the patchy horizontal distribution of zooplankton in reservoirs (Thorton et al. 1990, Betsill & van den Avyle 1994).

Both adult and juvenile *Daphnia lumholtzi*, an exotic cladoceran that recently invaded Lake Texoma, were positively correlated with the wind variables in the partial RDA (Figure 2). Peak abundance of *D. lumholtzi* occurred after the decline of the native zooplankton assemblage in mid-summer (Lienesch 1997, Work 1997). Because of this, *D. lumholtzi* was not found with high densities of other large zooplankton. This may help explain why *D. lumholtzi* seemed to respond differently to environmental variables than did the native species. The most probable explanation for the correlation between abundance of *D. lumholtzi* and the wind related variables was that *D. lumholtzi* only was present in the zooplankton assemblage from mid-June to mid-July. This period (day 14 to 45 of the study) also was characterized by high winds and waves (Fig. 3B). When the analyses were restricted to this time period, *D. lumholtzi* was still positively correlated with wave height although the correlation was weak ($r = 0.261$). One mode by which wind could have a positive effect on littoral abundance of *D. lumholtzi* is by creating surface currents (Wetzel 1983) capable of transporting zooplankton from the pelagic zone to the near shore area.

When the influence of 'day of study' was removed from daily fish abundance, temperature, turbidity, and lake level were no longer important in explaining fish abundance. Wind and wave height were the most informative variables explaining the residual variation in fish abundance. The abundances of the different species of fish did not have a common response to increased wave height. The trends we observed agree with those noted in the littoral zone of the Rappahannock River, Virginia, before and after a storm (Massmann & Ladd 1952). After the storm the abundance of *Dorosoma cepedianum* and *Morone* spp. increased and abundance of *Menidia beryllina* decreased. Although our sampling was much more extensive, we found the same responses by these fishes to increased wave action.

The increased abundance of certain species may be the result of inshore migration to take advantage of increased food availability. Massmann and Ladd (1952) noted that after the storm had passed, there was increased feeding activity at the water surface. Although *M. beryllina* are less abundant in the littoral zone on days with high waves, those that are captured on such days have fuller stomachs on average (unpublished data, D. Edds & W. J. Matthews). Wave action creates turbulence in the littoral zone and, therefore, may increase the vulnerability of both vertebrate and invertebrate prey to predation. As the waves break on the substrate along the edge of the lake, invertebrates and small fish may be transported into the water column where they are more easily detected by particulate feeding fishes. We hypothesize that increased abundance of certain species (e.g., *Morone chrysops*) is in response to increased food availability.

If food availability is the proximal cause of increases in the abundance of certain species, why do not all species respond similarly to increased wave action? One reason might be the trade-off between increased food availability and increased predation risk. The presence of predators affects use of habitat by minnows (Fraser & Cerri 1982, Power et al. 1985). Although juvenile *Menidia beryllina* were the only taxon to decrease significantly on days with increased wave height, adult *Cyprinella lutrensis* and *C. venustus* exhibited similar trends. *Menidia beryllina* are a major food source for all of the piscivorous fishes in the littoral zone. An untested hypothesis is that the decrease in *M. beryllina* may be in response to increased numbers of *Morone chrysops* and *M. saxatilis*. An alternative hypothesis is that *M. beryllina* migrate off shore to escape physical damage from the turbulence in the nearshore zone.

Wave action is an interesting phenomenon in that it is highly localized to the inshore area. The impact of wave action decreases further away from shore and with depth in the water column (Wetzel 1983), generating a horizontal and vertical gradient of disruption. Organisms which are sessile or are limited in their ability to migrate are most likely to be adversely affected by wave action. The distribution of aquatic macrophytes is limited by physical damage caused by wave action on exposed shoreline (Chambers 1987, Kautsky 1987). Unlike aquatic macrophytes, fish are highly mobile and capable of moving away from areas with unfavorable conditions. Many fishes in Lake Texoma migrate short distances to reach spawning areas or to find favorable conditions during periods of physiological stress. Adult *Morone saxatilis* migrate to the main basin of Lake Texoma in summer where they aggregate in cooler waters near the thermocline (Matthews et al. 1985). Both *M. saxatilis* and *M. chrysops* migrate up tributaries or the Red and Washita rivers to spawn each spring. Members of the sunfish family (Centrarchidae) and shad, *D. cepedianum* and *D. petenense*, typically migrate to shallow water for spawning (Pflieger 1975). The ability of fish to avoid inshore areas reduces the effect of high wave events on the population structure in the whole reservoir.

Although wave action may appear to be a disturbance to the littoral zone, it is a common phenomenon and many of the fish in Lake Texoma evolved in systems where large waves are common. Resh et al. (1988) proposed a definition of disturbance based on the average conditions encountered in the system under study. They proposed that events greater than 2 standard deviations from the long term mean constituted disturbances but they also acknowledged that disturbances were events that were not predictable (Resh et al. 1988). Under this definition, high discharges which occur annually in some creeks are not disturbances because they are predictable. Organisms in these systems have evolved in the presence of these events and in many cases are adapted to them (Harrell 1978, Meffe 1984, Minckley & Meffe 1987). A flood occurring in a normally low discharge period of the year may constitute a disturbance even though the discharge is less than that typical of an annual flood event (Resh et al. 1988). These unpredictable events may occur when vulnerable life history stages, such as larvae or juveniles, are present and therefore, may have more effect than the annual event. Although periods of high wave action could negatively affect fish populations through destruction of nests and larvae (Kramer & Smith 1962, Goff 1985,1986), it is unlikely that many juvenile or adult fish are killed due to physical damage caused by waves in Lake Texoma. Because of the swimming abilities of fishes in Lake Texoma, it is also unlikely that adults or juveniles are displaced by waves or the surface currents associated with high winds and waves.

Whereas Hubbs (1984) and Matthews (1986) reported diel differences in the abundance of fishes in the littoral zone of Lake Texoma, we observed that the distribution of fishes also can vary on a daily time scale. We assumed that the observed changes in fish abundance were due to offshore migration or movement to adjacent areas of shoreline that were protected from the waves. Although the assemblage of inshore areas varied on a daily time scale, the abundance of fishes in the reservoir were probably little affected by daily variability in environmental conditions. Although fish abundance only was measured at a small spatial scale, the inshore area, the variation observed could have effects on local processes. Daily changes in the inshore assemblage structure would have affects on competition, predator-prey interactions and system productivity.

Although it has been noted that native fishes are better adapted for surviving natural disturbances than are introduced fishes (Harrell 1978, Meffe 1984, Minckley & Meffe 1987), it is important to note where introduced fishes evolved when trying to predict their abilities to withstand the conditions in their new environment. Fish assemblages in reservoirs are artificial both from the standpoint that they are living in an unnatural environment and also in that many of them have been introduced. The status of native species is based on historical geographic range without any notion of what types of water the fish usually occurs in. Because of this, many 'native species' in reservoirs had evolved in, and were adapted to, lotic habitats. Populations of many native species are not adapted to living in lentic waters and will be eliminated or greatly reduced during the first few years after impoundment of a new reservoir (Patriarche & Campbell 1958, Timmons et al. 1978). Of the eight most abundant species in this study, three had been introduced; *M. beryllina*, *D. petenense*, and *M. saxatilis*. These three species are found along the Gulf and Atlantic coasts (Lee et al. 1980) where they would presumably encounter wave action more severe than any found in Lake Texoma. This complicates the issue of what constitutes a disturbance in that different species within an assemblage may view an event differently depending on their evolutionary histories.

We have shown that the littoral zone fish assemblage of Lake Texoma is affected by wave action and can change on short temporal scales. These results have ramifications for ecological studies that attempt to characterize littoral zone fish assemblages on the basis of samples taken on a single day. A better estimate of the littoral zone fish assemblage may result from sampling on multiple days during the period being characterized.

Acknowledgments

PWL was supported by a Centennial Research Fellowship from the University of Oklahoma. We want to thank K. Work and J. Stewart for field help and M. Palmer for assistance with the multivariate statistics. Coral McCallister helped prepare the figures.

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Table 1. Species and life-history stages collected in 52 samples.

Abbreviations are used in Figure 4.

Abb.	Species Name	Life-History Stage
	Dorosoma cepedianum	Adults
D. cep J	*Dorosoma cepedianum*	Juveniles
	Dorosoma petenense	Adults
D. pet J	*Dorosoma petenense*	Juveniles
	Dorosoma spp.	Juveniles
C. ven A	*Cyprinella venusta*	Adults
	Cyprinella venusta	Juveniles
C. lut A	*Cyprinella lutrensis*	Adults
	Cyprinella lutrensis	Juveniles
	Cyprinella lutrensis X *Cyprinella venusta* hybrid	Adults
	Hybognathus placitus	Juvenile
	Macrhybopsis storeriana	Adults
	Macrhybopsis storeriana	Juveniles
	Notemigonus crysoleucas	Adults

Table 1. Continued

N. ath A	*Notropis atherinoides*	Adults
N. ath J	*Notropis atherinoides*	Juveniles
	Notropis potteri	Adults
	Notropis potteri	Juveniles
	Pimephales vigilax	Adults
	Ictalurus bubalus	Adults
	Menidia beryllina	Adults
	Menidia beryllina	Juveniles
M. chr J	*Morone chrysops*	Juveniles
M. sax J	*Morone saxatilis*	Juveniles
	Morone spp.	Juveniles
	Lepomis megalotis	Adults
	Micropterus punctulatus	Adults
	Micropterus punctulatus	Juveniles
	Micropterus salmoides	Adults
	Micropterus salmoides	Juveniles
	Percina macrolepida	Adults
	Percina macrolepida	Juveniles
	Aplodinotus gunniens	Juveniles

Table 2. Taxa and life-history stages collected in 51 zooplankton samples. Abbreviations are used in Figure 3.

Abb.	Taxa Name	Life-History Stage
Cyclo A	Cyclopoid Copepods	Adults
	Cyclopoid Copepods	Copepodites
Calan A	Calanoid Copepods	Adults
	Calanoid Copepods	Copepodites
Nauplii	All Copepod Nauplii	Nauplii
D. lum A	*Daphnia lumholtzi*	Adults
D. lum J	*Daphnia lumholtzi*	Juveniles
D. spp	Other *Daphnia* species	Adults and Juveniles
Bosmina	*Bosmina* spp.	Adults and Juveniles
Diaphan.	*Diaphanosoma* spp.	Adults and Juveniles
Cerio.	*Ceriodaphnia* spp.	Adults and Juveniles

Table 3. Summary statistics for partial redundancy analysis on fish abundance data with environmental data and the zooplankton abundance data with the environmental data. The environmental variable 'day of study' was included as a covariable.

Axes	1	2	3	4
Fish Assemblage Data				
Eigenvalues:	0.148	0.075	0.039	0.032
Species-Environment Correlations	0.761	0.685	0.738	0.661
Cumulative percentage variance of:				
Species Data	17.7	26.7	31.4	35.3
Species-Environment relations	42.8	64.6	75.9	85.2
Sum of all unconstrained eigenvalues after fitting the covariable =				0.833
Sum of all constrained eigenvalues after fitting the covariable =				0.345
Zooplankton Assemblage Data				
Eigenvalues:	0.0175	0.080	0.034	0.022
Species-Environment Correlations	0.0859	0.667	0.644	0.601
Cumulative percentage variance of:				
Species Data	24.2	35.2	39.8	42.9
Species-Environment relations	51.6	75.1	85.0	91.5
Sum of all unconstrained eigenvalues after fitting the covariable =				0.732
Sum of all constrained eigenvalues after fitting the covariable =				0.339

List of Figures

Figure 1. Map of Lake Texoma (OK-TX) indicating the sampling site at the University of Oklahoma Biological Station.

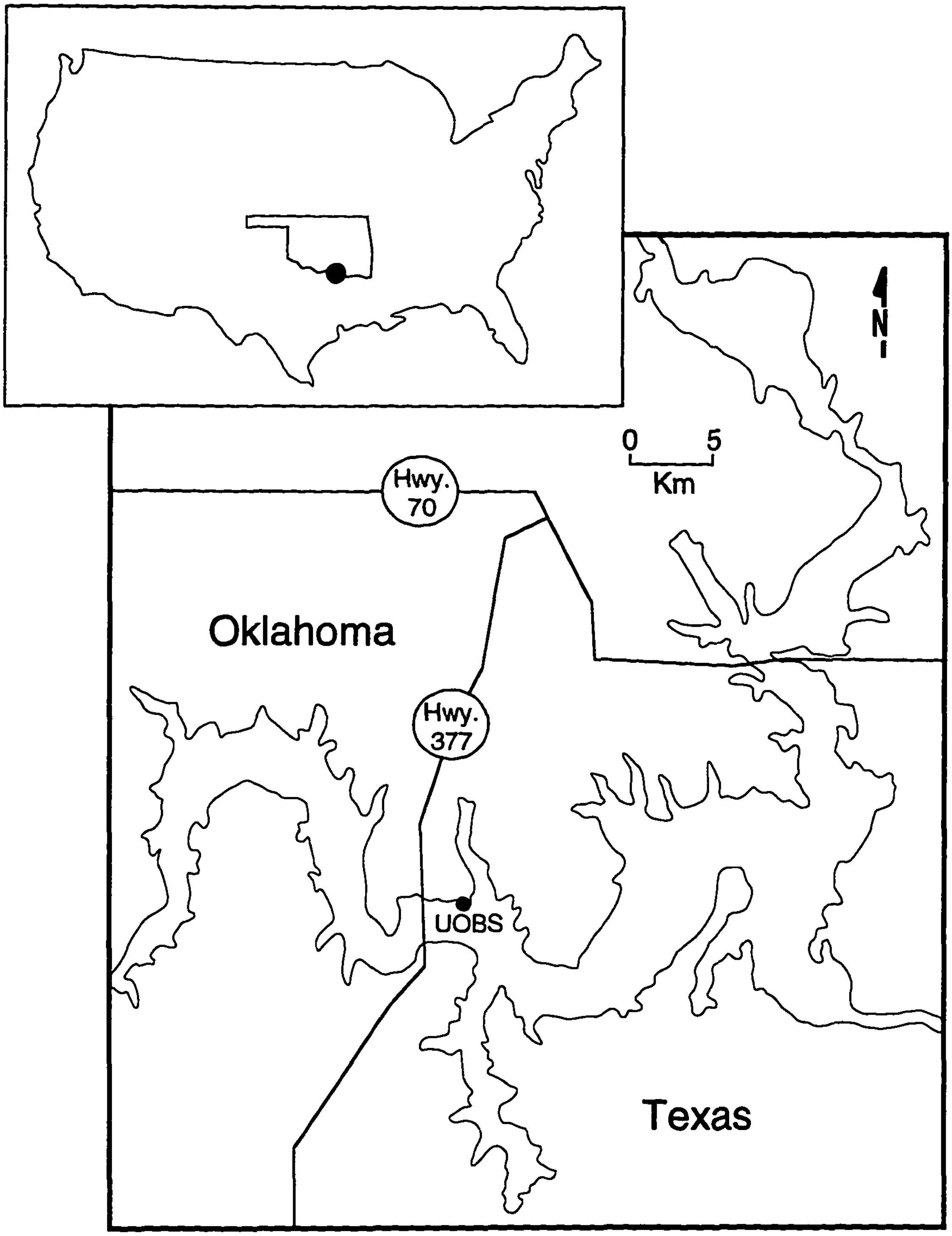
Figure 2. Changes in fish assemblage (a), wave height (b), temperature (c), turbidity (d), and lake level (e) throughout the 63 day sampling period (day 6 was 12 June 1993). The first three samples were eliminated as outliers. The change in fish assemblage was indicated by the sample score on the first axis from the partial redundancy analysis.

Figure 3. Biplot of environmental variables and zooplankton taxa from a partial redundancy analysis including 'day of study' as a covariable. The analysis is based on the daily environmental conditions and the abundances of zooplankton taxa. The biplot shows the first and second RDA axis. The abbreviations of the zooplankton taxa are the same as in Table 2. Environmental variables and zooplankton taxa with weak correlation to the first two axes (i.e. represented by short arrows) were not included in the diagram. For an explanation of the relationship between environmental variables, taxa, and RDA axes, see text.

Figure 4. Biplot of Lake Texoma's daily environmental conditions and abundance of fish taxa (a) from a partial redundancy analysis including the 'day of study' as a covariable. Plot of samples on the first two axes of the partial redundancy analysis (b). The abbreviations are the same as in Table 3. Details as in Figure 3.

Figure 5. Regression of the sample scores on partial redundancy axis 1 and 2 for each day against wave height. The sample scores were produced based on the abundances of fishes present in the Littoral zone of Lake Texoma on each day and therefore were used as indicators of the fish assemblage. The regression of sample scores against wave height was significant for both pRDA axes (P=0.0001 for axis 1 and p=0.0300 for axis 2).

Figure 6. Regressions of the residual log abundance of eleven fish taxa after regression with the day of study variable. Day of the study was regressed on the log abundance for each of the eleven most abundant fish taxa. The residual log abundance for each sample was then regressed on wave height from the day the sample was collected.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5
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Hwy. 70
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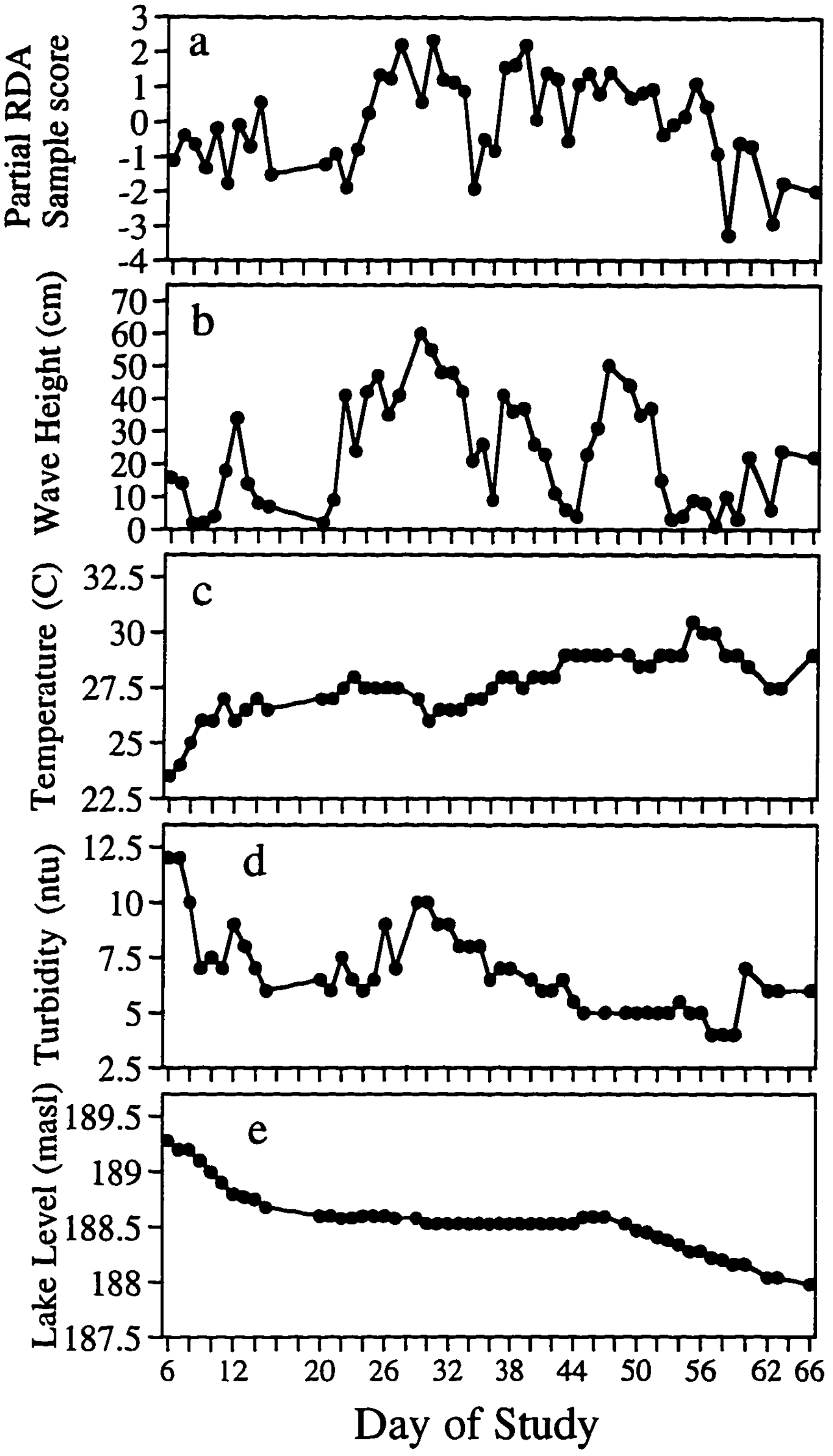
Partial RDA Sample score
3
2
1
0
-1
-2
-3
-4
a
Wave Height (cm)
70
60
50
40
30
20
10
0
b
Temperature (C)
32.5
30
27.5
25
22.5
c
Turbidity (ntu)
12.5
10
7.5
5
2.5
d
Lake Level (masl)
189.5
189
188.5
188
187.5
e
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12
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26
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38
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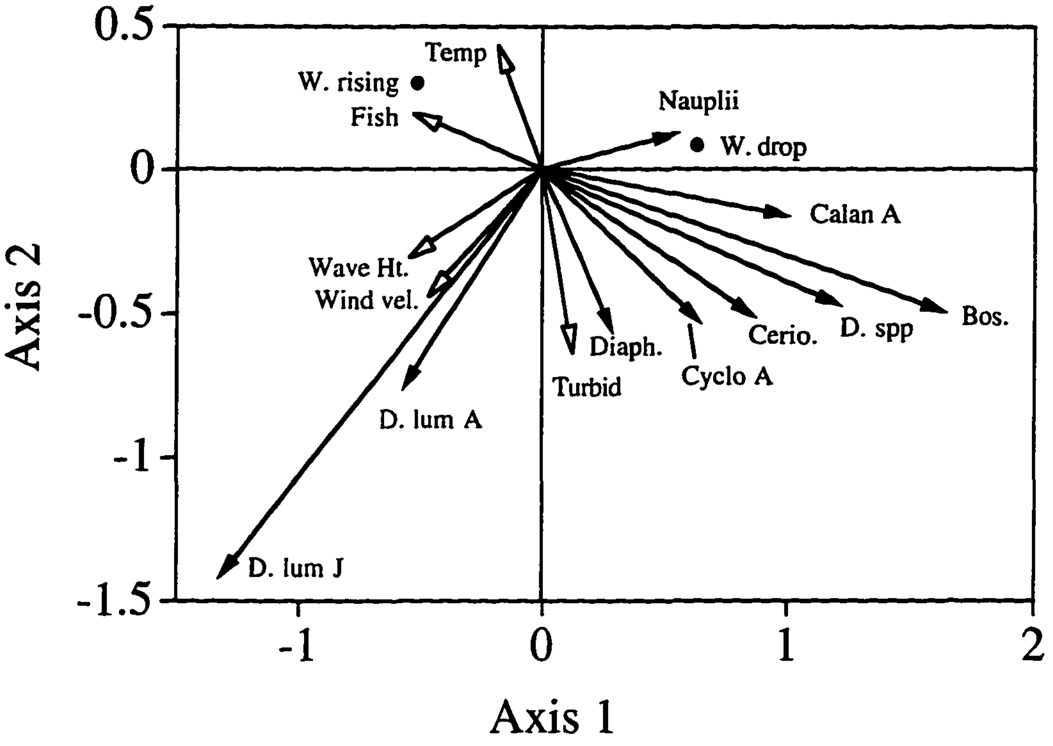
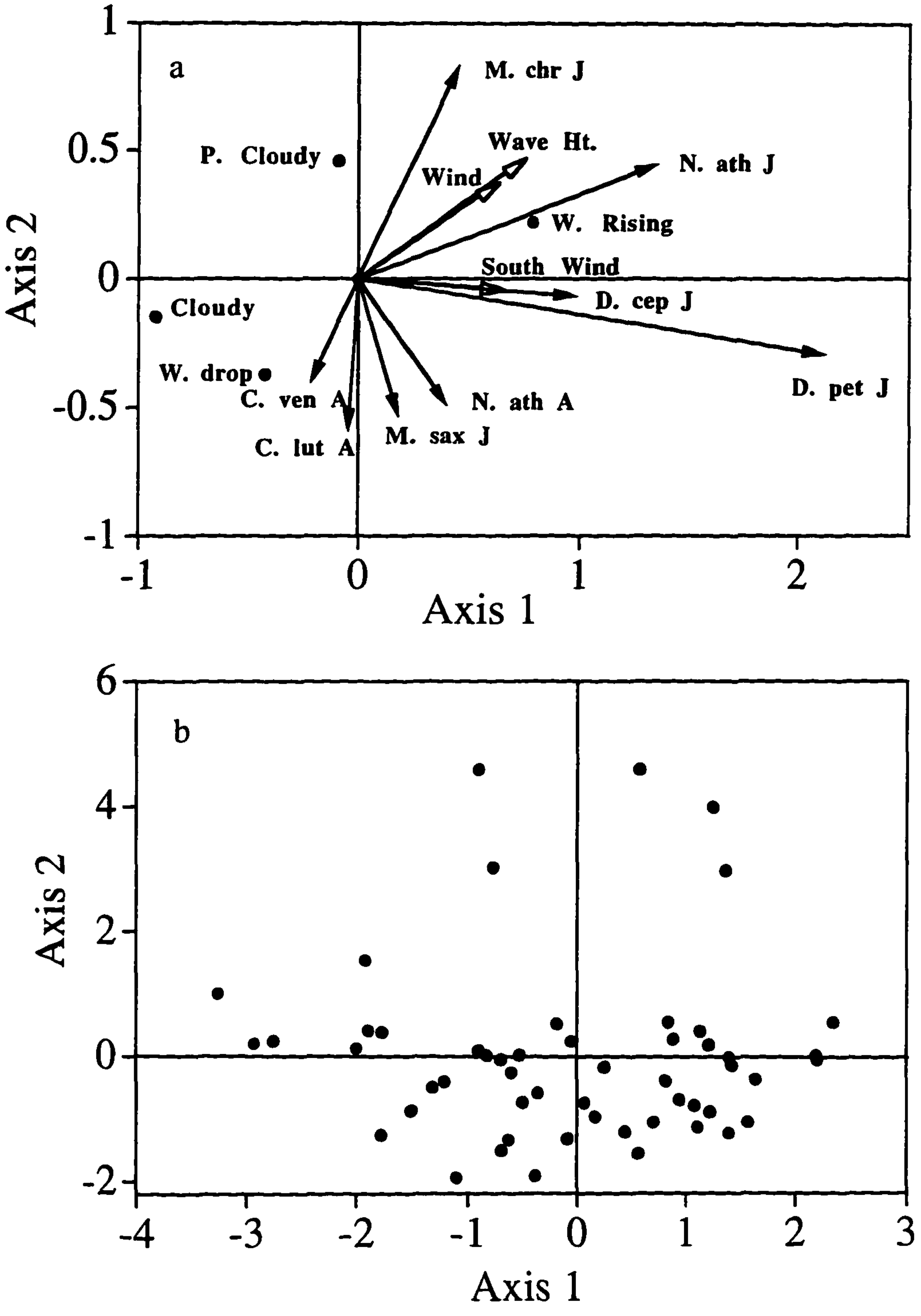
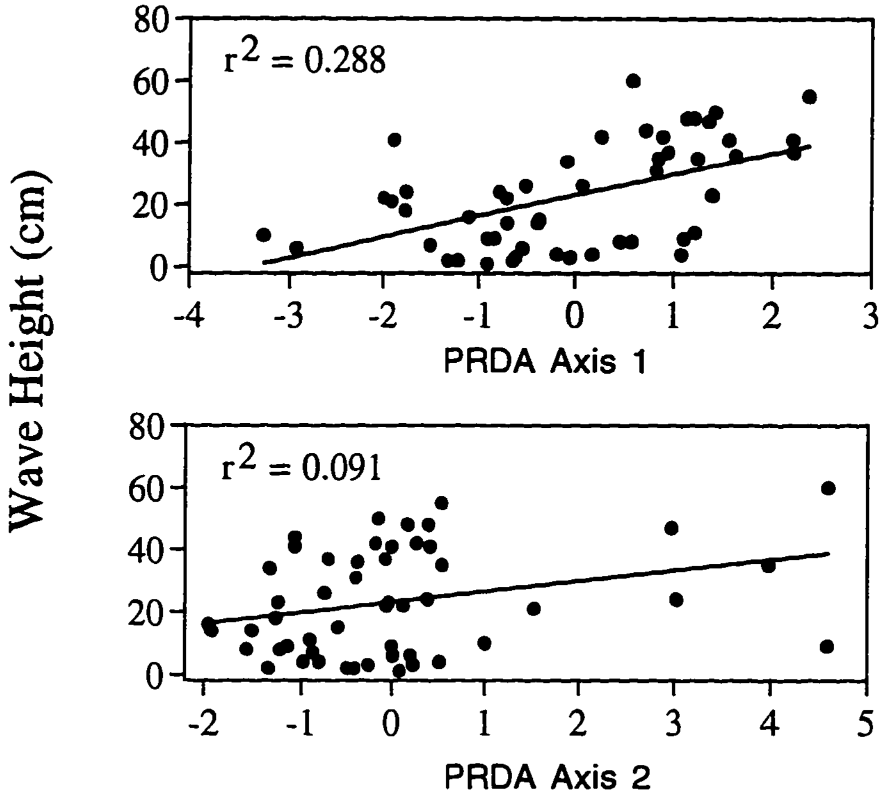
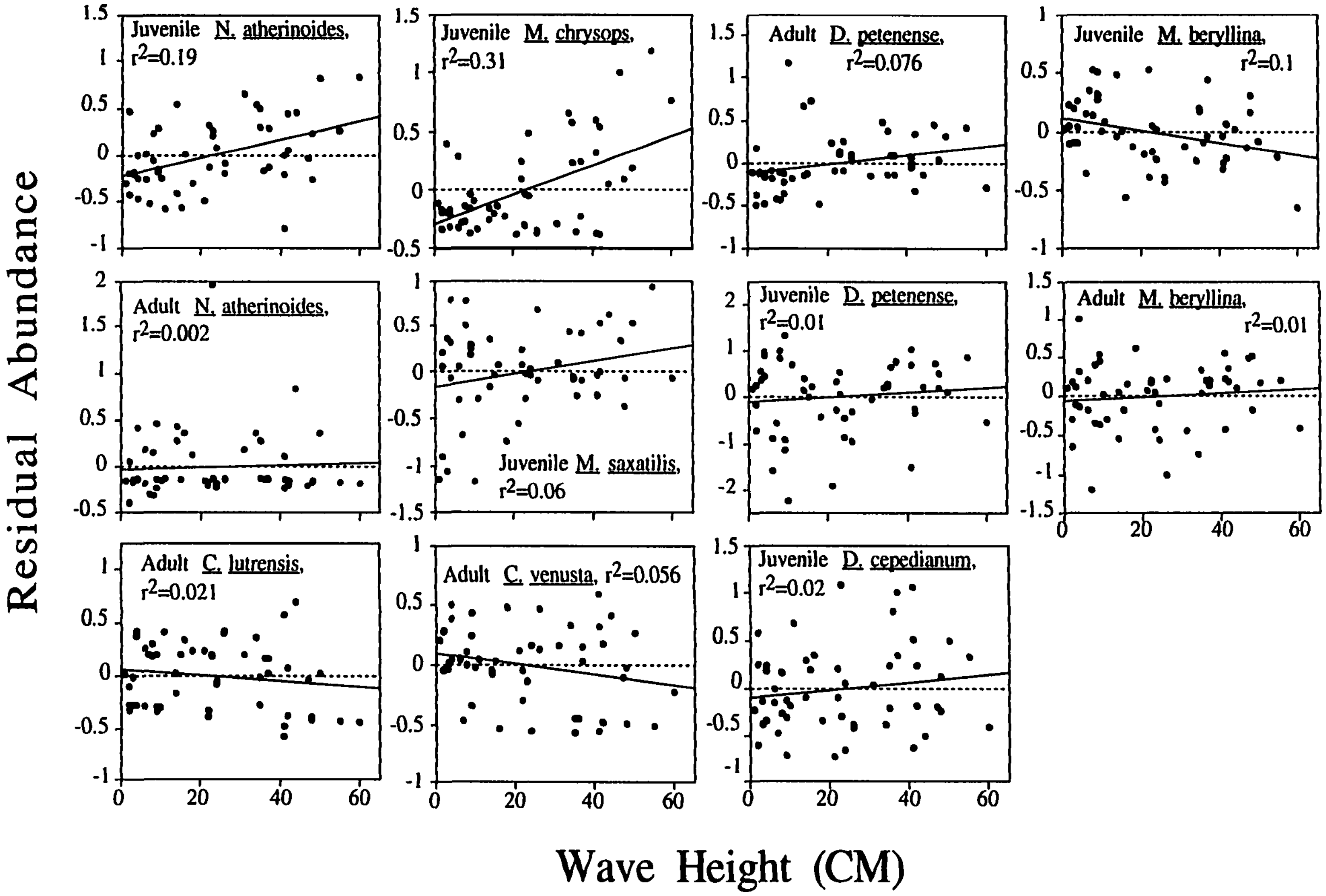
50
56
62
66
Day of Study


Temp
W. rising
Fish
Nauplii
W. drop
Calan A
Wave Ht.
Wind vel.
Bos.
D. spp
Cerio.
Diaph.
Cyclo A
Turbid
D. lum A
D. lum J
0.5
0
-0.5
-1
-1.5
-1
0
1
2
Axis 1
Axis 2


a
M. chr J
Wave Ht.
Wind
N. ath J
P. Cloudy
W. Rising
South Wind
D. cep J
Cloudy
D. pet J
W. drop
C. ven A
N. ath A
M. sax J
C. lut A
Axis 2
Axis 1
1
0.5
0
-0.5
-1
-1
0
1
2
b
Axis 2
Axis 1
6
4
2
0
-2
-4
-3
-2
-1
0
1
2
3


Wave Height (cm)
80
60
40
20
0
r^2 = 0.288
-4
-3
-2
-1
0
1
2
3
PRDA Axis 1
80
60
40
20
0
r^2 = 0.091
-2
-1
0
1
2
3
4
5
PRDA Axis 2


Juvenile N. atherinoides, r²=0.19
Juvenile M. chrysops, r²=0.31
Adult D. petenense, r²=0.076
Juvenile M. beryllina, r²=0.1
Adult N. atherinoides, r²=0.002
Juvenile M. saxatilis, r²=0.06
Juvenile D. petenense, r²=0.01
Adult M. beryllina, r²=0.01
Adult C. lutrensis, r²=0.021
Adult C. venusta, r²=0.056
Juvenile D. cepedianum, r²=0.02
Residual Abundance
Wave Height (CM)
0
20
40
60