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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

ECOSYSTEM EFFECTS OF OMNIVOROUS FISHES 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

Keith B. Gido
Norman, Oklahoma
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ECOSYSTEM EFFECTS OF OMNIVOROUS FISHES IN LAKE TEXOMA (OKLAHOMA-TEXAS)

A Dissertation APPROVED FOR
THE DEPARTMENT OF ZOOLOGY

BY

William Matthews (advisor)

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PREFACE

The three chapters of this dissertation have been prepared in submission format and include co-authors. Chapter 1 is formatted for *Ecological Applications*. Chapter 2 is formatted for *Journal of Fish Biology*, and Chapter 3 is formatted for *Ecology*.

ACKNOWLEDGMENTS

I am very fortunate to have come to the University of Oklahoma and to have worked with the many extraordinary people at this institution. This experience has been educational and enjoyable thanks to the faculty, graduate students, and staff in the Department of Zoology and at the Biological Station. I have listed individuals for their particular roles at the end of each chapter, however I would like to extend special thanks to several people. Foremost, I am greatly in debt to my major professor Bill Matthews for his friendship and guidance. No other person could have served as a better mentor. My committee members, Larry Canter, Mike Kaspari, Bill Shelton, and Caryn Vaughn always found time to comment on the design and writing of my dissertation. Interactions with the Matthews Lab was an integral part of my education. Jake Schaefer, my academic brother, and Edie Marsh-Matthews provided important field assistance, statistical advice, and critical evaluations of my chapters. Kirsten, Phil, Karl, Chad, and Keri all listened to and commented on my research ideas. I could not have completed the field research necessary for chapter one without the assistance of Bill Wolfinbarger, with whom I spent numerous weekends gill netting Lake Texoma. I will probably never be able to repay him for this. Andy Marsh provided necessary assistance with my field experiment in Chapter 3. My parents, Richard and Winnie Gido not only provided moral support, but were a loyal field crew. Finally, and most of all, I must recognize the support and understanding of my wonderful wife, Sarah. Thank you for not letting me take myself too seriously.

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ABSTRACT

Understanding the dynamics of reservoir fish assemblages has important social and economical implications on a global scale. Reservoirs not only provide flood control. water storage, and hydropower, but they provide a milieu for commercial fish production and recreational fishing opportunities. Fish assemblages in reservoirs are unique in that they typically consist of species native to the impounded river and introduced species in an environment that was created, and is partially regulated by man. The focus of my research is on benthic omnivorous fishes that can dominate the total fish biomass of these systems.

In the first chapter, I examined long-term changes in the total fish assemblage of Lake Texoma. Fish were sampled year-around using gill nets in 1954, 1981-84, and 1996-97. Assemblage structure, overall, was relatively stable across years as indicated by persistence of species, significant concordance in rank abundance, and overlapping sample scores in multivariate space. Regardless of these indices. some species varied in abundance across decades. Stepwise discriminant analysis selected six species that could be used to discriminate collections among decades. A more detailed evaluation of changes in the fish assemblage between the 1980s and the 1990s, that included size-structure and species associations, also showed little variation between decades. However, two species, smallmouth buffalo (*Ictiobus bubalus*) and striped bass (*Morone saxatilis*) < 250 mm, appeared to have increased in abundance in the 1990s. These data were then used as a baseline to assess the effect of a severe drought during the summer of 1998 on fish assemblage structure. Overall, percent similarity of the fish assemblage

sampled in 1998 with non-drought years was within the range of values for comparisons among non-drought years.

In the second chapter, I describe the feeding ecology of three benthic omnivores and develop hypotheses on the potential ecosystem-level effects of these species. Distribution, abundance, and diet of smallmouth buffalo, river carpsucker (*Carpiodes carpio*), and gizzard shad (*Dorosoma cepedianum*) relative to the availability of potential resources were examined during summer 1997 and 1998. During July and August, abundance of smallmouth buffalo was significantly greater at stations with depths of 10 m than at 1 or 3 m stations. There was no significant difference in abundance of gizzard shad or river carpsucker by depth or month. Relative proportions of detritus and zooplankton in the diet varied among species. Smallmouth buffalo primarily ate copepods, whereas gizzard shad primarily ate detritus. The diet of river carpsucker was intermediate in relative proportions of zooplankton and detritus to that of smallmouth buffalo and gizzard shad. Of the three species examined, only gizzard shad showed a significant decline in dietary crude protein, phosphorous, and organic content over the summer. This decline in nutritional value of food also corresponded to a decline in condition of gizzard shad. Overall, benthic invertebrates had a heterogeneous distribution within the reservoir, but percent organic content in sediments varied little over sample stations. The relative importance in ecosystem functioning of these large-bodied omnivorous fish, all of which are highly abundant in southern reservoirs, may partially depend on species specific feeding ecology and environmental conditions.

In the third chapter, I developed a model and a field experiment to further

examine the effects of these three species on ecosystem properties. In the first experiment I measured ammonia and phosphate excretion rates for each species. I then modeled nutrient loading for the reservoir that could be attributed to fishes on the basis of mean excretion rates, estimates of standing crop, and diel patterns of foraging activity. Gizzard shad had the highest mass-specific nutrient excretion rates, partly due to its smaller body size. Assuming a standing crop for the three species at 191.6 kg ha^{-1}, phosphorous loading by these fishes was estimated at 9.60 g $\text{ha}^{-1}\text{d}^{-1}$, which exceeds external loading rates from the watershed during low inflow periods. In the second experiment I used field enclosure/exclosures to examine the effect of foraging by these species on biota and organic matter in sediments. The exclusion of large fishes from foraging on benthic sediments was shown to significantly increase abundance of midge larvae (Chironomidae). However, in fish enclosures, only gizzard shad and smallmouth buffalo significantly depressed abundance of midges below that in exclosures; river carpsucker did not appear to affect midge abundance. Other sediment characteristics such as percent organic matter, algal abundance, and other macroinvertebrate abundances showed no significant differences among treatments. Omnivorous fishes have the potential to influence ecosystem-level properties in a variety of ways. However, because of the variable nature of reservoirs, effects of fishes are likely dependent on environmental conditions.

Chapter 1: Long-term variation in the offshore fish assemblage of Lake Texoma: stability in an unpredictable environment

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Abstract

Long-term variation in the offshore fish assemblage of Lake Texoma (Oklahoma-Texas) was examined across 43 years. Fish were sampled year-round using gill nets for the following time periods: 1954, 1981-84, and 1996-97. Assemblage structure, overall, was relatively stable across years as indicated by persistence of species, significant concordance in rank abundance, relatively low CV of species abundances among years, and overlapping sample scores in multivariate space. Regardless of these indices, some species were shown to vary in abundance across decades. Using stepwise discriminant analysis we were able to selected six species that could be used to discriminate collections among decades. A more detailed evaluation of changes in the fish assemblage between the 1980s and the 1990s, that included size-structure and species associations, showed little variation between decades. However, two species, smallmouth buffalo (*Ictiobus bubalus*) < 400 mm and striped bass (*Morone saxatilis*) < 250 mm were in greater abundance in the 1990s. The data from the 1980s and 1990s were also used as a baseline to assess the effect of a severe drought during the summer of 1998 on fish assemblage structure. Fish assemblage structure and condition of individuals after the drought was not different than during non-drought years. Based on this and previous studies, the fish assemblage in Lake Texoma appears to be relatively stable, however there is some evidence to suggest populations of introduced species are more susceptible to abiotic disturbances than native riverine fishes.

Introduction

Reservoir fisheries are economically important on a global scale for recreational and subsistence purposes (e.g., Fels and Keller 1973, Lowe-McConnell 1987, Fernando and Holcik 1991, Miranda and DeVries 1996). Thus knowledge of population dynamics and responses of various species (particularly game and forage fishes) to reservoir aging could have important management implications. However, the determination of the relative stability of these systems needs to be evaluated over long time periods (i.e., several population turnovers) due to the lag-response of many species to changes in the ecosystem (Connell and Sousa 1983). Such long-term studies also can answer basic ecological questions (Cody and Smallwood 1996) and be used as a baseline to compare the effects of species introductions (Elliott 1990). In this study, we examined long-term variability of the offshore fish assemblage in a large southern U.S. reservoir based on year-round sampling of the fish assemblage with gill nets. We use these data to characterize long-term variation and comment on the resistance and resilience of the fish assemblage to several biotic and abiotic disturbances at our study site.

From a basic ecological perspective, long-term monitoring of a reservoir fish assemblage is informative due to the artificial nature of reservoirs and their short history of occurrence (< 60 yrs). One might ask if fish assemblages in these systems have approached an equilibrium state or if they are continually developing (e.g., undergoing succession) or adapting to this new environment? Fish assemblages in natural lakes, which have a long history of co-occurrence, have developed tightly linked associations among species (e.g., MacLean and Magnuson 1977, Carpenter et al. 1985). Fish reproduction in lakes may also be timed to exploit seasonal pulses of zooplankton abundance, presumably a result of coevolution (Noble 1986). In contrast, species associations among reservoir fishes may be weakly linked and reproduction poorly synchronized with invertebrate prey abundance (Noble 1986). Moreover, reservoir fishes may be continually adapting to changes in their environment, such as unpredictable water fluctuations (e.g., June 1977) and the introduction of species (Li and Moyle 1981, Johnson et al. 1993, Wahl 1995).

Development of biotic assemblages in reservoirs has been relatively well studied within the first 5-20 years after filling. As sediments from the surrounding watershed and erosion of shorelines increase turbidity (Neel 1966, Benson 1980), reservoir phytoplankton assemblages often shift from nutrient- to light-limited species (e.g., Holz et al. 1997). Species composition and total species richness of zooplankton and benthic invertebrates can change as reservoirs age and as introduced species colonize the impoundment (Jones and Selgeby 1974, Taylor et al. 1993, Popp and Hoagland 1995, Work and Gophen 1995, Popp et al. 1996). These changes may affect fish assemblages. Growth rates and population densities are typically greatest immediately after filling of the reservoir because of increased availability of space and food resources (Patriarche and Campbell 1957, Gasaway 1970, Hashagen 1973, Walburg 1977, Shelton et al. 1979). This is typically followed by a decrease in abundance or species richness once the original, terrestrially derived nutrients are depleted (e.g., Paller et al. 1992, Ney 1996, Tereshchenko and Strel'nikov 1997).

While changes in reservoir fish assemblages < 25 years after impoundment are relatively well documented, few published studies have examined the fish assemblages in reservoirs after 40 years or more (but see Tereshchenko and Strel'nikov 1997). Several factors suggest that reservoir succession continues long after impoundment. First, the physical habitat changes throughout the life span of a reservoir. Sedimentation and erosion of shorelines continually simplify the environment, creating shallower sloped banks and turbid waters (Benson 1980). Second, many reservoirs are stochastically invaded by introduced fish, mussels, and zooplankton (Riggs and Bonn 1959, Work and Gophen 1995, Johnson and Carlton 1996). Thus, unstable food web dynamics may lead to extirpation of species that originally colonized the reservoir (Wydoski and Bennett 1981, Li and Moyle 1981, McComas and Drenner 1982). Finally, reservoirs may accumulate toxic wastes from the surrounding watershed that, over time, may adversely affect the fish assemblages (e.g., Bevelhimer and Adams 1996, Tereshchenko and Strel'nikov 1997).

The goal of our study was to examine fish assemblage structure of Lake Texoma over a 43-year post-impoundment period using data obtained from year-round gill net surveys conducted in 1956, 1981-84, and 1996-97. By sampling across six fixed habitats during 1981-84 and 1996-97 we also examined changes in species associations across habitats between these decades. Using these data as a baseline, we then assessed the stability (resistance and resilience) of the fish assemblage (sensu Connell and Sousa 1983) based on putative disturbances caused by (1) extreme weather conditions (including a severe drought during summer 1998) and (2) establishment of various introduced species.

Study area

Lake Texoma was created by the impoundment of the Red and Washita Rivers in 1943. At average pool, surface area of the reservoir is 36,000 ha, mean depth 8 m, maximum depth 26 m at the dam, and mean storage to inflow ratio (retention time) 1.1 yr. Several studies have documented the abundance and distribution of benthic invertebrates (Sublette 1957, Vaughn 1982), zooplankton (Threlkeld 1986, Work and Gophen 1995), and fishes (Riggs and Bonn 1959, Echelle et al. 1971, Matthews et al. 1985) in this system. Three major fish species introductions or invasions occurred in the reservoir since impoundment. Inland silverside, *Menidia beryllina*, was first recorded in 1953 (Riggs and Bonn 1959), threadfin shad, *Dorosoma petenense* in 1957 (Riggs and Moore 1958), and striped bass, *Morone saxatilis*, between 1965-74 (Harper and Namminga 1986). In addition, the exotic zooplankton *Daphnia lumholtzi* was first collected in the reservoir in 1991 (Work and Gophen 1995) and has persisted in high abundance through the period of this study. All collections for this study were made in the Red River arm of the reservoir, near the University of Oklahoma Biological Station (Fig. 1).

Methods

Environmental parameters - Reservoir elevation and temperature data were provided by the U.S. Army Corps of Engineers (Denison Dam). Water temperature was recorded daily near the dam at approximately 1.8 m depth since 1954. Ambient air temperature was taken from a weather station near Ardmore, Oklahoma, approximately 30 km north of Lake Texoma by the Oklahoma Climatological Survey.

Fish sampling - Fish were sampled with gill nets at least once per month during three time periods: January - December 1954, April 1981 - July 1984, and January 1996 - December 1997. We used data from these collections to examine patterns of long-term variation in the Lake Texoma fish assemblage. Although gill nets may selectively catch certain species (Jensen 1986) or size classes (McCombie and Fry 1960), they provide useful estimates of change in relative abundance (Hubert 1983). Our gill nets did not sample some abundant small-bodied fishes such as young shad (*Dorosoma* spp.) or inland silverside (*Menidia beryllina*). Thus, our analyses were restricted to larger-bodied species and size classes (e.g., fish > ca. 100 mm TL). In addition, our spatial scale of sampling was restricted to an area in the Red river arm of Lake Texoma, therefore patterns described herein may not be representative of the entire reservoir.

The 1954 fish collections were made by Dowell (1956) who used three four gill net sizes: (1) 38.1 m long x 1.8 m deep 'experimental' gill nets with five 7.62 m panels of mesh sizes 19, 25, 32, 38, 51 mm bar mesh (42% of samples); (2) 61 m long x 2.9 m deep gill nets with 76 mm bar mesh (41% of samples); and (3) 61 m long x 2.4 m deep (51 and 38 mm bar mesh) gill nets (18% of samples). Dowell had 13 sample stations in the vicinity of the University of Oklahoma Biological Station that included three coves, four shorelines, four mid-channels and one inundated creek (Fig. 1). Depths of these stations ranged from 2.1 to 12.8 m. Samples were taken throughout the year and the number of hours of gill netting ranged from 97 hrs in September to 1190 hrs in July. Most of his gill net sets were over a 24-hr period.

Samples from 1981-84 and 1996-96 were taken within the area of Dowell's stations. In the 1980s and 1990s, we used 'experimental' monofilament gill nets with multiple mesh sizes to estimate relative abundance of fishes at three sample locations that varied in depth from 2 m to 18 m in depth (Matthews et al. 1988). Each net was 61 m long and 1.83 m deep, with successive 7.6 m panels with mesh sizes of 19, 25, 38, 51, 64, 76, 89, and 102 mm bar measure. Nets were set approximately every two weeks from April 1981 to July 1984 and every three weeks between January 1996 and December 1997. Two nets (one 'surface' and one 'bottom') were set at each location in the afternoon and retrieved the following day, beginning at 0900 hours and ending by early afternoon (average set time was 20 hrs). Bottom nets were set with the lead line directly on the substratum, and surface nets were set with the top line ca. 0.5 m below the surface. All fish were identified to species, weighed, and measured. In addition to the above sampling, one sample at each of the three locations (surface and bottom) was taken in September 1998 to examine the immediate effects of a severe drought on the fish assemblage.

Data analysis - For statistical comparisons among all three decades, we used years in which sampling occurred for all 12 calendar months (1981 and 1984 were excluded). To compare assemblage structure across time periods, we standardized the number of individuals captured by the number of gill net hours. In addition, multiple samples from a given month were pooled to give a mean catch per unit effort (CPUE) for each species per month. Because the two introduced species, striped bass and threadfin shad, were not established in the reservoir until after the 1954 sampling, they were excluded from these comparisons. By excluding these species, we focused on variation in species abundances that may have occurred due to these introductions.

Because there is disagreement regarding methods for assessing changes in fish assemblage structure (Ebeling et al. 1990, Grossman et al. 1990, Matthews 1998), we attempted to gain a consensus from several methods. Changes in rank abundance of fishes that represented > 1% of the total individuals captured were examined among years using Kendall's W (e.g., Ross et al. 1985). We used coefficients of variation (CV; e.g., Winemiller 1989, Grossman et al. 1990) of monthly abundances (mean number/ hour gill netting) for each species to estimate variation in individual species abundances within and among years. If there were large changes in the fish assemblage across sampling periods, we would predict CV within years to be lower than CV among years.

Two multivariate approaches also were used to examine changes in the fish assemblage. First, a detrended correspondence analysis (DCA) was used to examine variation in the fish assemblage across the three time periods. DCA is a multivariate ordination technique based on reciprocal averaging and is useful in analyzing a species by sample data matrix (Gauch 1982). In this analysis, the gradient length for each axis is a measure of faunal turnover. A gradient of four standard deviations is approximately equal to one complete turnover in species composition (Gauch 1982). The monthly average CPUEs for the 11 most abundant species (those with relative abundances > 1%) were used as individual samples (i.e., n=12 for 1954, n=24 for 1982-83, and n=24 for 1996-97). Eigenvalues and sample scores were calculated using PC-ORD (McCune & Mefford 1995).

Secondly, we used a stepwise discriminant function analysis to identify those species that varied most among decades using monthly abundances as individuals samples. This analysis constructs a model in which species abundances are used to discriminate among groups (in this case decades). The stepwise procedure only includes those species that significantly ($P < 0.05$) contribute to the model. Prior probability of classifying individual samples was weighted by the number of months sampled that decade. Abundances of each species were log (x+1) transformed prior to analysis to better approximate a normal distribution. Of those species identified by the discriminant analysis, we examined difference in abundance among years using a Mann-Whittney U test with Bonferroni corrections for multiple comparisons among species. All statistics were calculated using SPSS (SPSS Inc. 1996).

Because the same sampling gear and locations were used in the 1981-84 and 1996-97 collections, more detailed analyses were performed on these data. For these comparisons we analyzed changes in the size structure of numerically dominant fish species in the assemblage and examined concordance of species associations across years. We separated striped bass, gizzard shad, blue catfish (*Ictalurus furcatus*), smallmouth buffalo (*Ictiobus bubalus*), and white bass (*Morone chrysops*) into size classes (Table 1) based on length-frequency histograms. As above, a DCA was used to examine variation between sample periods and a discriminant analysis was used to identify those species that changed most in abundance between the two time periods. In this case, each sample represented the pooled number of individuals across the three locations for a particular sample date (n = 67 samples in 1981-84 and 29 samples in 1996-97).

Changes in species association between 1981-84 and 1996-97 were estimated with

Pearson product moment correlations of abundance between species pairs across the three locations and two depths (n = six habitats) in 1981-84 and 1996-97. Warm (April - September) and cold (October - March) seasons were analyzed separately because of seasonal differences in the fish assemblage (Matthews et al. *in press*) The correlations between species pairs were used to construct matrices representing similarity in distribution for the twelve most common species. We used a Mantel test (Mantel 1967). which provides a correlation coefficient between two triangular matrices (Jackson and Somers 1989, Legendre and Fortin 1989), to test concordance of species matrices across years, with warm and cold seasons considered separately. A significant correlation between matrices indicates similar species associations in the years being compared and the Mantel statistic indicates the strength of correlation between matrices (McCune and Mefford 1995). Significance levels for concordance among matrices were made using a Bonferonni corrected alpha level (Sokal and Rohlf 1995). All calculations were performed in PC-ORD (McCune and Mefford 1995).

Finally, species abundance data from the 1980s and 1990s were used to assess the effect of a severe drought on the fish assemblage at our study site. In summer 1998 a drought occurred in southern Oklahoma in which air temperature remained above 37.7 °C for 51 consecutive days (Fig. 2) and total rainfall for the months of July, August, and September was only 6.96 cm. These conditions in concert with low winds and reservoir volume (due to little tributary inflow) may have negatively affected fishes by decreasing suitable habitat (e.g., by thermal stratification). To assess the potential effect of this drought, locations were resampled in September 1998. We used a percent similarity index (PSI, Matthews 1998) to determine if the fish assemblage in September 1998 was qualitatively different from September samples of other years. In addition, a one-way *t*-test was used to determine if mean condition (Weight/$SL^3 * 10^3$, Anderson and Gutreuter 1983) of the six most abundant fish species was lower after the drought than during September of non-drought years (1996 and 1997).

Results

Since filling of the reservoir in 1944, reservoir elevation has fluctuated between 183 and 194 m (Fig. 2). In addition there were several notable increases in elevation during 1957, 1982 and 1990. Water temperature rarely exceeded 27 °C between 1954 and 1966 but often remained above 27°C for long periods in years after 1966. However, this trend is not consistent with air temperature that has varied with no apparent trend toward increasing temperature after 1966. Water temperature rarely dropped below 4°C, however, there were three prolonged periods of low water temperatures (Fig. 2).

The most notable change in the fish assemblage since 1954 was the introduction and establishment of striped bass and threadfin shad. In the 1980s and 1990s striped bass ranked second in abundance whereas threadfin shad ranked seventh in 1981-84 and third in 1996-97 (Table 2). Although these species are presently abundant and represent a substantial change in the fish assemblage, further comparisons among decades focused only on native species. All species collected in 1954 were captured in the 1980s or 1990s and only one of the ten most abundant species in 1954 was not among the ten most abundant species in the 1980s and 1990s. Rank abundance of the 11 most abundant species also was highly concordant among years (Kendall's W = 0.88, $X^2 = 44.11$, $P < 0.001$). Mean CV across years for these 11 species was 58.1% (range 11.0 to 108.3%), suggesting moderately fluctuating abundances (sensu Grossman et al. 1990). However, in comparison, mean CV for these species within years was higher than the among-year CV (88.6 vs. 58.1%) and only two species, goldeye and smallmouth buffalo, had higher among- than within-year CVs.

The DCA comparing monthly abundances of species across the three decades showed high overlap among years (Fig. 3). Overall, axes lengths were relatively short (< 2.5 SD) and primarily reflected seasonal variation within years rather than differences among years or decades. While the fish assemblage at our study site as a whole appeared to be relatively stable, there was some variation in individual species abundances across decades. The stepwise discriminant function analysis identified six species that could be used to discriminate among the three decades ($P < 0.001$, Table 3). Mean abundances of all these species also was significantly different among decades (Mann-Whitney U, df = 2, $P < 0.002$). The discriminant function was relatively accurate when tested against a random selection of cases; only 10% were mis-classified (i.e., placed in the wrong decade).

When a DCA was performed on samples in which size classes of the numerically dominant species were considered separately (1981-84 and 1996-97 only), there was almost complete overlap of decades in multivariate space (Fig. 4). Regardless, CDA was able to identify five species/size classes that significantly discriminated between the 1981-84 and 1996-97 sample periods (Table 4). However, this discriminant function was less accurate than above in that 32.2% of randomly selected cases were mis-classified by the model. Moreover, only two of the five species/size classes showed significant differences in abundance between the two time periods, smallmouth buffalo > 400 mm ($Z = -2.842$, $df = 12$, $P = 0.003$) and striped bass < 250 mm ($Z = -2.355$, $df = 12$, $P = 0.018$).

There was no evidence of change in species associations across habitats between decades based on Mantel tests. There was significant concordance in species association in four of the six possible comparisons between cold seasons in the 1980s and 1990s whereas, only two of the four possible comparisons within either time period was significant (Table 5). During the warm season, all possible comparisons were found to be significantly concordant. However, Mantel correlations were relatively low (< 0.60) suggesting a large amount of unexplained variation in species associations among years.

Percent similarity of the fish assemblage taken in September 1998 (post-drought) and the September collection from 1997 (pre-drought) was 61.8 %. This value was intermediate and within the range of variation (55.3 to 72.6%) from comparisons of September collections from adjacent years during non-drought conditions. In addition, relative abundances for all species but *C. carpio* captured in September 1998 fell within 95% confidence intervals of those species abundances during non-drought years (Fig. 5). Thus, relative abundances of species did not appear to be influenced by the drought and did not change more than in non-drought years. In addition, mean condition of the six dominant species in the assemblage was not significantly different in September collections from the drought year and September collections in non-drought years ($P > 0.05$, Fig. 6).

Discussion

Long-term variation in the fish assemblage

The offshore fish assemblage of Lake Texoma (excluding introduced species) in our study area remained relatively stable across 43 yrs as evidenced by persistence of species, concordance among years in rank abundance, and high overlap of monthly DCA scores. Although the fish assemblage in Lake Texoma likely experienced considerable changes in the first few years after impoundment, our data suggest that typical aging processes of the reservoir since 1954 (e.g., sediment accumulation and species introductions) have not resulted in marked changes in the original fish assemblage. However, several of the species in this assemblage, although persistent, showed shifts in relative abundance over time. The most notable change was that of goldeye (*Hiodon alosoides*), that ranked second in abundance in 1954 and dropped to twelfth in 1996-97. Conversely, smallmouth buffalo increased in rank from ninth to fifth between 1954 and 1996-97. Because sampling was not continuous throughout this time period we cannot link a particular event or events (e.g., introduction of striped bass) to changes in species abundances. However, Hubbs (1984), based on annual gill net samples of Lake Texoma between 1972 and 1983, suggested the decline in goldeye was due to competitive interactions with the introducted striped bass. Changes in abundance of smallmouth buffalo do not appear to be linked to a particular event because their increase has occurred gradually. Not only did they increase from 1954 to 1981-84, but they also increased between 1981-84 and 1996-97.

Differences between samples collected in 1954 and those taken after 1981 may be due, in part, to sampling differences or management practices. For example, maximum mesh size used by Dowell (1956) was 76 mm, whereas gill nets used in the 1980s and 1990s had a maximum mesh size of 102 mm. Although fishes captured in the large mesh only represented a small proportion of the total number of individuals caught in any sample, many of those were smallmouth buffalo. Thus, low apparent abundance of smallmouth buffalo in 1954 may have been due to differences in gear efficiency instead of absolute changes in abundance. In addition, commercial fishing for smallmouth buffalo (Parrack et al. 1970) was legal in Lake Texoma through the early 1970s, and may have been partially responsible for the observed low abundance of smallmouth buffalo in 1954. However, differences in sampling gear or commercial fishing cannot explain the change in relative abundance of smallmouth buffalo between the 1980s and 1990s. Despite potential biases in sampling and management practices, the fish assemblage in 1954 was remarkably consistent with that sampled in the 1980s and 1990s.

Resistance and resilience of the fish assemblage to disturbance

According to Connell and Sousa (1983), several criteria are necessary to determine the stability (i.e., resistance and resilience) of biotic assemblages, including: 1) populations are examined over sufficiently long time periods (i.e., several population turnovers) and 2) base-line information on an "equilibrium state" must be adequately established. Because of extensive gill netting and the time-span of our samples, we are able to make inferences on the stability of this assemblage based on several putative disturbance events that occurred in Lake Texoma. First, a prolonged period of high temperature, low precipitation, and low wind during summer 1998 presumably increased stratification and expanded the anoxic hypolimnion of the reservoir. During this period, numerous dead blue catfish and freshwater drum were noticed floating or on the shoreline near our study site and over 20,000 adult striped bass were reported to have died in the main body of the reservoir (Texas Parks and Wildlife, unpublished data). However, our sampling in September 1998 did not indicate a change in the relative abundance of common species including blue catfish and freshwater drum. Moreover, mean condition of the common species was similar between drought and non-drought years suggesting growth and reproduction was not adversely affected by the drought. We were unable to detect a change in the abundance of adult striped bass because they migrate to the main body of the reservoir and are in very low abundance at in our study site during this time (Matthews et al. 1989). At least for freshwater drum and blue catfish, the observed mortalities either represented a small proportion of the total assemblage or they were washed into the reservoir from the tributary river. Therefore, the majority of the native species in our study area appear to be resistant to these conditions.

Fishes endemic to the Red River drainage basin appear to be more resistant to disturbance events than introduced lacustrine fishes. Native fishes evolved in a large river ecosystem that normally experienced large fluctuations in temperature and reductions in flow. However, introduced species, in particular large striped bass, are adversely affected by high temperature and hypoxia during the summer (Matthews 1985, Coutant 1985, Matthews et al. 1989). Because striped bass are intolerant of high water temperatures, thermal stratification shrinks their suitable habitat to a small area just above the thermocline (Coutant 1985). Native fishes, on the other hand, appear to tolerate the warmer waters and are less restricted in habitat during these conditions.

A second event suggests that introduced species are more sensitive to fluctuations in temperature that, in turn, can affect predator prey associations. Low water temperature and intense predation by striped bass were hypothesized to have caused a complete winter kill of threadfin shad in February of 1982 (Harper and Namminga 1986). In the summer following this event, the condition of striped bass, the major predator of threadfin shad, was greatly reduced (Harper and Namminga 1986, Matthews et al. 1988). Although this event negatively affected on striped bass condition, there was no notable decline in their abundance in subsequent years. This was presumably because of the presence of an alternative prey source (gizzard shad) and the reestablishment of threadfin shad in the reservoir through restocking.

A number of abiotic events occurred between sampling periods that could have affected the offshore fish assemblage in our study area. Foremost, was a record flood that occurred in 1990 (between our 1984 and 1996 sampling events), when the water level rose 7 m above normal pool elevation. This event may have favored certain species and caused a shift in relative abundance of taxa within the assemblage. Because we did not sample during this time, we cannot comment on the resistance of the assemblage to this event, however, we do know that by 1996, the fish assemblage was similar to that in 1984, suggesting at minimum a resilient assemblage.

Species introductions can also be considered a disturbance event. The effect of such introductions on native fish populations in reservoirs appears to be quite variable.

Our study agrees with that of Combs (1980) in that the introduction of striped bass had little effect on the native fish species of reservoirs. Because striped bass occupy pelagic areas, whereas native fishes are typically restricted to littoral and riverine portions of the reservoir, interactions among these species may be minimal (Fernando and Holcik 1991). However, McComas and Drenner (1982), suggested the complete replacement of the native planktivore, brook silverside (*Labidesthes sicculus*) by the introduced inland silverside in Lake Texoma was due to competitive exclusion; inland silverside is a more efficient forager than brook silverside. And, Hubbs (1984) suggested the decline in abundance of goldeye was because of competitive interactions with striped bass. Although the effects of species introductions on native fishes are largely unpredictable (Li and Moyle 1981, Moyle et al. 1986) most species introductions into Lake Texoma have had little effect on the native riverine fishes of the reservoir.

Conclusions

Research on reservoir fish assemblages has shown that stochastic abiotic events such as turbid inflows (Matthews 1984), hypoxia in summer (Coutant 1985, Matthews et al. 1985), fluctuation in water level et al. 1984, Cohen and Radonski 1993, Guy and Willis 1995), and invasion of introduced species (Wydoski and Bennett 1981) may be important in structuring fish assemblages. Regardless, the fish assemblage at our study site on Lake Texoma has appeared to resist such events in terms of species persistence and relative abundances of most species, and has remained stable since the early 1950s. Therefore, our data suggest few changes in the reservoir fish assemblage as the reservoir ages. However, our study indicates that introduced species are less resistant to abiotic conditions than the native species. We suggest that continued long-term investigation of this system will provide necessary information to refine our knowledge of how various reservoir fishes respond to disturbance events.

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Table 1. Size classes for taxa used in analysis of the fish assemblage of Lake Texoma.

Species	Length (mm)
striped bass	< 200
	200 to 300
	> 300
gizzard shad	< 150
	150 to 250
	> 250
smallmouth buffalo	< 400
	≥ 400
blue catfish	< 300
	≥ 300
white bass	< 225
	≥ 225

Table 2. Relative abundances, rank abundance, and CV (within and between years) for fish species taken by gill netting Lake Texoma from 1955 - 1997. Coefficient of variation is only given for the 11 most abundant taxa excluding introduced striped bass and threadfin shad. Species codes are used in Figures 3 and 4.

		Percent abundance					Rank abundance					Coefficient of variation	
Species	Code	1956	1982	1983	1996	1997	1956	1982	1983	1996	1997	Inter-annual	Intra-annual
gizzard shad	gs	27.4	43.9	50.1	39.9	36.1	1	1	1	1	1	43.8	63.8
striped bass[1]	sb	-	27.0	23.2	23.9	21.7	-	2	2	2	2	-	-
white bass	wb	14.0	6.4	8.4	7.0	4.6	3	5	4	4	6	37.3	80.9
freshwater drum	fd	4.1	22.9	10.2	4.6	5.8	7	3	3	6	4	41.4	144.7
threadfin shad[1]	ts	-	3.0	5.6	11.0	17.2	-	7	7	3	3	-	-
goldeye	ge	17.6	2.7	2.4	0.9	0.5	2	9	9	11	12	108.3	102.6
white crappie	wc	10.3	2.2	7.0	1.2	0.7	4	11	5	9	10	66.0	71.4
common carp	cp	7.9	2.3	1.9	2.1	2.3	5	10	11	7	8	92.9	109.4
smallmouth buffalo	sm	2.6	3.0	2.9	5.3	5.5	9	8	8	5	5	71.6	56.9
blue catfish	bc	1.2	6.9	6.5	1.7	2.8	14	4	6	8	7	48.7	66.0

channel catfish	cc	2.2	3.1	2.2	1.0	1.0	10	6	10	10	9	11.0	67.6
river carpsucker	rc	4.2	1.4	0.4	0.5	0.5	6	12	14	12	11	48.3	71.4
longnose gar	lg	3.1	0.5	0.8	0.2	0.5	8	13	12	13	13	69.3	139.8
largemouth bass		1.3	0.5	0.5	0.2	0.4	11	14	13	14	14		
bluegill		1.3	0.4	0.2	0.1	0.2	12	15	16	17	15		
shortnose gar		1.2	0.4	0.3	0.1	<0.1	13	16	15	18	20		
spotted gar		0.5	<0.1	0.2	0.2	0.1	16	19	18	15	16		
flathead catfish		0.5	0.1	0.2	0.1	0.1	16	18	17	16	17		
bigmouth buffalo		0.6	<0.1	0.1	<0.1	0.1	15	20	20	20	18		
black crappie		<0.1	0.2	0.1	<0.1	<0.1	18	17	19	19	19		
Total individuals		7167	2007	3535	3128	2788						$\bar{x} = 58.1$	$\bar{x} = 88.6$
Net-nights		271	120	138	86	90							

[1] introduced or established after 1954

Table 3. Wilks's Lambda, significance, and loadings from a canonical discriminant function analysis performed to discriminate Lake Texoma fish collections taken from three different decades based on species captured in gill nets. Only those species that significantly contributed to the stepwise discriminant function are included in the table (all P-values < 0.001).

Species	Wilks' Lambda	Function 1	Function 2
smallmouth buffalo	0.546	- 0.207	0.732
river carpsucker	0.313	0.484	0.015
white crappie	0.204	0.377	-0.187
blue catfish	0.136	-0.264	-0.510
longnose gar	0.112	0.232	-0.056
goldeye	0.100	0.444	-0.083

Table 4. Wilks's Lambda, significance, and loadings from a canonical discriminant function analysis performed to discriminate Lake Texoma fish collections taken from 1981-84 and those taken in 1996-97 based on species and size classes captured in gill nets. Only those species and size classes that significantly contributed to the stepwise discriminant function are included in the table (all P-values < 0.001).

Species	Wilks' Lambda	Function 1
smallmouth buffalo - lg	0.842	0.681
striped bass - *sm*	0.783	0.523
threadfin shad	0.750	0.555
white crappie	0.727	-0.226
smallmouth buffalo - sm	0.712	0.070

Table 5. Mantel statistics (matrix correlations) and significance for comparisons of species associations among years. Significance indicates that species occurrences across habitats were similar between years being compared.

Cold season	1981	1982	1983	1996
1982	0.156			
1983	0.137	0.366^{***}		
1996	0.096	0.453^{***}	0.340^{***}	
1997	-0.004	0.349^{**}	0.337^{***}	0.340^{***}

Warm season	1981	1982	1983	1996
1982	0.333^{*}			
1983	0.550^{**}	0.473^{**}		
1996	0.525^{***}	0.322^{*}	0.504^{***}	
1997	0.553^{***}	0.458^{***}	0.588^{***}	0.512^{***}

* = $P < 0.05$, * = $P < 0.01$, and *** = $P < 0.001$

List of Figures

Figure 1. Location of the sample stations located in the Red River arm of Lake Texoma near the University of Oklahoma Biological Station. Circles represent sample station for collections taken in 1954 and squares represent sample stations for collections taken in the 1980s and 1990s.

Figure 2. Reservoir elevation, reservoir temperature, and ambient air temperature data since filling of Lake Texoma in 1944. Time periods in which the fish assemblage was sampled are highlighted in grey. Temperature is reported as the number of days above or below limits that are potentially stressful to fishes. Reservoir temperature was taken at 1.8 m below the surface.

Figure 3. Results from a detrended correspondence analysis of the fish assemblage of Lake Texoma across three decades. Upper left graph shows species scores (codes for species names are given in Table 2). Shaded area represents the range of sample scores within a particular decade and the outer polygon references the total space occupied by sample scores from all years combined.

Figure 4. Species scores and polygons representing the range of DCA scores for the fish assemblage of Lake Texoma from 1981-84 and 1996-97. Codes for species names are as in Table 2. The suffixes -l, -m, -s represent large, medium, and small size classes, respectively.

Figure 5. Relative abundances of 13 species based on September gill net samples in Lake Texoma during drought and non-drought years. Error bars for non-drought years

represent 95% confidence intervals.

Figure 6. Mean condition of the six most abundant fishes taken from September collections in drought (1998) and non-drought (1996-97) years. Vertical bars represent one standard error.

Figure 1

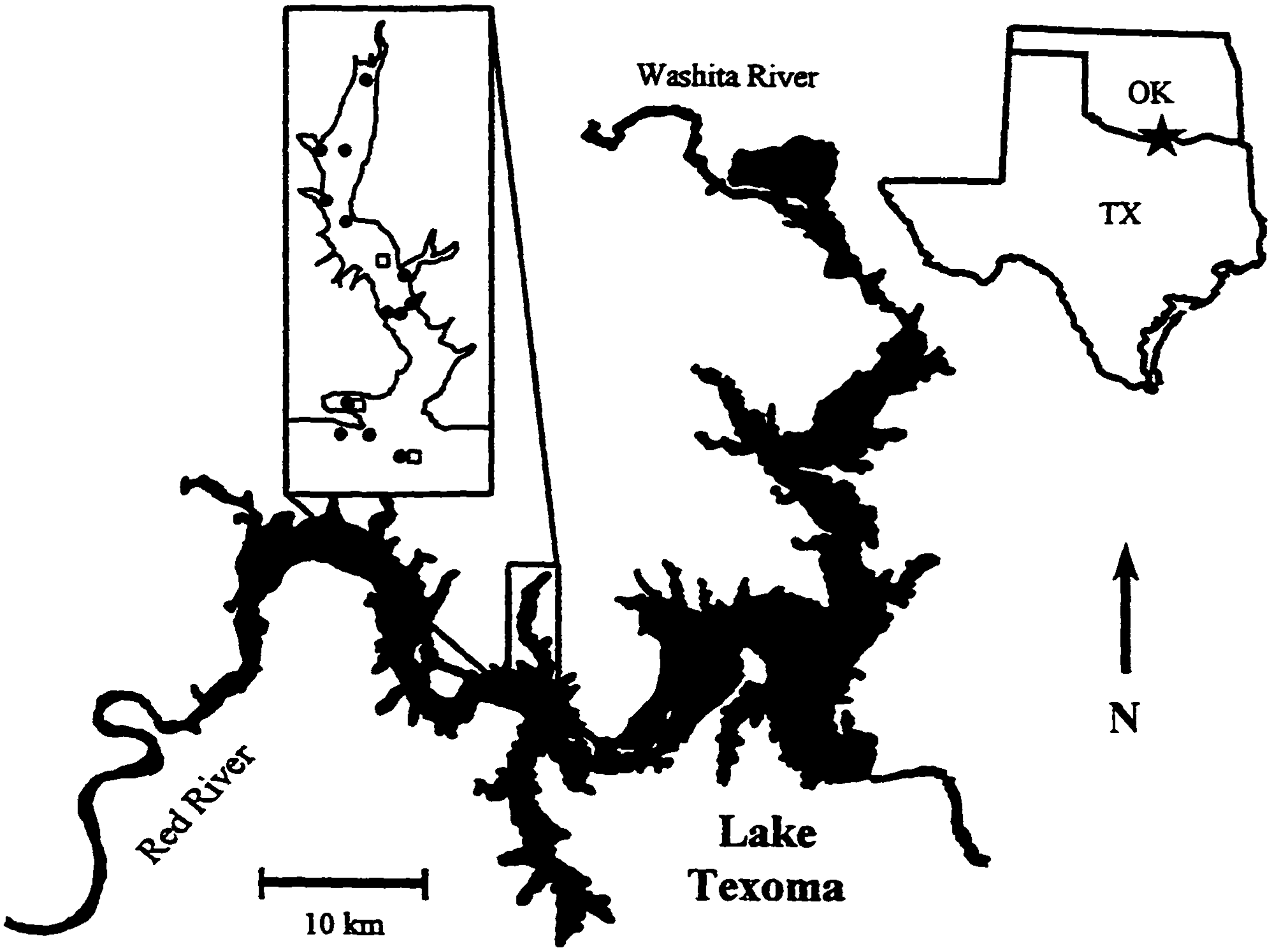


Figure 2

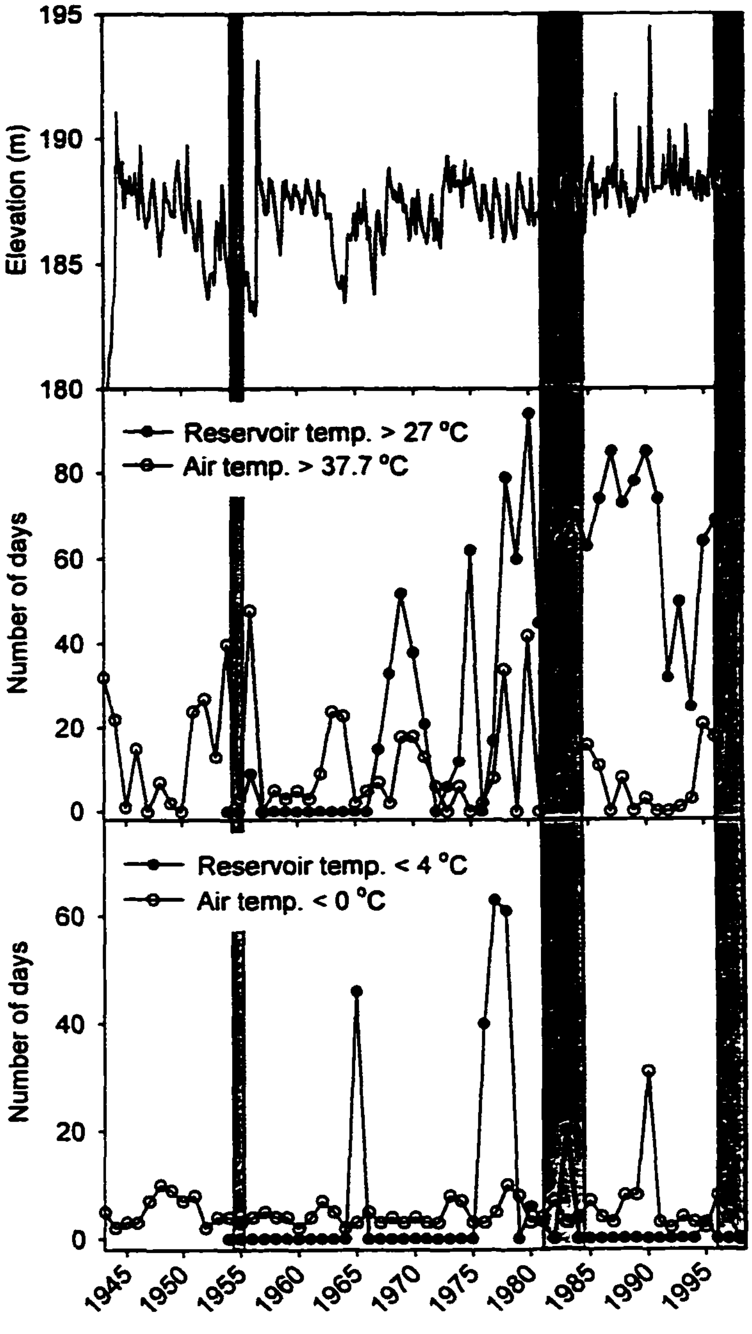

195
190
185
180
Elevation (m)
Reservoir temp. > 27 °C
Air temp. > 37.7 °C
80
60
40
20
0
Number of days
Reservoir temp. < 4 °C
Air temp. < 0 °C
60
40
20
0
Number of days
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995

Figure 3

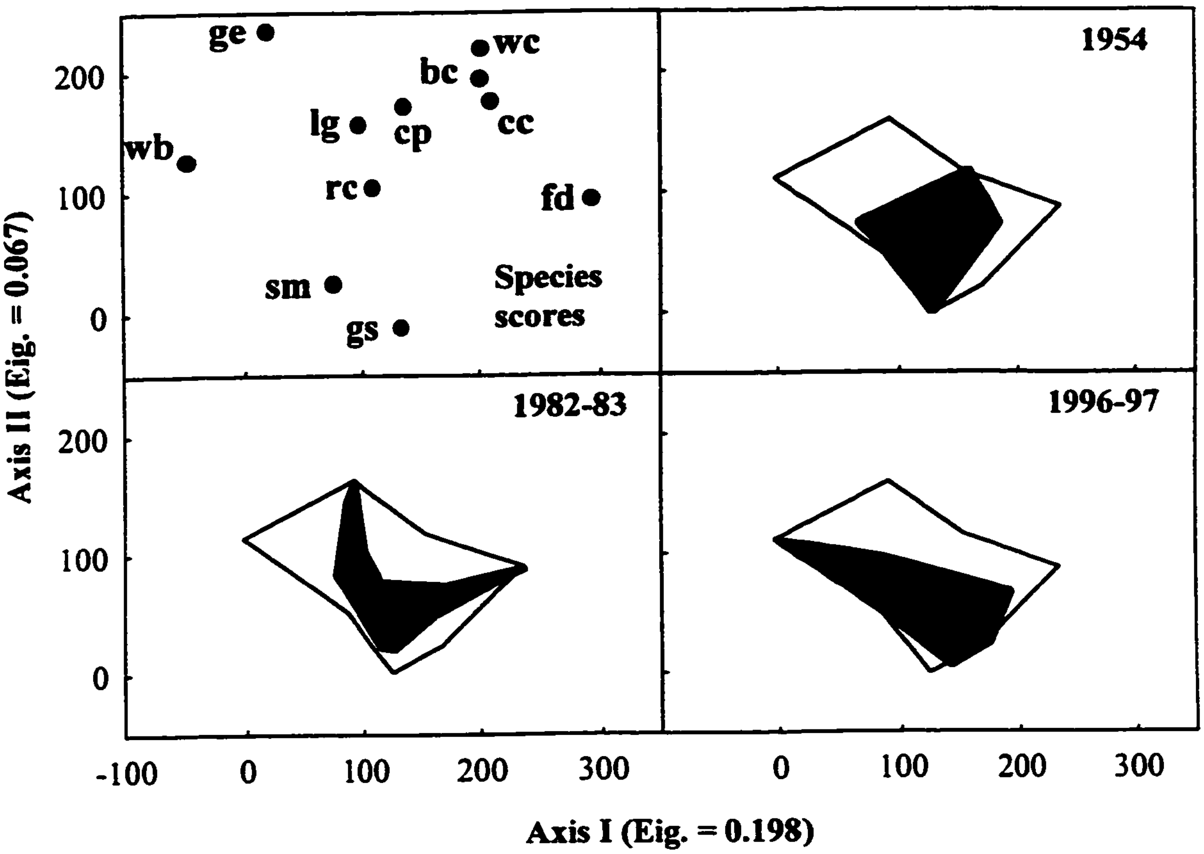

ge
wc
bc
cc
lg
cp
wb
rc
fd
sm
gs
Species scores
1954
1982-83
1996-97
200
100
0
-100
300
Axis II (Eig. = 0.067)
Axis I (Eig. = 0.198)

Figure 4

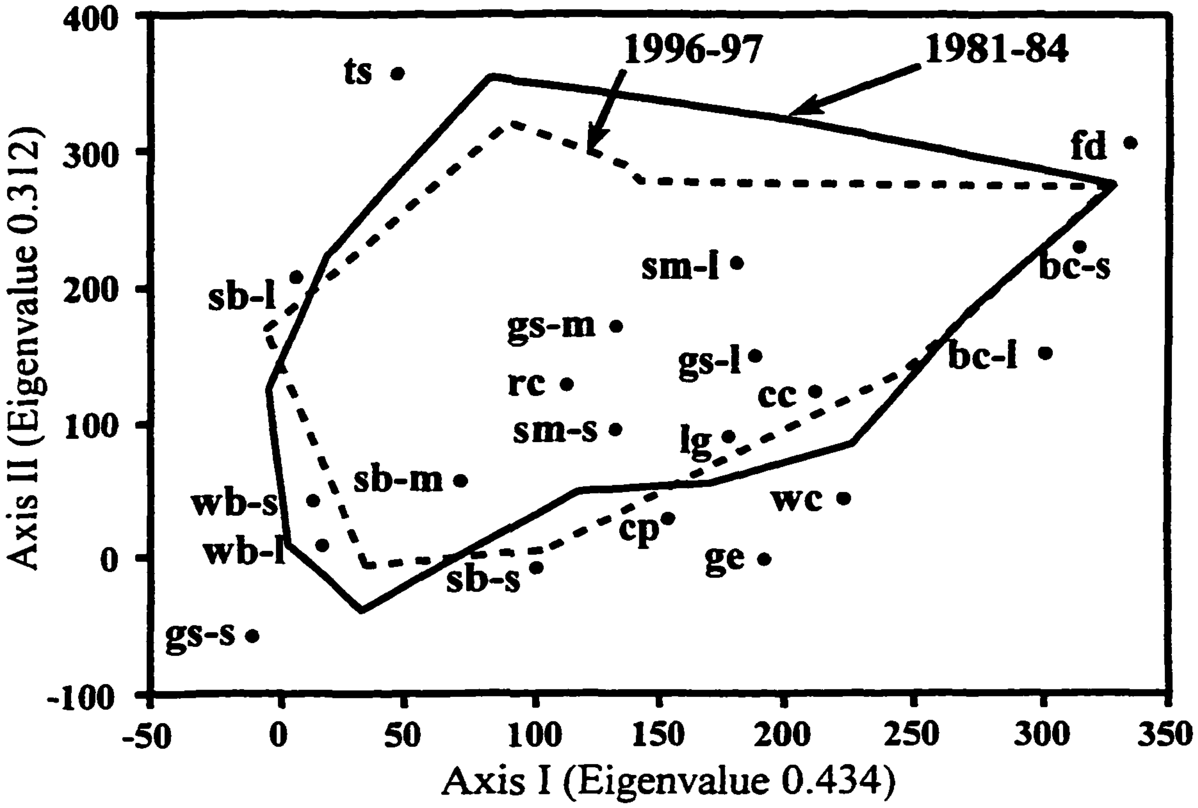
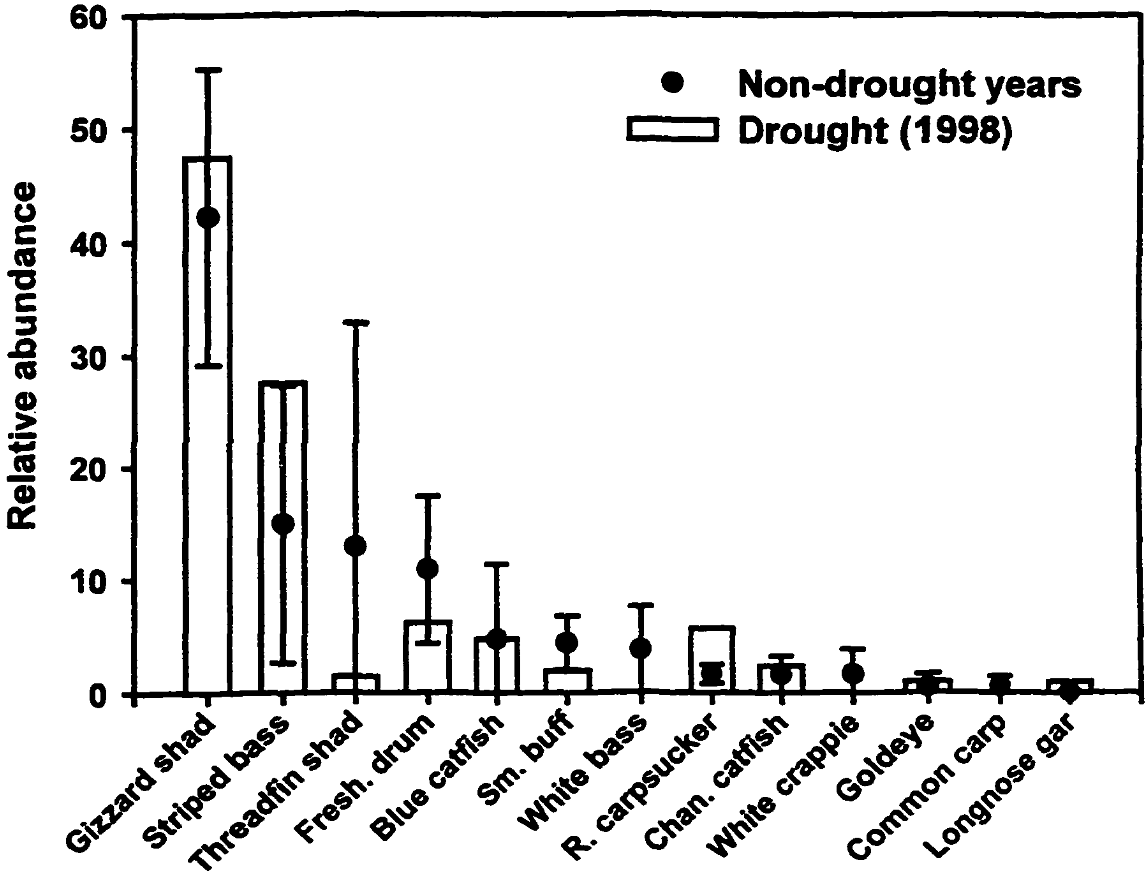
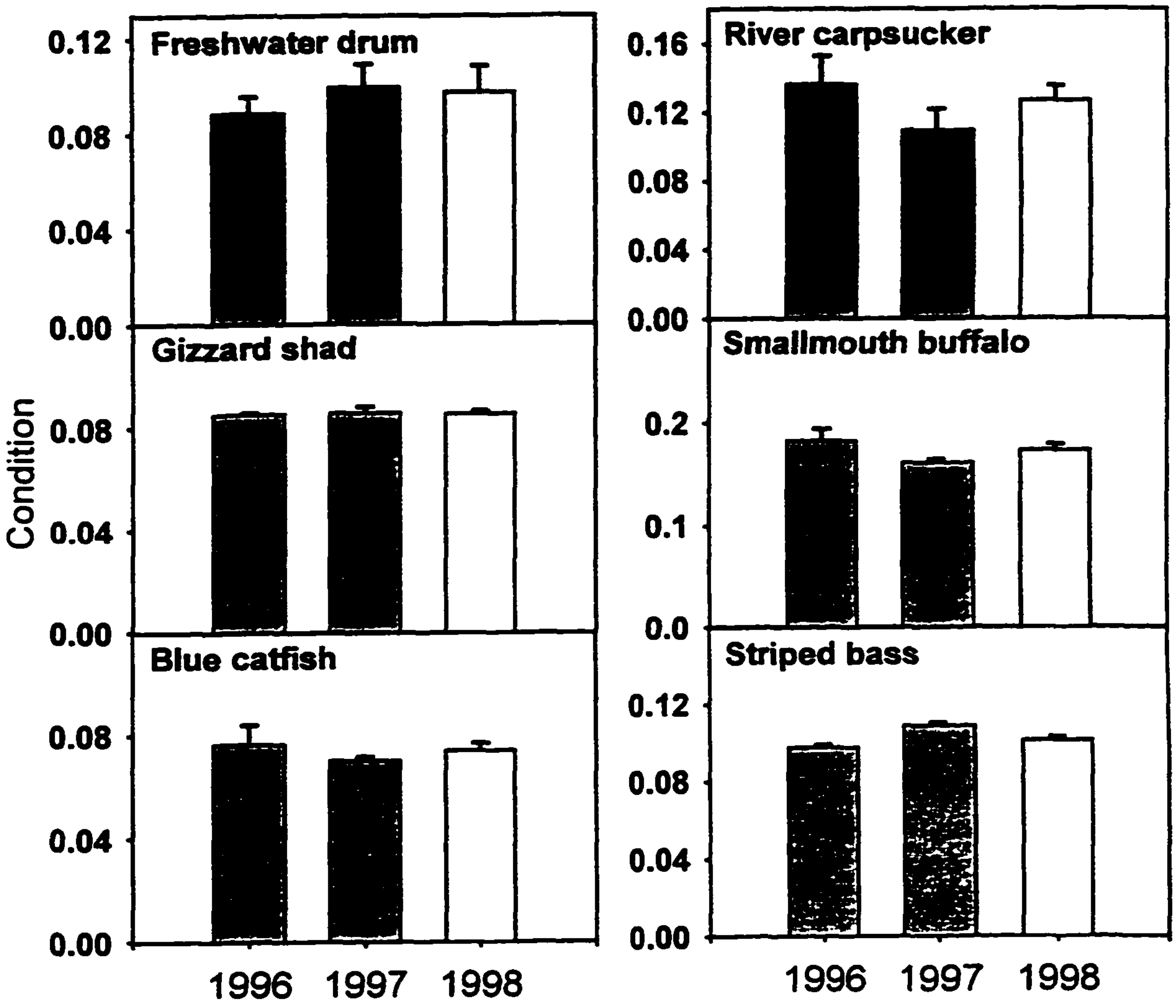

1996-97
1981-84
ts
fd
sm-l
bc-s
sb-l
gs-m
gs-l
bc-l
rc
cc
sm-s
lg
sb-m
wb-s
wc
cp
wb-l
ge
sb-s
gs-s
400
300
200
100
0
-100
-50
0
50
100
150
200
250
300
350
Axis II (Eigenvalue 0.312)
Axis I (Eigenvalue 0.434)

Figure 5



Relative abundance
0
10
20
30
40
50
60
● Non-drought years
Drought (1998)
Gizzard shad
Striped bass
Threadfin shad
Fresh. drum
Blue catfish
Sm. buff
White bass
R. carpsucker
Chan. catfish
White crappie
Goldeye
Common carp
Longnose gar

Figure 6



Freshwater drum
River carpsucker
Gizzard shad
Smallmouth buffalo
Blue catfish
Striped bass
Condition
0.12
0.08
0.04
0.00
0.16
0.12
0.08
0.04
0.00
0.08
0.04
0.00
0.2
0.1
0.0
0.08
0.04
0.00
0.12
0.08
0.04
0.00
1996
1997
1998
1996
1997
1998

Chapter 2: Feeding Ecology of Three Omnivorous Fishes in Lake Texoma (Oklahoma-Texas, USA)

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Abstract

The feeding ecology of three omnivorous fish species in a large southern U.S. reservoir was investigated to determine their potential functional roles in this ecosystem. Distribution, abundance, and diet of *Ictiobus bubalus* (smallmouth buffalo), *Carpiodes carpio* (river carpsucker), and *Dorosoma cepedianum* (gizzard shad) relative to the availability of potential resources, were examined during summer 1997 and 1998. In July and August, abundance of *I. bubalus* was significantly greater at stations with depths of 10 m than at 1 or 3 m stations. There was no significant difference in abundance of *D. cepedianum* or *C. carpio* by depth or month. Relative proportions of detritus and zooplankton in the diet varied among species. *Ictiobus bubalus* primarily ate copepods, whereas *D. cepedianum* primarily ate detritus. The diet of *C. carpio* was intermediate in relative proportions of zooplankton and detritus to that of *I. bubalus* and *D. cepedianum*. Of the three species, only *D. cepedianum* showed a significant decline in dietary crude protein, phosphorous, and organic content over the summer. This decline in nutritional value of food also corresponded to a decline in condition of *D. cepedianum*. Overall, benthic invertebrates had a heterogeneous distribution within the reservoir, but percent organic content in sediments varied little over sample stations. The relative importance in ecosystem functioning of these species, all of which are highly abundant in southern reservoirs, may partially depend on species-specific feeding ecology and environmental conditions.

Keywords: reservoir fishes, detritus, diet, benthic invertebrates, *Dorosoma cepedianum*, *Ictiobus bubalus*, *Carpiodes carpio*

Introduction

Fish assemblages in North American reservoirs typically are dominated by omnivorous fishes like gizzard shad, *Dorosoma cepedianum* (Lesueur), smallmouth buffalo, *Ictiobus bubalus* (Rafinesque), and river carpsucker, *Carpiodes carpio* (Rafinesque) (Mensinger, 1971; Robison & Buchanan 1988). These species can have important effects on ecosystem processes like nutrient cycling and bioturbation of sediments (Lamarra, 1975; Brabrand et al., 1990; Stein et al., 1995; Drenner et al., 1996; Flecker, 1996). Their relative effect on ecosystem processes, however, depends on their abundance, modes of feeding (e.g., bioturbators), and abiotic conditions (e.g., spatial and temporal variation in nutrient loading from the watershed and sedimentation rates). To assess the potential roles of these large-bodied omnivores in reservoirs, a requisite first step is understanding where and when they forage and how this relates to resource availability (e.g., Power, 1997).

I examined feeding ecology of three omnivorous fish species in the context of the distribution and abundance of their food resources in a large North American reservoir (Lake Texoma, Oklahoma-Texas). The abundance of these fishes in this system may depend on the availability and nutritional quality of food resources. Fishes that are facultative detritivores will only switch to detritus if higher nutritional quality prey declines (Ahlgren, 1990b; Lobon-Cervia & Rincon, 1994; Valladolid & Przybylski, 1996; Yako et al., 1996) and they grow best when detritus is supplemented with invertebrate prey (Mundahl & Wissing, 1987; Ahlgren, 1990*a*; Bowen et al., 1995). Thus spatial differences in resources quality also may influence distribution or condition of these fishes. Spatial variation in benthic invertebrate abundance in flood control reservoirs may vary with wave exposure (Cooper, 1977), dissolved oxygen (Sublette, 1957; Cooper, 1980; Cooper & Knight, 1985) and particulate organic matter (Vaughn, 1982). Moreover, detritus quality may vary throughout lentic systems. For example, detritus from wind-exposed shoreline habitats maintained fathead minnow (*Pimephales promelas*) better than detritus from profundal habitats (Lemke & Bowen, 1998).

The goal of this study was to correlate the distribution, abundance, and diet of three omnivorous fishes (*D. cepedianum*, *I. bubalus*, and *C. carpio*) to spatial and temporal variation in quality and quantity of resources in Lake Texoma. I then used this information to develop hypotheses about interspecific differences in the potential effects of these fishes on nutrient dynamics. Food habits of these species have been well documented (Dalquest & Peters, 1966; Minckley et al., 1970; Tafanelli et al., 1971; Summerfelt et al., 1972; Pierce et al., 1981; Mundahl & Wissing, 1987). All three are benthic foragers and facultative detritivores that can consume large amounts of zooplankton. Whereas most of these studies quantified patterns of variation in diet, only studies of *D. cepedianum* have examined this variation in the context of resource quality (Pierce et al., 1981; Mundahl & Wissing, 1987; Mundahl & Wissing, 1988; Mundahl 1991). Because *D. cepedianum* appears to have a potentially important functional role in reservoir ecosystems by processing detritus (Stein et al., 1996; Vanni 1996; Schaus et al. 1997), it is possible these other species may perform similar functions.

Materials and Methods

Study area

Lake Texoma is a 36,000 ha impoundment of the Washita and Red rivers on the Oklahoma-Texas border, U.S.A. Reservoir releases and resulting fluctuations in water level are primarily for hydropower and flood control. Near my study sites, secchi depth transparency typically ranges from 100 to 125 cm, but can decrease to 15 cm during turbid inflow episodes (Matthews, 1984). Study sites were located ca. 35 km uplake from the Denison Dam, within the Red River arm of Lake Texoma near the University of Oklahoma Biological Station (Fig. 1). Nine sampling stations were established in three coves (three stations per cove) located on the north shore of the reservoir. Within each cove, stations were located at depths of 1, 3, and 10 m. One and 3 m stations were within a given cove, whereas the 10 m station was located directly outside each cove in the main body of the reservoir. All sites were located off-shore at least 20 m. Because depth profile, size, and wind exposure were similar among the three coves, each was a replicate for statistical analyses.

Field Collections

Fish Abundance and Diet - Samples were collected monthly from June to August 1997 and 1998 at each station using experimental gill nets (46 m x 1.8 m) with mesh sizes ranging from 51 to 101 bar-measure mesh. Gill nets were set with the lead line on the bottom during daylight for 2 to 4 h. At each station one or two individuals of each species (*D. cepedianum*, *C. carpio*, and *I. bubalus*) were sacrificed for gut content analysis (i.e., maximum of 18 individuals of each species per sample date); the remaining fish were counted and released. Intestines from sacrificed fish were immediately removed and transported on ice to a freezer.

For analysis of diet, gut contents were taken from the esophagus (*D. cepedianum*) or anterior quarter of the intestine (*I. bubalus* and *C. carpiodes*) and preserved in 70% ethanol. Esophageal contents of *I. bubalus* and *C. carpiodes* were not used because food items were rarely found in this region. Moreover, food items in the anterior gut were very much intact and did not appear to have undergone much digestion. Gut contents from each fish were stirred to create a homogeneous mixture of food items; then a 1 ml subsample was taken from this mixture for dietary analysis. A preliminary investigation showed that replicate samples were very similar (< 5% difference in percent volume of major food items) because of the small size of dietary items. The subsample was placed in a Sedgwick-Rafter counting slide and analyzed at 100X magnification. Relative volumes of food items on the entire slide were determined by a modified point system (Hynes, 1950). Invertebrates were identified to major taxonomic groups. Because all of the species had a relatively "fine-grained" diet, determination of the nature of vegetative food items was difficult. Therefore, I classified vegetative debris, algae, and amorphous organic matter as detritus. Inorganic sand grains were ignored in my analysis.

Contents of the anterior one-fourth of the intestine (for all species) also were examined for crude protein, total phosphorous, and percent organic matter to assess nutritional value of the diet. Up to five individuals of each species were examined each month; only fish with intestines more than 75% full were considered in these analyses. Intestinal contents were oven-dried at 60° C for 24 hrs and cooled in a desiccator, then ground with mortar and pestle to homogenize the contents. Total Kjedahl nitrogen and total phosphorus were determined from a 0.25 g subsample of the ground contents that were digested in concentrated sulfuric acid at 440° C for 5 min. Total nitrogen was determined by the Nessler method and total phosphorous by the ascorbic acid method (APHA 1985). Total nitrogen was converted to crude protein by multiplying by 6.25. Total organic content was estimated in the remainder of the sample by ash-free dry weight (AFDW) based on the difference in weight of dried samples from those combusted in a muffle furnace at 550° C for 1 hr.

Benthic invertebrates and detritus - Abundance of benthic invertebrates and the organic fraction in benthic sediments were estimated from core samples. Core samples were taken with a combination of an acrylic tube (8 cm diameter) and an Eckman dredge (15 x 15 cm). First, a sample of the benthic substratum was brought to the surface with the dredge and a subsample was then taken from within the dredge with the corer before opening the bottom of the dredge. This allowed retrieval of core samples from deep stations with only minimal disturbance of organisms and organic matter at the surface-water interface. Only the top 1 cm of each core sample was retained for analysis.

Two samples were taken at each station for each sample date (n = 18) and stored at 4° C. In the laboratory, a 5 g (wet-weight) subsample from each core was dried at 60° C for 24 hrs and organic content was determined by combustion as above.

The remaining sample was passed through a 210 μm sieve to retain organic debris and macroinvertebrates. Macroinvertebrates were identified to major taxonomic categories and enumerated under a stereoscope at 60X magnification. Herein, all invertebrates, including those associated with the sediment-water interface (i.e., Copepoda and Ostracoda) are considered "benthic invertebrates."

Sedimentation Rates - To estimate rates of sedimentation, one cylindrical sediment trap was placed on the bottom at each station concurrent with the gill net sampling in 1997. Traps were retrieved 48 hrs ± 2 hrs (SD) after deployment. Each trap had a diameter of 9.9 cm and depth of 30.5 cm (height:diameter ratio > 3:1; Blomqvist & Kofoed, 1981) and was placed so the opening was 40 cm above the substratum. Before removal, each trap was capped in place (using SCUBA) and then brought to the surface. Sediment samples were allowed to settle for 1 hr and then the excess water was decanted. The dry weight of each sample was determined after drying at 60° C for 24 hrs and percent organic content was determined by combustion (as described above).

Data Analysis

Differences in abundance among depths, months, and years for each species of fish, major benthic invertebrate taxa, percent organic content in core samples, and sedimentation rates were tested using a repeated measures ANOVA with month as the repeated factor (SPSS, 1996). Subsample means were used for benthic invertebrates and percent organic content from core samples. Thus, for all variables there were three replicates (one per cove) at each depth. Log (x+1) transformations of fish and benthic invertebrate abundances were performed to maximize homogeneity of variances. Multiple comparisons among depths and months were analyzed with Tukey HSD tests (SPSS, 1996).

Principal component analysis (PCA) was used to characterize differences in diet among species and across sample dates (Crow, 1978). Prior to analysis, percent volume of major resource categories for each species was arcsine square root transformed to reduce deviation from normal distributions. Eigenvalues and loadings were calculated using PC-ORD (McCune & Mefford, 1995) based on a correlation matrix of variables. A one-way ANOVA (SSPS, 1996), was used to detect differences among species in crude protein, total phosphorous, N:P ratio, and organic content of the diet. In addition, a general factorial ANOVA was used to test for differences in these variables between years and among months for each species.

A Fulton-type condition index (weight/length^3; Anderson & Gutreuter, 1983) was used to assess the condition of the three species throughout the summer. In order to increase sample size, lengths and weights of fish taken from a separate gill net survey in the same area of the reservoir (Gido, unpublished data), were used to calculate mean condition from June to August in 1996 and 1997. No analyses were performed in summer 1998 because of low sample size. Differences in condition among months were determined using a one-way ANOVA. Similarly, differences in sedimentation rates and percent organic contents of sediments among depths and months were examined using a general factorial ANOVA. All Post hoc comparisons among depths and months were made by Tukey HSD tests (SPSS, 1996).

Results

Fish Abundance and Diet - Abundance of the three fish species varied considerably across months, depths, and years (Fig. 2). No significant differences in mean total abundance were found among months for any species. Mean abundance of *D. cepedianum* was significantly higher in 1997 than in 1998 ($F_{1,9}$=7.22, P = 0.025), but its abundance did not vary among station depths or months. There was a significant difference in mean abundance among depths for *I. bubalus* ($F_{2,9}$=7.07, P=0.014), but not between years or among months. This difference was primarily due to greater mean abundance of *I. bubalus* at 10 m stations during July and August. Because only two *C. carpio* were taken in 1997, comparisons of mean abundance among depths and months were only made for 1998 and were not significant (P > 0.10).

Principal component analysis revealed differences in diet among the three species; however, there was much overlap (Fig. 3). The first three axes accounted for 48% of variation in diet among species (Table 1). Based on variable loadings, the first axis represented a contrast between individuals that consumed large volumes of cyclopoid copepods (hereafter referred to as copepods) and *Daphnia* spp. with those that consumed detritus. This axis identified both interspecific differences and seasonal differences in diet of these species. The second axis represented the relative proportions of ostracods, *Bosmina* spp., and terrestrial insects in the diet and primarily identified intraspecific variation in the diet of *D. cepedianum*. Axis three (not shown) represented a contrast between individuals that consumed *Daphnia* spp. and those that consumed zooplankton ephippia and *Bosmina* spp and showed weak interspecific differences between *I. bubalus* and the other two species.

Averaged across months, copepods accounted for the greatest percent volume in the diet of *I. bubalus* ($\bar{x}$ = 50.0%), whereas *D. cepedianum* consumed primarily detritus ($\bar{x}$ = 80.2%, Table 2). The diet of *C. carpio* was intermediate between these species in percent volume of copepods ($\bar{x}$ = 32.3%) and detritus ($\bar{x}$ = 55.7%). In addition, all species tended to have a greater relative volume of copepods in the diet in June ($\bar{x}$ = 40.5%) than in July or August ($\bar{x}$ = 26.2%).

One-way ANOVA revealed significant differences among species for crude protein, total phosphorous, N:P ratio, and percent organic matter in the diet ($P < 0.001$, Fig. 4). Mean values for all variables were greatest in the diet of *I. bubalus*, and least in *D. cepedianum*. Excluding 1997 data because of low sample size, gut contents of *C. carpio* had intermediate levels of all variables except N:P ratio. Low values of crude protein, phosphorous, and percent organic matter in the diet of *D. cepedianum* were likely due to large volumes of sand in gut contents and low protein content of detritus. No significant differences between years or among months for crude protein, total phosphorous, or percent organic matter were observed in the diet of *I. bubalus*. However, there was a significant year*month interaction for N:P ratio ($F_{2,14} = 5.406$, $P = 0.018$). This interaction occurred because of a decline in N:P into the summer of 1997 and an increase in N:P into the summer of 1998. Because of the low abundance of *C. carpio* in 1997, only differences among months for 1998 were tested. No significant differences were found for any of the variables. Dietary nutrient content of *D. cepedianum* showed a significant effect of month for all measures of diet quality ($P < 0.025$). These differences were attributed to a general decline in all variables from June to August.

No significant differences were observed in the mean condition of *I. bubalus* and *C. carpio* among months. Mean condition of *D. cepedianum* in 1996 and 1997 was significantly lower, however, during July and August than in June ($P < 0.05$, Fig. 5).

Benthic Invertebrates and Detritus - Chironomidae (41.2%), Copepoda (29.8%), and Ostracoda (22.9%) accounted numerically for 94% of the total individuals in the core samples. All taxa showed heterogeneous distributions across station depths and months (Fig. 6). Mean CV of paired samples was 38.3, 56.1, and 32.8% for Chironomidae, Copeopda, and Ostracoda, respectively; indicating some variation between paired samples. Mean abundance of ostracods was not different ($P > 0.05$) among months, but varied significantly among depths ($F_{2,10} = 7.509$, $P = 0.010$) and years ($F_{1,10} = 8.408$, $P = 0.016$). Ostracods were typically more abundant at 1 m and 3 m stations, and overall were more abundant in 1997. Mean chironomid abundance varied differently across months and years as shown by the significant interaction between these variables ($F_{2,20} = 20.254$, $P < 0.001$). Mean chironomid abundance was greater in June than in July or August and greater overall in 1997. Mean chironomid abundance in June also was higher at 1m than at the 3 m or 10 m stations. Mean copepod abundance also varied significantly across months and depths (month*depth interaction, $F_{4,20} = 9.030$, $P = 0.002$). The greatest mean abundance of copepods occurred at the 10 m stations, although this difference was only significant for July and August.

Organic Matter in Core Samples and Sedimentation Rates - No differences in percent organic matter in core samples were detected for months, depths, or years ($P > 0.05$, Fig. 7). However, in 1997 there were significant differences in sedimentation rates among depths ($F_{2,13} = 8.389$, $P = 0.005$) and months ($F_{2,13}=7.837$, $P = 0.006$, Fig. 8). Mean sedimentation rate was greatest in July, and, in all months, was significantly greater at the 3 m and 10 m stations than at 1 m stations. No differences ($P < 0.05$) in percent organic matter in sediment samples were found among months or depths.

Discussion

Interspecific differences in feeding ecology

Differences in feeding strategies among fish species may influence their relative importance in reservoir ecosystems. In this study, *D. cepedianum* ingested large amounts of detritus and inorganic sediments, whereas *I. bubalus* and *C. carpio* filtered invertebrates and detritus without ingesting much inorganic matter. Thus, *D. cepedianum* would presumably have a greater effect on fragmentation and decomposition of detritus, microorganisms, and algae in sediments in Lake Texoma. The effect of foraging by *C. carpio* and *I. bubalus* on fragmentation and decomposition of detritus is more likely through processing of detritus and sediments rather than by direct consumption. For example, stirring of sediments by these species while feeding may influence ecosystem processes by altering exchange equilibria of the sediment water interface (e.g., by oxygenation), which can effect phosphorus transport between sediments and the water column (Wetzel, 1983; Palmer et al., 1998; Scheffer, 1998). In addition, resuspension of phytoplankton by foraging fishes can also increase overall primary productivity in the water column (Breukelaar et al., 1994; Scheffer, 1998).

Another important effect of these fishes is the transportation of nutrients from benthic sediments to the water column through excretion (Lamarra, 1975; Vanni, 1996; Schaus et al., 1997). Excretion of nutrients by *D. cepedianum* in an Ohio reservoir equaled or exceeded input of nutrients from the watershed (Vanni, 1996; Schaus et al., 1997). In this case, nutrients were assimilated directly from detritus in sediments and excreted into the water column. Because *I. bubalus* and *C. carpiodes* consume large numbers of benthic invertebrates (cyclopoid copepods and chironomids) that consume detritus, the path of nutrients from detritus into the water column may be more complex. Benthic invertebrates can influence decomposition of organic materials and release of phosphorous from sediments by bioturbation, microbial grazing, shredding, and repackaging of sediments (Gallepp, 1979; Pelegri & Blackburn, 1996; Palmer et al., 1998). Thus, because foraging by *I. bubalus* and *C. carpiodes* may reduce the abundance of these animals, this may have cascading effects through the detrital food web (Scheffer 1998). Although detailed experiments would be necessary to quantify the effects of these fishes on ecosystem dynamics of Lake Texoma, the results of this study suggest that foraging by *D. cepedianum* should have a relatively large effect on release of nutrients from benthic sediments due to direct assimilation and excretion of nutrients from detritus, as suggested in other studies of this species (Vanni, 1996; Schaus et al., 1997). The effects of the two catostomids, however, should be weaker (or opposite) due to indirect effects caused by foraging on benthic invertebrates.

In Lake Texoma, the diets of *D. cepedianum*, *C. carpio*, and *I. bubalus* differ in invertebrate species composition, nutrients, and organic content. These differences are partially due to the different feeding strategies of these fishes. Based on morphology and diet, *D. cepedianum* can be classified as a "scooper" (Gerking, 1994), that scoops mud from the bottom and sorts and discards unwanted matter through the gill rakers. On the other hand, *I. bubalus* and *C. carpio* are "suction feeders" that suck detritus and invertebrates from the bottom and sieve these materials through their gill rakers. Percent organic matter in gut contents of all fishes was higher than in core samples, indicating selective consumption of food items from the substrata. In comparison to the two catostomids, the percent organic content in the diet of *D. cepedianum* was low (< 20%) owing to the consumption of large quantities of inorganic sand along with detritus. The food materials and percent organic matter found in the diet of *D. cepedianum* were similar to those found in previous studies of this species (Mundahl & Wissing, 1987; Pierce et al., 1981). Apparently, this species either compensates for the low nutritional quality of its food by increasing consumption rates or assimilation efficiency (Grimm, 1988), or by supplementing its diet with small amounts of invertebrates when available (Yako et al., 1996).

Ictiobus bubalus and *C. carpio* fed more selectively than *D. cepedianum*. primarily ingesting detritus and invertebrates while consuming little inorganic material. Food items consumed by these species were also similar to those reported previously (Walburg & Nelson 1966; Summerfelt et al., 1972; Tafanelli et al., 1971). but the percent volume of detritus in their diets was typically less. Other investigators reported mean volumes of detritus of 68% in *C. carpio* (Summerfelt et al., 1972) and greater than 65% in *I. bubalus* (Tafanelli et al., 1971) in Oklahoma reservoirs corresponding values in my study were 57% and 36% for *C. carpio* and *I. bubalus*. respectively. Because the other studies were carried out over the entire year. these differences may be due to the greater proportion of zooplankton in the diet during summer. In any case, these studies agree with the findings of this study that both species are facultative detritivores and consume detritus when availability of invertebrates is low (i.e.. July and August).

Spatial and Temporal Variation in Diet and Food Resources

Reservoir ecosystems present a spatially and temporally heterogenous environment for fishes. External inputs from the watershed, wave action. and fluctuation in water level influence deposition and oxidation of sediments and detritus. In addition, mid-summer succession of zooplankton (Threlkeld. 1986) and benthic invertebrate (Sublette, 1957) assemblages creates seasonally available food resources for many reservoir fishes. Declines in invertebrate abundance, particularly copepods, at the 1 m and 3 m stations from June to August corresponded to declines in the relative volume of invertebrates in the diet of the three fish species. However, only *D. cepedianum* showed a decline in condition in late summer. These data suggest that when invertebrate prey are less abundant *D. cepedianum* shift to a diet with lower nutritional value (i.e., detritus).

Omnivorous fishes will switch to a lower quality diet when invertebrate abundance declines (Brabrand, 1985, Mundahl & Wissing, 1988; Ahlgren, 1990*b*; Lobon-Cervia & Rincon, 1994; Ahlgren, 1996). In an Ohio reservoir, *D. cepedianum* switched from a mixed zooplankton and detritus to a primarily detritus diet, resulting in lower growth and condition during summer (Mundahl & Wissing, 1987). Juvenile *Catostomus commersoni* (Lacépede) fed only detritus lost weight, whereas those fed invertebrates gained weight (Ahlgren, 1990*a*). Because of the limited availability of invertebrates, many fish consume detritus to supplement their diet (Bowen et al., 1995). However, the nutritional quality of this resource is not adequate to sustain growth and reproduction. It is also possible that a combination of low resource availability and interspecific competition among these species could cause a switch in diet (Brabrand, 1985).

Whereas the nutrient and organic contents of the diet, and condition of *D. cepedianum* declined from June to August, there was no significant decline in these parameters for *I. bubalus* or *C. carpio*. Even though the relative volume of detritus in the diet of these species appeared to increase into the summer, they may be able to maintain condition by supplementing their diet with invertebrates. Even a small proportion of invertebrate prey in the diet of *C. commersoni* increased growth and condition (Ahlgren, 1990*b*). Moreover, in Lake Texoma *I. bubalus* used deeper habitats (i.e., 10 m stations), that had a greater abundance of copepods during July and August.

Differences among habitats in nutritional quality of detritus in sediments may also influence the distribution and abundance of detritivorous fishes. showed that Nutritional quality of detritus in sediments can be greater in areas that were exposed to turbulence from waves than in profundal zones sheltered from waves (Lemke & Bowen, 1998). Condition of male *Sarotherodon* was lowest in habitats with low quality foods Bowen (1984). In Lake Texoma, there was no significant difference among stations in percent organic matter in core samples. This homogeneous distribution of organic matter in upper layers of sediments may be due to deposition of sediments of similar organic composition. Thus, even though spatial differences in benthic invertebrates occurred, organic matter in sediments was relatively constant across habitats. Homogeneous distribution of organic matter in sediments may correspond to broad spatial distribution of *D. cepedianum*, and perhaps *C. carpio*, that have higher proportions of detritus in their diet.

Because benthic fishes must process sediments to attain nutritionally important food material (Mundahl, 1991; Minckley et al., 1970), the rate of sediment deposition presumably can influence their effect on benthic communities. For example, Mundahl (1991) showed that *D. cepedianum* processed < 4% of the sediments deposited in an Ohio reservoir. He concluded that because of high rates of deposition of sediments foraging by *D. cepedianum* should have little effect on benthic communities. Typical of many reservoirs (Neel, 1966), sedimentation rates in Lake Texoma were high and varied with depth. Therefore, the relative importance of sediment processing by fishes in Lake Texoma would presumably be greatest in coves where sedimentation rate is lowest.

Conclusions

The success of omnivorous species like *D. cepedianum*, *I. bubalus*, and *C. carpio* in many southern reservoirs is likely due to their ability to switch to lower quality food items (e.g., detritus) when invertebrate prey are in low abundance (e.g., Cherry & Guthrie, 1975) and the ability of adults to avoid predation because of their large body size (Stein et al., 1995). Because these species occur in such high abundances they have potentially important effects on reservoir ecosystem processes by virtue of recycling of nutrients or bioturbation of sediments. Interspecific differences in distribution, abundance, and foraging behavior of these species along with variable abiotic conditions will likely influence their relative importance in reservoir ecosystems. This study suggests *Dorosoma cepedianum* should have the largest per capita effect on ecosystem processes given; 1) low organic content in their diet and presumably high rates of sediment processing and 2) consumption of detritus and release of phosphorous (through excretion) that would otherwise be locked in sediments. Further experiments should focus on the cumulative effects of these species on resuspension of sediments and recycling of nutrients in reservoirs.

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Table 1. Eigenvalues and variable loadings for the first three principal component axes derived from an analysis of relative volume of food items in the diet of three omnivorous fishes in Lake Texoma. Asterisk indicates items considered important for that axis.

Axis	PC1	PC2	PC3
Eigenvalue	2.132	1.382	1.214
Percent variance explained	22.2	13.7	12.1
Food item			
Copepoda	-0.882*	0.153	-0.165
Daphnia	-0.517*	0.065	0.454*
Chironomidae	-0.319	0.004	0.328
Ostracoda	0.105	-0.673*	0.082
Bosmina	-0.206	-0.617*	-0.466*
Unknown zooplankton	0.161	-0.275	-0.315
Detritus	0.916*	0.112	0.216
Rotifer	-0.297	0.096	0.211
Ephippia	-0.131	0.313	-0.591*
Terrestrial insect	-0.222	-0.565*	0.326

Table 2. Percent volume (±SD) of major resource items found in the anterior portion of the gut for three species of omnivores in Lake Texoma.

	D. cepedianum			*I. bubalus*			*C. carpio*		
	June	July	Aug	June	July	Aug.	June	July	Aug.
Food item	(n=11)	(n=13)	(n=12)	(n=12)	(n=11)	(n=7)	(n=5)	(n=3)	(n=3)
Rotifera	0.9 (1.9)	0.1 (0.3)	0.7 (1.4)	5.4 (5.2)	0.0	0.0	4.0 (3.7)	0.3 (0.5)	0.0
Crustacea									
Copepoda	19.5 (29.7)	0.0	0.2 (0.6)	55.0 (16.7)	41.4 (24.5)	53.6 (20.3)	47.0 (20.4)	13.3 (9.4)	36.7 (20.5)
Cladocera	0.0	0.4 (1.3)	0.1 (0.3)	2.1 (3.2)	0.0	0.1 (0.3)	0.0	3.3 (4.7)	2.0 (2.2)
Ephippia	0.0	0.2 (0.5)	0.4 (1.4)	0.0	6.4 (7.4)	4.3 (4.7)	0.0	0.0	3.3 (4.7)
Ostracoda	0.9 (2.9)	4.2 (4.2)	2.2 (5.6)	1.3 (3.0)	3.9 (10.0)	0.7 (1.7)	1.0 (2.0)	1.7 (2.4)	0.0
Insecta									
Chironomidae	0.0	0.5 (1.4)	0.0	6.7 (9.0)	4.2 (8.6)	8.6 (11.2)	9.0 (5.8)	0.0	11.7 (6.2)
Detritus	60.5 (24.0)	90.0 (14.2)	90.0 (8.2)	29.6 (13.2)	44.1 (21.7)	32.7 (9.9)	39.0 (21.0)	81.7 (10.5)	46.3 (11.6)

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Figure 1. Location of the nine sample stations located on the north shore of Lake Texoma near the University of Oklahoma Biological Station. Samples were taken at depths of 1, 3, and 10m in each cove.

Figure 2. Mean abundance (individuals per hour gill netting) of fish species taken from three coves on Lake Texoma by station depth, month, and year. Vertical bars represent 1 standard error.

Figure 3. First two principal component axes from an analysis of the diet of three omnivorous fish species in Lake Texoma. Top left graph represents differences in diet among species; I = *Ictiobus bubalus*, D = *Dorosoma cepedianum*, C = *Carpiodes carpio*. Other graphs represent monthly changes in diet for each of the three species.

Figure 4. Mean values for crude protein, total phosphorous, N:P ratio, and percent organic matter in the diet of three omnivorous fish species in Lake Texoma, June-August 1997 and 1998. Vertical bars represent 1 standard error.

Figure 5. Mean condition of three omnivorous fish species in Lake Texoma across summer months for 1996 and 1997. Vertical bars represent 1 standard error.

Figure 6. Mean abundance of three major taxa of benthic invertebrates in core samples taken from three coves in Lake Texoma by station depth, month, and year. Vertical bars represent 1 standard error.

Figure 7. Ash-free dry mass (AFDM) of core samples taken from three coves in Lake Texoma by station depth, month, and year. Vertical bars represent 1 standard error.

Figure 8. Sedimentation rates taken from three coves on Lake Texoma across three depths in 1997. Vertical bars represent 1 standard error.

Figure 1

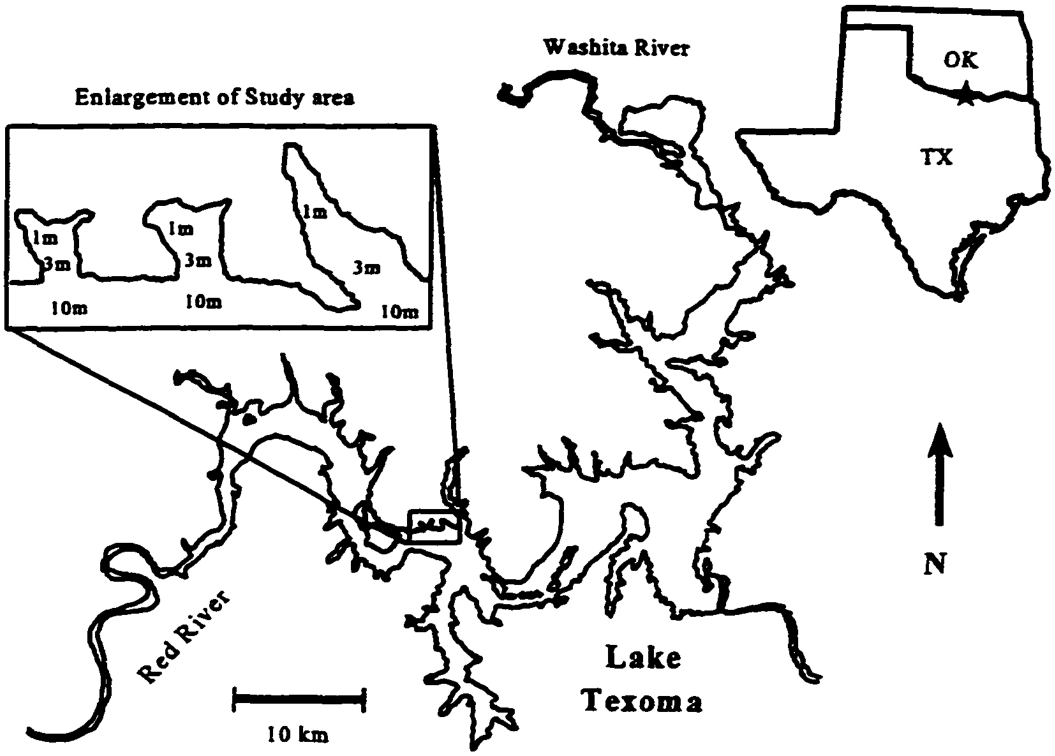
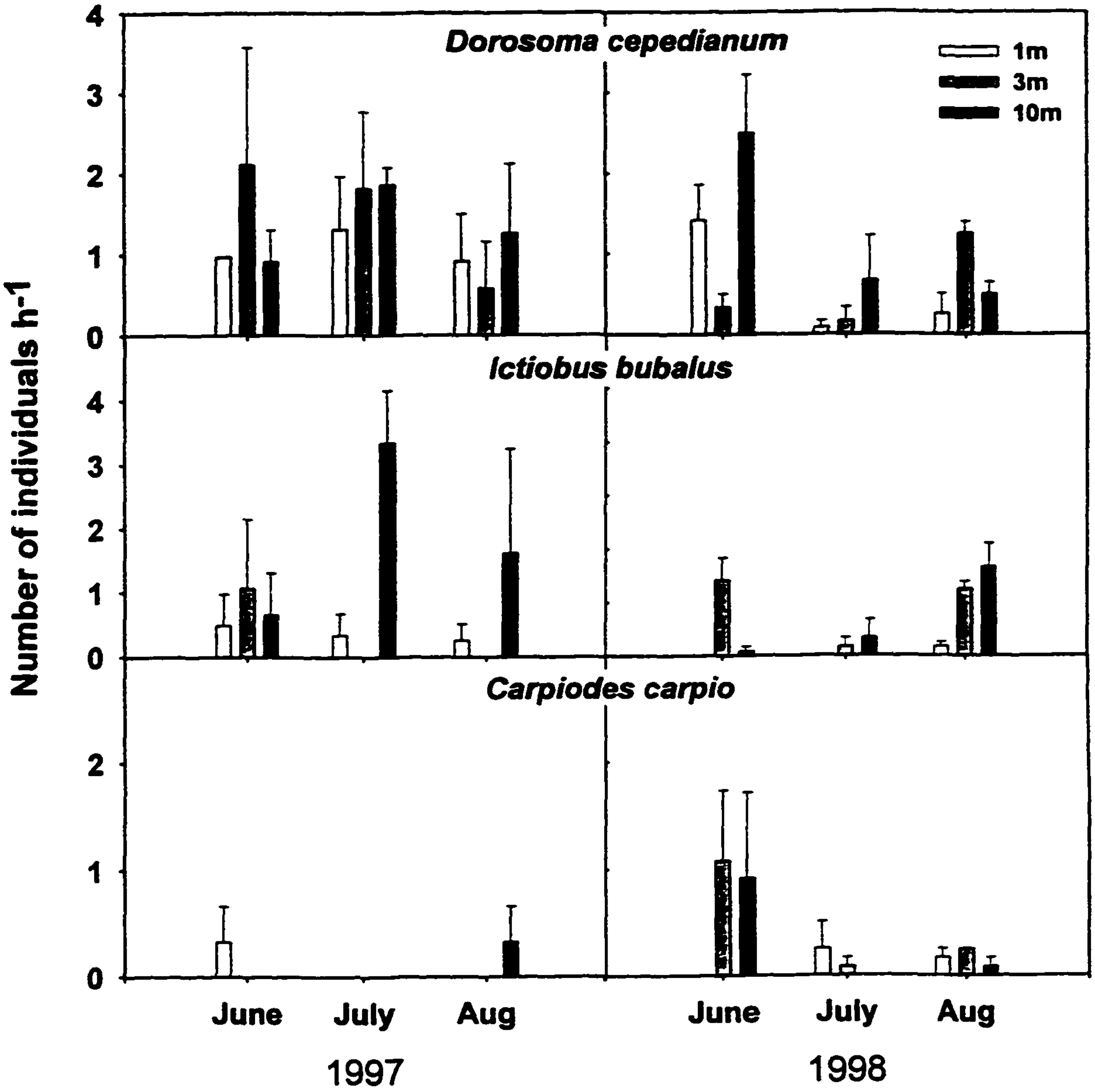

Washita River
Enlargement of Study area
1m
3m
10m
1m
3m
10m
1m
3m
10m
OK
TX
N
Red River
10 km
Lake
Texoma

Figure 2



Dorosoma cepedianum
Ictiobus bubalus
Carpiodes carpio
1m
3m
10m
Number of individuals h-1
0
1
2
3
4
June
July
Aug
1997
1998

Figure 3

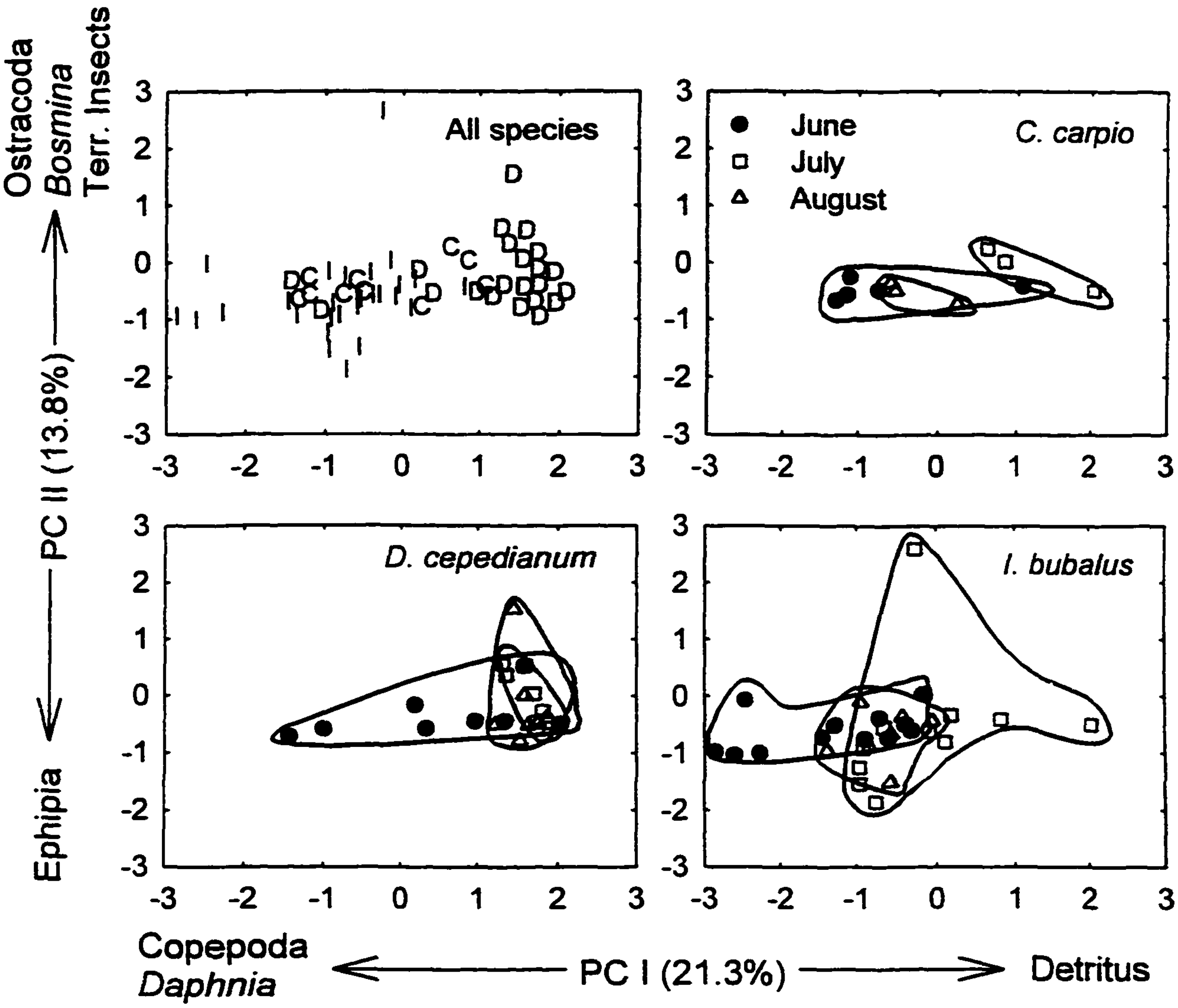
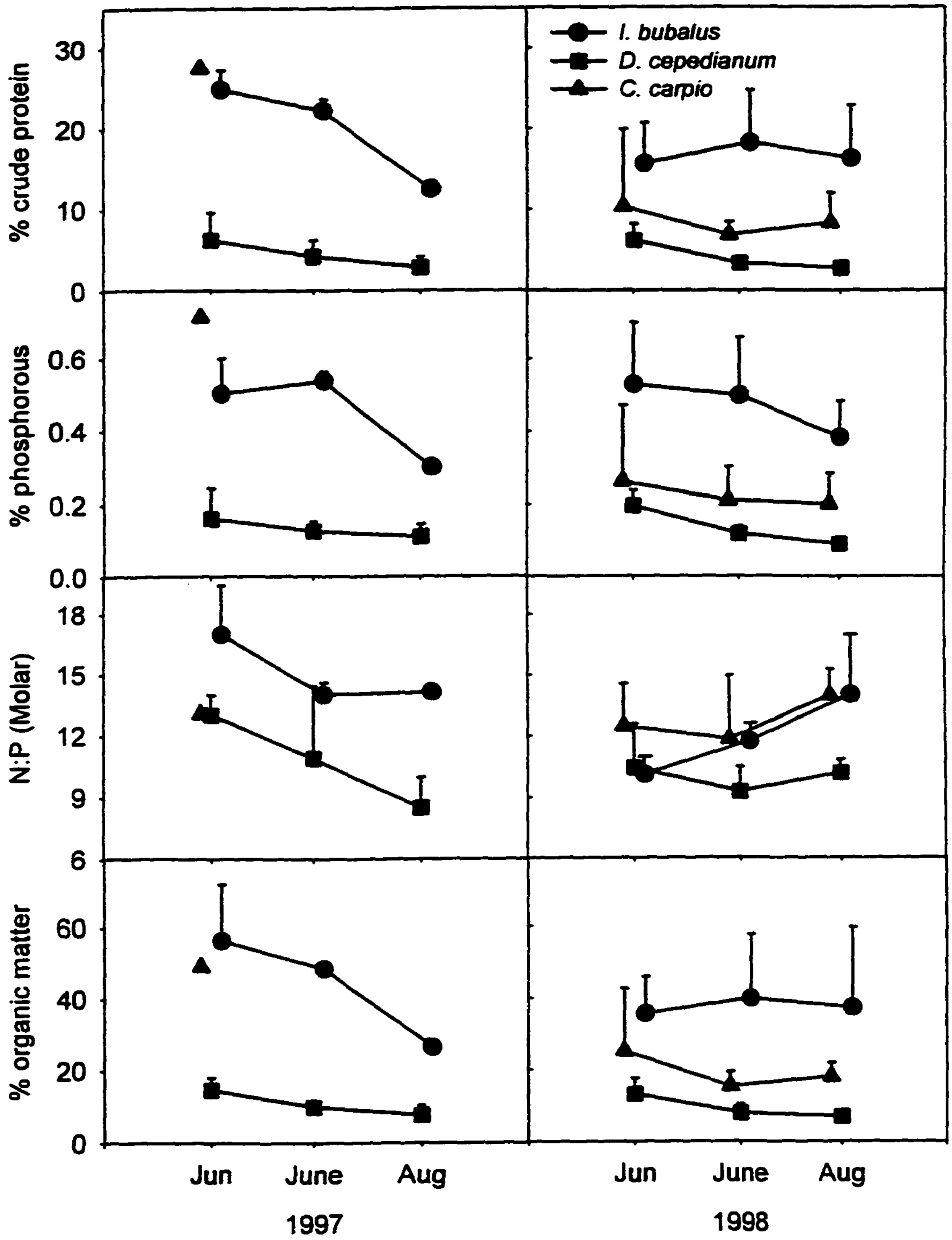

All species
C. carpio
● June
□ July
△ August
D. cepedianum
I. bubalus
Ostracoda
Bosmina
Terr. Insects
PC II (13.8%)
Ephipia
Copepoda
Daphnia
PC I (21.3%)
Detritus
3
2
1
0
-1
-2
-3

Figure 4



I. bubalus
D. cepedianum
C. carpio
% crude protein
0
10
20
30
% phosphorous
0.0
0.2
0.4
0.6
N:P (Molar)
6
9
12
15
18
% organic matter
0
20
40
60
Jun
June
Aug
1997
Jun
June
Aug
1998

Figure 5

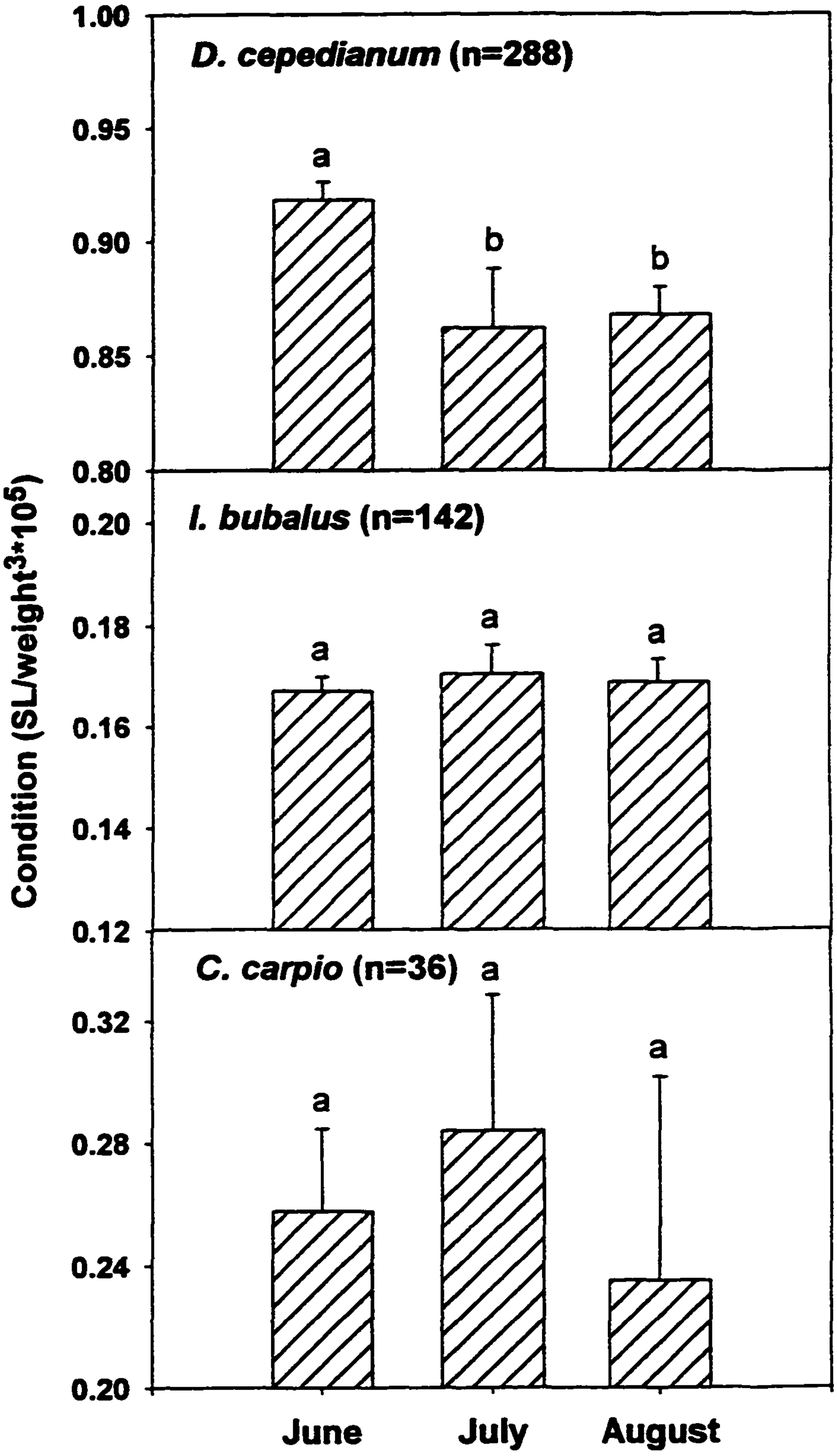

D. cepedianum (n=288)
I. bubalus (n=142)
C. carpio (n=36)
Condition (SL/weight^3*10^5)
1.00
0.95
0.90
0.85
0.80
0.20
0.18
0.16
0.14
0.12
0.32
0.28
0.24
0.20
a
b
b
a
a
a
a
a
a
June
July
August

Figure 6

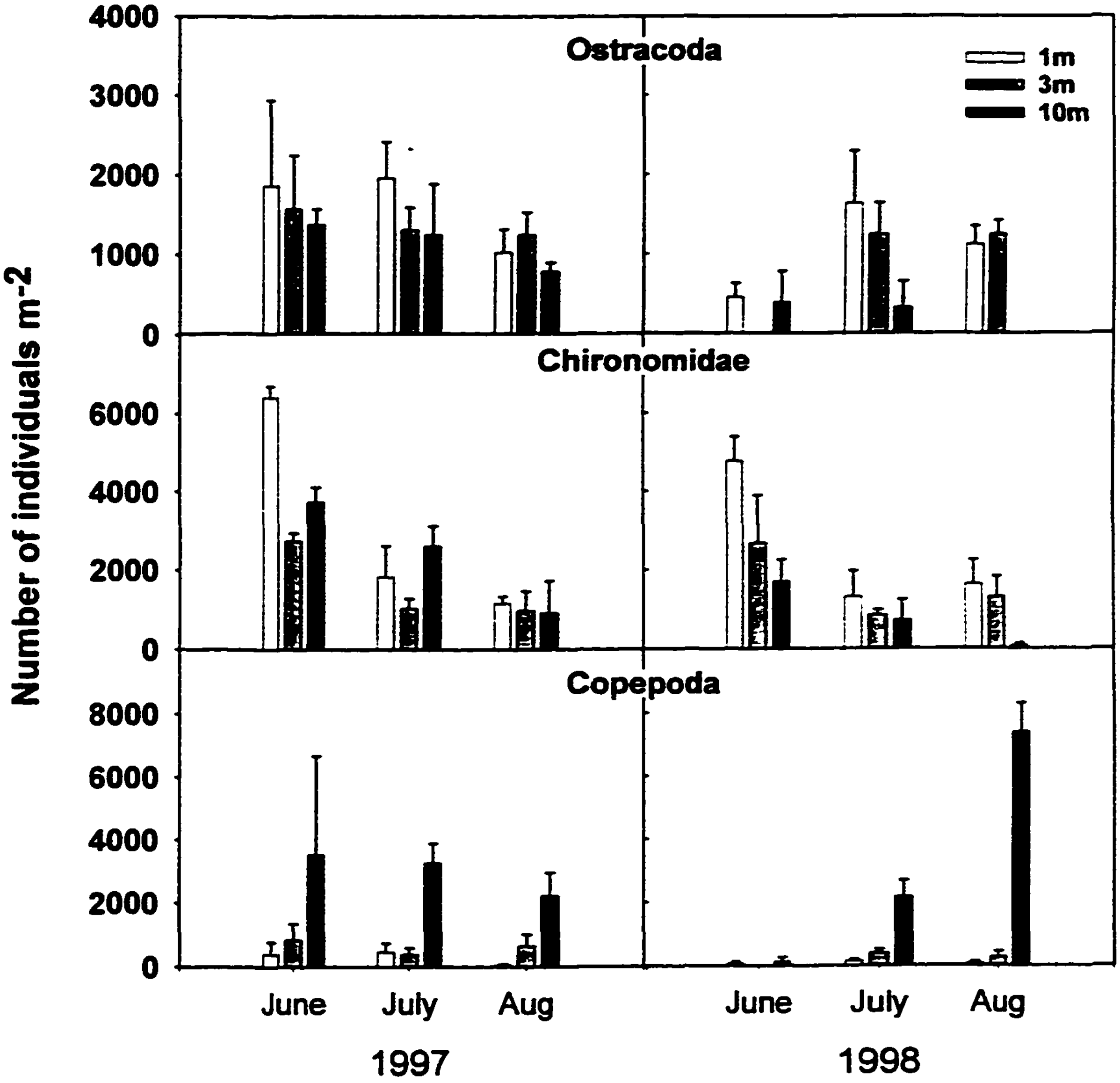

Number of individuals m-2
Ostracoda
1m
3m
10m
4000
3000
2000
1000
0
Chironomidae
6000
4000
2000
0
Copepoda
8000
6000
4000
2000
0
June
July
Aug
1997
June
July
Aug
1998

Figure 7

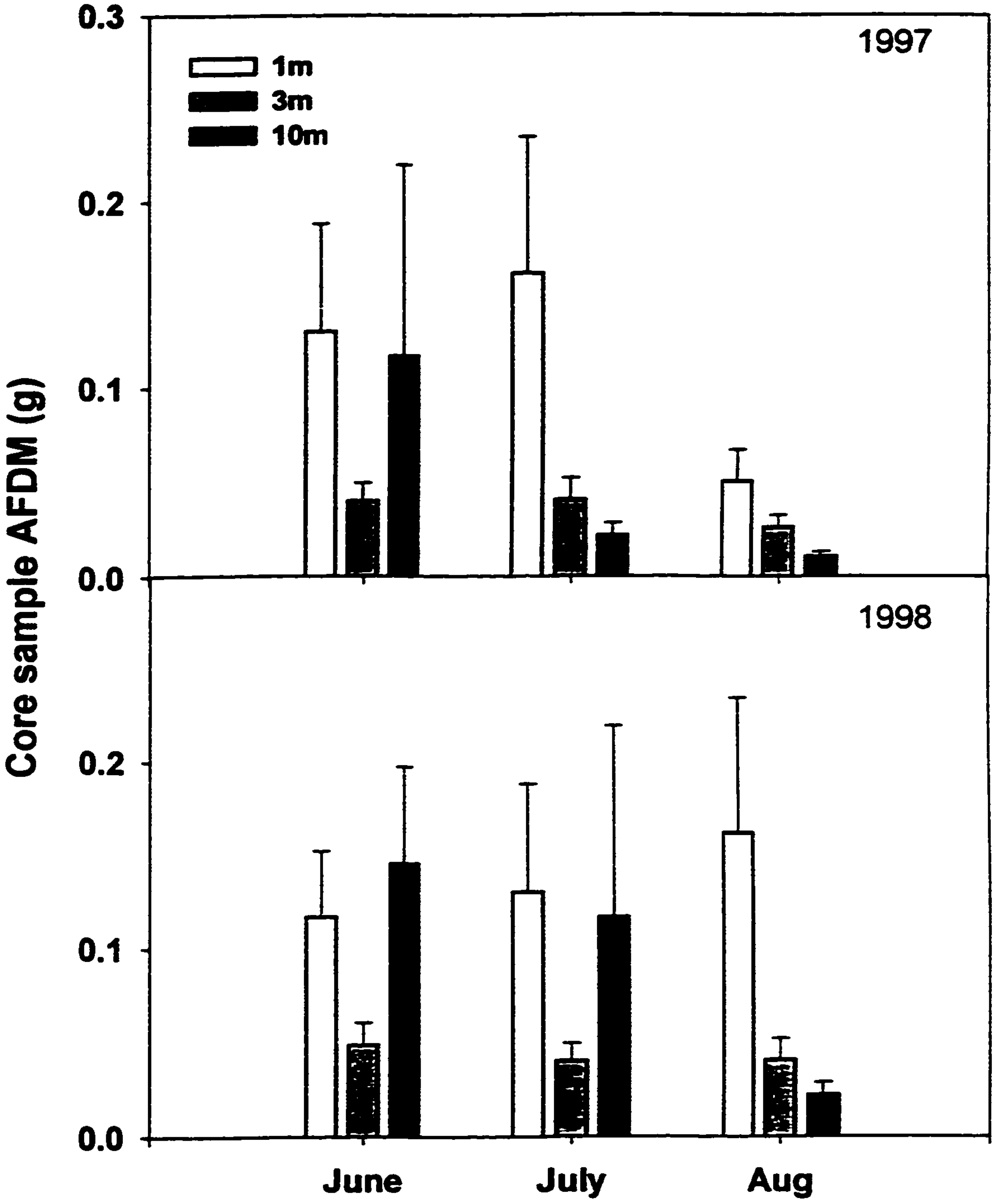
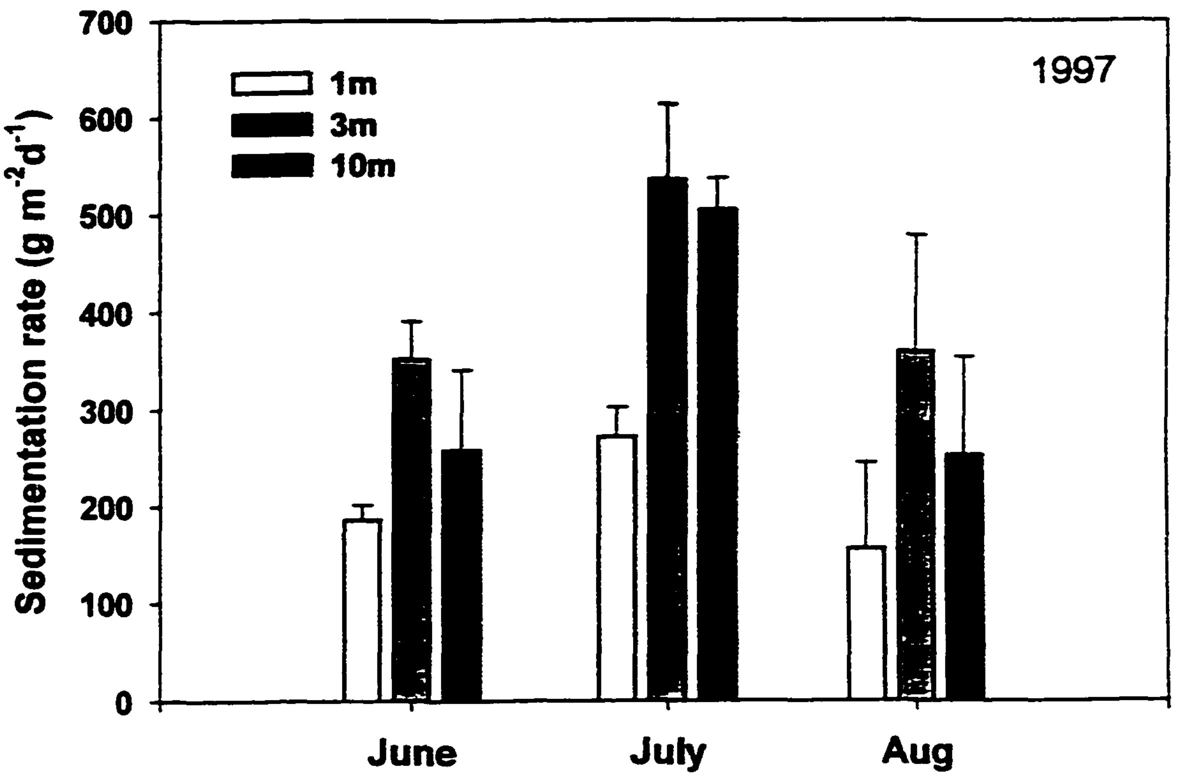

0.3
0.2
0.1
0.0
0.2
0.1
0.0
Core sample AFDM (g)
1997
1998
1m
3m
10m
June
July
Aug

Figure 8


1997
1m
3m
10m
Sedimentation rate (g m-2d-1)
0
100
200
300
400
500
600
700
June
July
Aug

Chapter 3: Ecosystem effects of three omnivorous fishes in a large impoundment (Lake Texoma, Oklahoma-Texas)

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Abstract

Ecosystem-level effects of three omnivorous fishes, gizzard shad (*Dorosoma cepedianum*), smallmouth buffalo (*Ictiobus bubalus*), and river carpsucker (*Carpiodes carpio*), in a large southern reservoir (Lake Texoma, Oklahoma and Texas) were examined in two experiments. Ammonia and phosphate excretion rates were measured for each species. Nutrient loading for the reservoir attributable to fishes on the basis of mean excretion rates, estimates of standing crop, and diel patterns of foraging activity was modeled. *Dorosoma cepedianum* had the highest mass-specific nutrient excretion rates, partly due to its smaller body size. Assuming a standing crop for the three species of 191.6 kg ha^{-1}, phosphorous loading by these fishes was estimated at 9.60 g $ha^{-1}d^{-1}$, exceeding external loading rates from the watershed during periods of low inflow. Field enclosures and exclosures were used to examine the effect of foraging by these species on the biota and organic matter in the sediments. Chironomid and ostracod abundance significantly increased when large fishes were excluded. However, when fish were enclosed in cages, only *D. cepedianum* and *I. bubalus* significantly depress abundance of midges below that of exclosures; *C. carpio* had no significant effect on invertebrate abundances. Organic matter, algal abundance, and abundance of other macroinvertebrates did not differ significantly among treatments. Omnivorous fishes have the potential to influence ecosystem-level properties in a variety of ways. However, because of the variable nature of reservoirs, effects of fishes are likely dependent on environmental conditions.

Introduction

Effects of organisms on their environment has attracted much recent attention (e.g., Jones and Lawton 1995). This issue is important for ecosystem conservation and management, particularly if the focal species are considered "strong interactors" (sensu Paine 1980). Because of the rapidly changing environment caused by human activities, there is concern that a loss of native species or introduction of exotics will alter ecosystem functioning. In particular, researchers have suggested that many species in an assemblage perform similar roles in the ecosystem (i.e., species redundancy; Walker 1992, Lawton and Brown 1993), thus changes due to the loss of a single species are compensated for by other species. Conversely, if each species performs a unique role in the ecosystem (i.e., the rivet hypothesis; Ehrlich and Ehrlich 1981) the loss or addition of a species has the potential to have a substantial effect on the ecosystem. Knowledge of the effects of fishes in ecosystems is also important to managers interested in the use of these organisms to improve water quality or to enhance sport fish production (e.g., through biomanipulation; Carpenter et al. 1987, Gophen 1990, Stein et al. 1996, Drenner et al. 1998, Matthews 1998).

Numerous studies have shown that fishes can have important effects on ecosystem processes. Fishes can directly affect primary productivity through control of grazer populations (e.g., Power 1990, Carpenter et al. 1985) or through transport and recycling of nutrients (Hurlbert et al. 1972, Lamarra 1975, Andersson et al. 1978, Carpenter et al. 1985, Power et al. 1985, Persson 1997). Mechanical disturbance of substrata by fishes may cause changes in turbidity, organic matter standing crop, and associated invertebrate abundances (Lamarra 1975, Gelwick and Matthews 1992, Flecker 1996, Gelwick et al. 1997, Pringle and Hamazaki 1998). Moreover, Breukelaar et al. (1994) showed that fishes can enhance primary productivity by resuspending phytoplankton from sediments to surface waters.

The relative importance of a species in ecosystem functioning may depend on its abundance (Power et al. 1996, Power 1997), population size structure (Meahner et al. 1998), trophic level (Carpenter et al. 1992a, Schindler et al. 1993), or mode of feeding (Matthews 1998). In addition, abiotic conditions often mediate the magnitude of a species effect in an ecosystem (Brabrand et al. 1990, Power et al. 1996). For example, top-down trophic effects (e.g., Carpenter et al. 1985) are most important in oligotrophic systems with well-defined trophic levels (McQueen et al. 1986, Power 1992). Large-bodied benthic fishes that can process large amounts of sediments (e.g., *Prochilodus*, Flecker 1996) are likely to disrupt sediment processes than are smaller fishes. Additionally, indirect effects of nutrient enrichment by fishes (e.g., Schindler et al. 1996, Vanni 1996) likely are important only in systems in which nutrient loading from the watershed is low (Brabrand et al. 1990). Therefore, species effects in ecosystems must be examined in the context of variable biotic and abiotic factors (Power et al. 1996, Power 1997).

Here, I quantify potential ecosystem effects of three omnivorous fishes in a reservoir. North American reservoirs often contain large numbers of benthic omnivorous fishes that historically have been labeled "rough fish" or undesirable for the production of game fishes. In turn, there have been extensive efforts to reduce or extirpate populations of these fishes (Lambou and Stern 1958, Mathis and Hulsey 1959, Hoffarth and Conder 1964). However, research on these omnivores in lentic systems indicates they may have important effects on basic ecosystem function (e.g.,Vanni 1996, Schaus et al. 1997, Horppila 1998).

Defining ecosystem effects of omnivores is difficult because they consume organisms at more than one trophic level (e.g., Polis and Strong 1996). Also, many omnivorous fish are facultative detritivores with the ability to transport nutrients from detritus in the sediments into the water column (Lamarra 1975, Brabrand et al. 1990, Drenner et al. 1996, Vanni 1996, Schaus et al. 1997) thus linking benthic and pelagic processes. By consuming invertebrate detritivores (e.g., chironmids), benthic fishes also can diminish effects of these invertebrates on decomposition of detritus or cycling of nutrients. Perhaps the greatest effect of omnivores on ecosystem processes may be to increase nutrient turnover rates (e.g., Vanni 1997) which in turn may increase the ability of a system to rebound from pulsed disturbances (DeAngelis et al. 1989, Carpenter et al. 1992a).

This study was conducted in two phases. Phase I modeled the potential effects of these omnivores on primary productivity through nutrient excretion. Phase II tested the hypothesis that these fishes affect the structure of benthic communities and organic matter processing. I show that the combined effects of these species are likely to influence ecosystem level properties, however, there are differences in the occurrence and magnitude of effects among species.

Study Area

Lake Texoma is a 36,000 ha impoundment of the Washita and Red Rivers on the Oklahoma-Texas border U.S.A. Reservoir releases and resulting fluctuations in water level are primarily for hydropower and flood control. Secchi depth transparency typically ranges from 100 to 125 cm, but can decrease to 15 cm during turbid inflow episodes (Matthews 1984). Mean productivity at my study site, measured between June and August 1998 at 0.5 m below the surface, ranged from 98.7 to 191.8 ($\bar{x}$ = 149.8) mg C m^{-3} h^{-1}. Reservoir temperature ranges between 2° and 32° C in some years. Locations of fish collections and the field experiment were ca. 35 km uplake from Denison Dam, within the Red River arm of Lake Texoma. Experimental cages were placed in a shallow cove (Mayfield Flats) west of the University of Oklahoma Biological Station that was sheltered from the prevailing south winds [see Patten (1975) for a detailed map].

Fishes studied were smallmouth buffalo (*Ictiobus bubalus*), gizzard shad (*Dorosoma cepedianum*), and river carpsucker (*Carpiodes carpio*). All are facultative detritivores, but they differ in the relative proportions of detritus, algae, and invertebrates in their diets. *Dorosoma cepedianum* primarily consumes detritus and algae, *I. bubalus* primarily consumes cyclopoid copepods, and *C. carpio* has a diet intermediate to the other two species (Dalquest and Peters 1966, Tafenelli et al. 1971, Summerfelt et al. 1972, Gido 1999). All three species are abundant in Lake Texoma and comprised > 50% of the off-shore fish biomass captured during gill net surveys (Matthews et al. in press).

Methods

Nutrient excretion

Excretion rates— Ammonia (NH_4^+) and phosphate (PO_4^{-3}) excretion rates were measured in the field for each species using methods similar to those of Mather et al. (1995) and Schaus et al. (1997). Most fish were collected by seine, however because of difficulty capturing *I. bubalus* and *C. carpio*, several individuals were captured by gill nets run at 30 min intervals. *Dorosoma cepedianum* were collected only by seine. All fish collections were between 1400 and 1600 hrs when nutrient excretion rates were likely greatest (e.g., Schaus et al. 1997). Fish were immediately placed in Styrofoam coolers lined with a polyethylene bag and filled with prefiltered (Whatman GF/F filters) water collected from Lake Texoma. Water samples (250 ml each) were taken immediately after a fish was placed in the cooler and after 1 hr. These samples were placed on ice immediately after collection and analyzed within 24 hr. Care was taken to minimize stress to fishes by minimal handling, placement in dark chambers (coolers), and providing sufficient volumes of water so oxygen was not depleted. Although stress due to capture may affect nutrient excretion rates, Mather et al. (1995) showed no difference in excretion rates between *D. cepedianum* captured in the field and laboratory reared individuals accustomed to handling.

Ammonia concentration was determined by the Phenate Method with light transmittance measured at 640 nm (APHA, 1985). Total Dissolved Phosphorous (TDP) was determined by the Ascorbic Acid Method and transmittance measured at 880 nm (APHA 1985). In a preliminary study, samples filtered through Gelman A/E

(0.45 μm pore size) filters gave similar values (< 2% difference) as TDP, suggesting little particulate phosphorous suspended in the water. Thus, values of TDP are close approximations of soluble reactive phosphorous (SRP) that has been measured in previous studies (e.g., Schaus et al. 1997). Additional water samples were taken 1 hr after fish were removed from coolers to test for nutrient uptake by microbes (e.g., Meyer and Schultz 1985). Differences in ammonia and TDP concentrations between the time fish were removed from coolers and 1 hr thereafter averaged -94.2 (SE 201.0) and -2.2 (SE 4.76) μg/l, respectively. Because neither value was significantly different from zero (t-test, $P > 0.05$), uptake by microbes was assumed to be negligible and no adjustments were made.

Estimates of whole lake effects--Nutrient excretion rates were extrapolated to estimate nutrient loading by fishes (L) to the entire reservoir. Nutrient loading (kg ha^{-1} d^{-1}) was defined as:

$$L_s = E_s \times SC_s \times FD_s$$

where, E is the mass specific ammonia and TDP excretion rates (kg N or P kg^{-1} h^{-1}) described above, SC is standing crop (kg ha^{-1}), FD is the proportion of day spent foraging (d), and subscript "s" denotes species. Estimates of SC for each species in Lake Texoma were taken from an average of Oklahoma reservoirs based on cove rotenone surveys (Table 3, Jenkins 1976). Because nutrient excretion rates likely vary over a 24 hr period, loading rates were adjusted to the proportion of each day a fish spent foraging (FD). FD was estimated by examination of gut fullness across daylight hours. I assumed a significant decline in gut fullness indicated cessation of feeding.

To measure this, fishes were collected with monofilament gill nets with mesh sizes from 25 to 102 mm bar measure at four hour intervals: from 800 to 1200 hrs, 1200 to 1600 hrs, and 1600 to 2000 hours. The alimentary canal from a maximum of six individuals was taken from each time period (i.e., maximum of 18 individuals/day) and immediately placed on ice. In the laboratory, gut contents were cleared from the entire length of intestine and dried to a constant weight at 60° C (for approximately 48 hrs). Relative mass of dried gut contents was used to determine differences in feeding activity across time periods. Because nutrient excretion continues into the night, I estimated excretion rates at night as 80% of mean daily rates; from Schaus et al. (1997) who estimated night time excretion rates for *D. cepedianum* at 82% of maximum daily rates.

To quantify the relative importance of nutrient excretion by fishes, loading by fishes was compared to external loading from the watershed. Data on available nutrient concentrations (total nitrogen and total phosphorous) in major tributaries to Lake Texoma were taken from Oklahoma Department of Environmental Quality for the months of June, July, and August between the years of 1976 and 1993. To estimate a range of external loading rates, mean nutrient concentration was multiplied by mean inflow from tributary streams during summer 1995-1998 (taken from U.S. Army Corps of Engineers, Denison Dam, unpublished data). These estimates assume nutrient concentrations in tributaries are constant and loading rate is a linear function of inflow.

Data analysis--Interspecific differences in ammonia, TDP excretion and N:P ratio were determined with ANCOVA with body weight as the covariate. The relationship between log body mass (individual species and all species combined) and nutrient excretion rate or N:P ratio of excretion was determined with pearson product moment correlations. To examine diel differences in gut fullness, a full factorial ANOVA was used to detect differences among the main effects of month, time of day and any interaction terms.

Cage experiments

Experimental design--Experimental field cages were used to examine the effects of these omnivorous fishes on organic matter processing and biota in sediments. Cages were constructed with 2.54 cm mesh plastic netting that allowed smaller fishes (e.g., juvenile *Lepomis* and *Morone* spp., *Menidia beryllina*, and *Pimephales vigilax*) to pass through while retaining or excluding the large bodied (> 100 mm TL) focal species. Sixteen cylindrical cages, each 1.94 m in diameter, were placed within a sheltered cove in the Red River arm of Lake Texoma. Cages were open at the bottom and edges were secured to the substrate with metal posts and concrete weights. All cages were placed in approximately 1.5 m water with minimal disturbance to enclosed sediments. Fish were captured with a 40 m x 1.5 m seine and immediately placed in cages. The experiment was a randomized block design with five treatments and four replicates each (Table 1). In one treatment, four samples were taken in the proximity of the cages as a measure of ambient conditions. In a second treatment (exclosure) no fish were added. Because of their large body size, cages with

I. bubalus were stocked at higher densities than cages with *D. cepedianum* and *C. carpio*. Based on reports of standing crop for these fishes in Oklahoma reservoirs (Jenkins 1976), these densities probably represent maximum densities for this system. However, these fish are often found in feeding aggregations and likely reach these densities on smaller spatial and temporal scales (W. J. Matthews, personal observation). Fish were added to cages on 22 July and removed on 12 August 1998. At the end of the experiment, a 3 m x 1.5 m seine with 5 mm bar mesh was used to collect all fishes (including those fishes that could passively move into cages).

Response variables--To examine changes in sediment biota, one core sample (8 cm diameter) was taken from a random position within each cage and at random locations outside of cages at the beginning of the experiment and every four days thereafter. Only one core was taken during each sampling interval because I did not want to disturb the substratum more than necessary. In addition, previous research indicated invertebrate abundance in paired sediment cores are similar in this cove; CV of replicate samples averaged 21% (Gido 1999). Only the upper 10 mm of core sediments were retained, because organisms and detritus deeper in sediments are most likely inaccessible to these fishes (Mundahl and Wissing 1987). Samples were preserved in 5% formalin. In the laboratory, water was added to each sample to bring it to a total volume of 200 ml. This sample was shaken vigorously to suspend all silt, sand, and organic matter and three 4 ml aliquots were drawn from this homogenate. The remainder of the sample was passed through a 210 μm sieve to retain macroinvertebrates and large organic debris. After macroinvertebrates were removed from the debris, the sample was dried at 60 °C for 24 hrs and then ashed at 550 °C for 1 hr to determine percent organic matter. Algal abundance was determined from one aliquot from each core sample. From this aliquot a subsample was placed in a Palmer counting cell and algal cells were counted in 50 fields of view at 400X magnification (Flecker 1996). Filamentous algal strands were considered one cell because they were small and varied little in size.

Data analysis--Differences in response variables among treatments in the cage experiment were determined with a repeated measures ANOVA with day after start of experiment as the repeated factor. Because of the low number of replicates (n=4), an alpha level of 0.10 was set a priori to reduce the likelihood of a Type II error. If significant differences were found, post hoc comparisons were examined with Ryan's multiple comparison procedure (Toothaker 1991).

Results

Nutrient excretion

Excretion rates— Nutrient excretion was measured for fishes during summer (May - August) 1998 when water temperature ranged from 25.5 to 30.5 °C. Using body mass as a covariate, mass specific excretion rates were significantly different among species for ammonia ($F_{2,36} = 6.24$, $P = 0.005$) and TDP ($F_{2,36} = 13.62$, $P < 0.001$) but not for N:P ratio ($F_{2,36} = 1.93$, $P=0.161$)(Fig. 1). Mean excretion rate for ammonia was more than twice as high for *D. cepedianum* (8.47 μmol g^{-1} h^{-1}) than for *I. bubalus* (3.28 μmol g^{-1} h^{-1}) and mean excretion rate of TDP was almost three times higher for

D. cepedianum (0.104 μmol g^{-1} h^{-1}) than for *I. bubalus* (0.038 μmol g^{-1} h^{-1}). The slope of the relationship between body mass and mass-specific excretion rates and N:P ratio was not significantly different among species ($P > 0.320$). However, only *C. carpio* had a significant negative relationship between ammonia and TDP excretion rates and log body mass ($P < 0.04$), likely due to the larger size range of individuals examined. With the three species combined, there was a highly significant negative correlation for both ammonia and TDP excretion rates with log body mass (Fig. 1).

Estimates of whole lake effects— No significant differences were found in gut fullness and time of day for any species ($P > 0.09$), suggesting continuous feeding throughout daylight hours (Fig. 2). Thus, I assumed excretion rates to be continuous for a minimum of 12 h d^{-1}. In a survey of 20 Oklahoma reservoirs, including Lake Texoma, Jenkins (1976) reported standing crop estimates for *D. cepedianum* (117.6 kg ha^{-1}), *I. bubalus* (52.7 kg ha^{-1}) and *C. carpio* (21.3 kg ha^{-1}) based on cove rotenone data (Table 3). Because of the uncertainty of extrapolating these number to Lake Texoma, I have plotted loading rates by these fishes as a function of standing crop; assuming relative densities of 61.1 %, 27.5 %, and 11.1 % for *D. cepedianum*, *I. bubalus*, and *C. carpio*, respectively (sensu Jenkins 1976). Estimates of nutrient loading from the watershed ranged from 5.422 to 0.0196 kg ha^{-1} d^{-1} for total nitrogen and from 1.240 to 0.004 kg ha^{-1} d^{-1} for total phosphorous (Fig. 3, shaded areas). Assuming a standing crop of 191.6 kg ha^{-1}, nutrient loading by fishes can exceed that of external loading during low inflow periods. Such a period occurred in Lake Texoma during summer 1998 when inflow to the reservoir was low due to a drought.

Cage experiments

Core samples were dominated taxonomically by several species of midge larvae (primarily *Glyptotendipes* spp.), ostracods, oligochaetes, and cyclopoid copepods. Less abundant taxa in core samples included water mites (Hydracarina), and phantom midges (*Chaoborus* spp.). Algal counts were dominated by several species of diatoms with few filamentous green and blue-green algae.

Mean chironomid and ostracod densities differed significantly across treatments as detected by repeated measures ANOVA ($P < 0.04$; Fig. 4). Although no post hoc comparisons were significant for mean ostracod densities, there was a trend for more ostracods in fish exclosures than in ambient core samples. For mean chironomid densities, post hoc comparisons revealed significant differences among treatments on days 12 and 16, but not on day 20. In the fish exclosure and *C. carpio* treatments, chironomid density was significantly greater than ambient (outside cages) on day 12. On day 16, chironomid density in fish exclosures was significantly greater than all other treatments except cages with *C. carpio*. Overall, the presence of *I. bubalus* and *D. cepedianum* appeared to depress chironomid densities, whereas *C. carpio* did not.

Gut contents of three of the four *I. bubalus* taken at the end of the experiment contained chironomid larvae, indicating that they directly preyed on these organisms (Table 2). Both *D. cepedianum* and *C. carpio* had primarily detritus and algae in their diet with a few ostracods. However, *D. cepedianum* appeared to primarily consume vegetative detritus whereas *C. carpio* primarily consumed filamentous algae. Because filamentous algae were rare in sediment cores, I presumed *C. carpio* grazed mostly on algal growth on cage walls.

The presence of small fishes that could pass through cage mesh could have affected abundance of sediment biota by foraging inside cages. Although there was no significant difference among treatments in mean total density of smaller fishes (ANOVA $F_{3,15} = 1.25$, $P = 0.335$), there were relatively high densities in all cages: bluegill (*Lepomis macrochirus*), *Morone* spp., and bullhead minnow (*Pimephales vigilax*) densities were 42.6 (± 28.0 SD), 13.0 (±9.3 SD), and 3.2 (±1.7 SD) individuals per cage, respectively. Thus, even benthos in fish exclosures were likely subject to some predation.

Discussion

Nutrient excretion

This study indicated that large-bodied, omnivorous fishes can contribute substantially to the nutrient budget of Lake Texoma through transport and recycling of nutrients. The relative importance of fishes in regulation of primary productivity depends on several factors. First, nutrients excreted by fishes must be a limiting factor for primary producers. Light, rather than nutrients, may be the most important limiting factor for primary productivity in many reservoirs because of high turbidity (Jenkins 1982, Ploskey 1986, Holz et al. 1997). The relative contribution of nutrients from reservoir watersheds is variable and dependent on inflow. Because watershed nutrient loading into Lake Texoma is typically high, loading by fishes may be of little importance. For example, during summer 1995 when inflow from tributaries was high, phosphorous loading from the watershed was estimated to exceeded 1 kg ha^{-1} d^{-1}. However, in the summer of 1998, total inflow from tributaries to Lake Texoma ranged from 5.4 to 88.0 m^3 s^{-1} and mean predicted phosphorous loading was only 4.5 x 10^{-3} kg ha^{-1} d^{-1}. Thus, given a predicted density of 192 kg ha^{-1} of omnivorous fishes, the estimate of internal nutrient loading (9.60 x 10^{-3} kg ha^{-1} d^{-1}) was more than twice that of the loading from the watershed. Moreover, these estimates are likely conservative because decreases in reservoir volume during periods of low inflow would concentrate the effects of fishes (i.e., by increasing biomass per unit area). Assuming nutrients are limiting, nutrient excretion by benthic omnivorous fishes likely will influence primary productivity during periods of low inflow.

Benthic fishes can stimulate primary productivity (Lamarra 1975, Andersson et al. 1978, Brabrand et al. 1990) or alter species composition of phytoplankton (Drenner et al. 1996, Schaus et al. 1997) through excretion. In addition, because these fish feed at multiple trophic levels, they also can increase primary productivity through suppression of grazing zooplankton (e.g., Drenner et al. 1996, Drenner et al. 1998). The net effect of these fishes likely is to increase cycling and transport of nutrients, which in turn should positively affect primary productivity. Such an increase in nutrient processing and turnover theoretically can affect resistance and resilience of primary producers to changes in watershed nutrient loading (DeAngelis et al. 1989, Carpenter et al. 1992b). In addition, excretion of nutrients during periods when external loading is low may stabilize producer populations. This may be particularly important in reservoirs that are subject to highly variable inflow.

Other factors may contribute to the internal nutrient loading by fishes in reservoir ecosystems. First, foraging activities that increase turbidity or reduce abundance of detritus processing macroinvertebrates (see below) may potentially decrease primary productivity or nutrient turnover. Secondly, fishes are more likely to increase productivity if they transport nutrients that would otherwise be unavailable to phytoplankton from benthic sediments to the water column than if they were simply recycling nutrients in the water column by foraging on suspended phytoplankton or zooplankton (Brabrand et al. 1990, Kraft 1992, McQueen et al. 1992). Third, size structure of the assemblage must be considered because of the negative relationship between body size and mass-specific nutrient excretion (Schaus et al. 1997, Fig. 1). An assemblage dominated by the larger-bodied *I. bubalus* may contribute substantially less to the nutrient budget of a reservoir than an assemblage comprised of smaller-bodied *D. cepedianum*. Finally, the importance of fishes is dependent on standing crop. Based on a literature review of cove rotenone studies in reservoirs (Table 3), fish densities used in this study were typical of many reservoirs. And in some systems, the standing crop of omnivorous fishes was reported to be > 2000 kg ha^{-1} (S. Miranda, unpublished data). Thus, fishes are likely to have the greatest effect in systems with low inflow rates and high standing crop (of small fish), whereas in large reservoirs such as Lake Texoma, these effects are probably only important during periods of low inflow.

Cage experiments

Exclusion of large fishes caused an increase in chironomid and possibly ostracod densities in cages. In enclosures, benthic foraging by *I. bubalus* and *D. cepedianum* maintained chironomid abundance at levels similar to those outside of cages. Examination of gut contents at the end of the experiment suggested that consumption of chironomids by *I. bubalus* was responsible for decreasing abundance of these organisms. However, chironomid abundance also was reduced in enclosures with *D. cepedianum*, which appear to forage primarily on detritus and algae (Dalquest and Peters 1966, Mundahl and Wissing 1987, Gido 1999). Although *D. cepedianum* rarely consume chironomids. they also could affect them by disturbing sediments or by competition for resources (i.e., detritus and algae). For example, Vadas (1990) suggested that omnivores may affect invertebrate abundances through simultaneous competition and predation. Cages with *C. carpio* were most similar to exclosure treatments, showing little effect of this species on benthic macroinvertebrates. Based on gut contents at the end of the experiment, this species apparently foraged on filamentous green algae attached to plastic netting. Therefore. the effect of this species on benthic organisms in uncertain.

No response variables other than chironomid and ostracod densities were significantly affected by the presence of these large fishes. Of particular interest, algal and detrital abundance (AFDM) were not different among treatments even though the fish species, particularly *D. cepedianum*, foraged heavily on these items. Several factors could have contributed to this result. First, high sedimentation rates of silt, detritus, and algae may have dampened the effects of fishes. In addition, foraging by small fishes (that could pass through the mesh walls) in exclosures may have reduced differences between exclosures and fish enclosures. Finally, because each treatment had only four replicates, detection of small differences among treatments would not have been possible. For example, on the last four sample dates mean algal counts were lower, but not significantly so, in *D. cepedianum* enclosures than in other treatments (Fig. 4.). Although this trend would be predicted based on the diet of this *D. cepedianum* (i.e., algae and detritus), differences among treatments were weak.

It is important to note that fish were stocked at relatively high densities in this experiment; at lower densities no effect on invertebrate abundances might have been observed. However, differences in chironomid abundance between exclosure and ambient treatments likely was due to the exclusion of the large-bodied focal species. Other fishes in this system were unlikely to have an effect because they were either in low abundance (e.g., *Cyprinus carpio*, common carp) or piscivores that do not forage on benthic organisms (e.g., adult *Morone* spp.).

What effects might benthic foraging by omnivores have on ecosystem level properties? Bioturbation of sediments is an important factor regulating dynamics of aquatic ecosystems (Palmer et al. 1998). Disturbance of sediments by fishes likely increases oxidative decomposition and thus the release of nutrients from sediments to the water column (factors not directly measured in this study). However, consumption of benthic invertebrates that are, themselves, bioturbators may reduce the magnitude of this effect. For example, most chironomid species in shallow waters of Lake Texoma are in the genus *Glyptotendipes*, which are filter-feeding detritivores (Vaughn 1982 and references therein). Studies on related species report effects on nutrient cycling by increasing rates of oxidative decomposition of detritus (e.g., Pelegri and Blackburn 1996, Hansen et al. 1998). Mechanical disturbance by fishes is likely of much greater magnitude than disturbances caused by benthic invertebrates; however, the combined effects have not been examined.

Conclusion

North American reservoirs are characterized by high abundances of omnivorous fishes (Stein et al. 1995), detritus-based food webs (Cherry and Guthrie 1975), and highly variable abiotic conditions (e.g., water level fluctuation and sediment deposition). Stein et al. (1995) provide a strong argument that the presence of large-bodied omnivorous fishes in southern U.S. reservoirs regulates trophic interactions. Because adults of these species are resistant to predation (due to predator gape limitation), they suggest that trophic interactions less likely to be regulated by top-down factors and more likely regulated by competition and nutrient cycling. Whereas the focus of their study was primarily *D. cepedianum*, other large-bodied fishes such as *I. bubalus* and *C. carpio* are abundant in reservoirs and may have similar functional roles in the ecosystem. Evidence from this and a previous study (Gido 1999) suggest these species are similar to some extent. Primarily, all are benthic foragers and are likely to affect sediment-water exchange equilibrium through mechanical disturbance or predation on benthic organisms. In addition, all species forage, at least facultatively, on detritus, thus increasing turnover rates and pumping of nutrients from sediments into the water column. However, there are major difference among species in the relative proportion of detritus in their diet; *I. bubalus* primarily forages on copepods, *D. cepedianum* primarily forages on detritus, and *C. carpio* is intermediate between the two (Gido 1999). *Dorosoma cepedianum*, because of their higher mass-specific nutrient excretion rates, greater proportion of detritus in their diet, and high abundances, are more likely to regulate ecosystem properties than the other two species.

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Table 1. Experimental design of cage experiment.

Treatment	Number of individuals/cage	Biomass ($kg\ ha^{-1}$)	*Replicates*
Ambient	-	-	4
Control	0	0	4
Dorosoma cepedianum	3	1140 - 1210	4
Carpiodes carpio	1	956 - 1033	3*
Ictiobus bubalus	1	1816 - 2118	4

* Mortality in one treatment occurred during experiment so omitted from analysis.

Table 2. Percent composition of gut contents for fishes removed at the end of field cage experiments.

Food item	*I. bubalus*	*D. cepedianum*	*C. carpio*
Rotifera	0.0	0.2	1.0
Copepoda	1.8	0.0	0.5
Zooplankton ephippia	1.3	0.0	0.0
Chironomidae	13.0	0.0	0.0
Ostracoda	2.5	1.6	0.5
Vegetative debris	12.4	22.6	4.0
Amorphous debris and algae	69.0	75.6	94.0

Table 3. Estimates of standing crop (kg ha^{-1}) for total fish and three omnivorous fishes based on cove rotenone surveys in reservoirs.

Reservoir	Total fish	*I. bubalus*	*D. cepedianum*	*C. carpio*	Source
Oklahoma reservoirs	276	52.7[a]	117.6	21.3	Jenkins (1976)
Clear lake	227	27	195		Lambou and Stern (1958)
Lake Catherine	187		137		Mathis and Hulsey (1959)
West Point reservoir	351-934		103 - 798		Timmons et al. (1979)
Acton Lake			417		Schaus et al. (1997)
NRRP data base[b]		24.2 (37.6)	118.5 (177.0)	9.2 (22.4)	S. Miranda (unpubl. data)

[a] buffalofishes

[b] mean (SD) standing crop estimates (cove rotenone) from 360 reservoirs across the United States compiled by the National Reservoir Research Program (NRRP).

Figure Captions

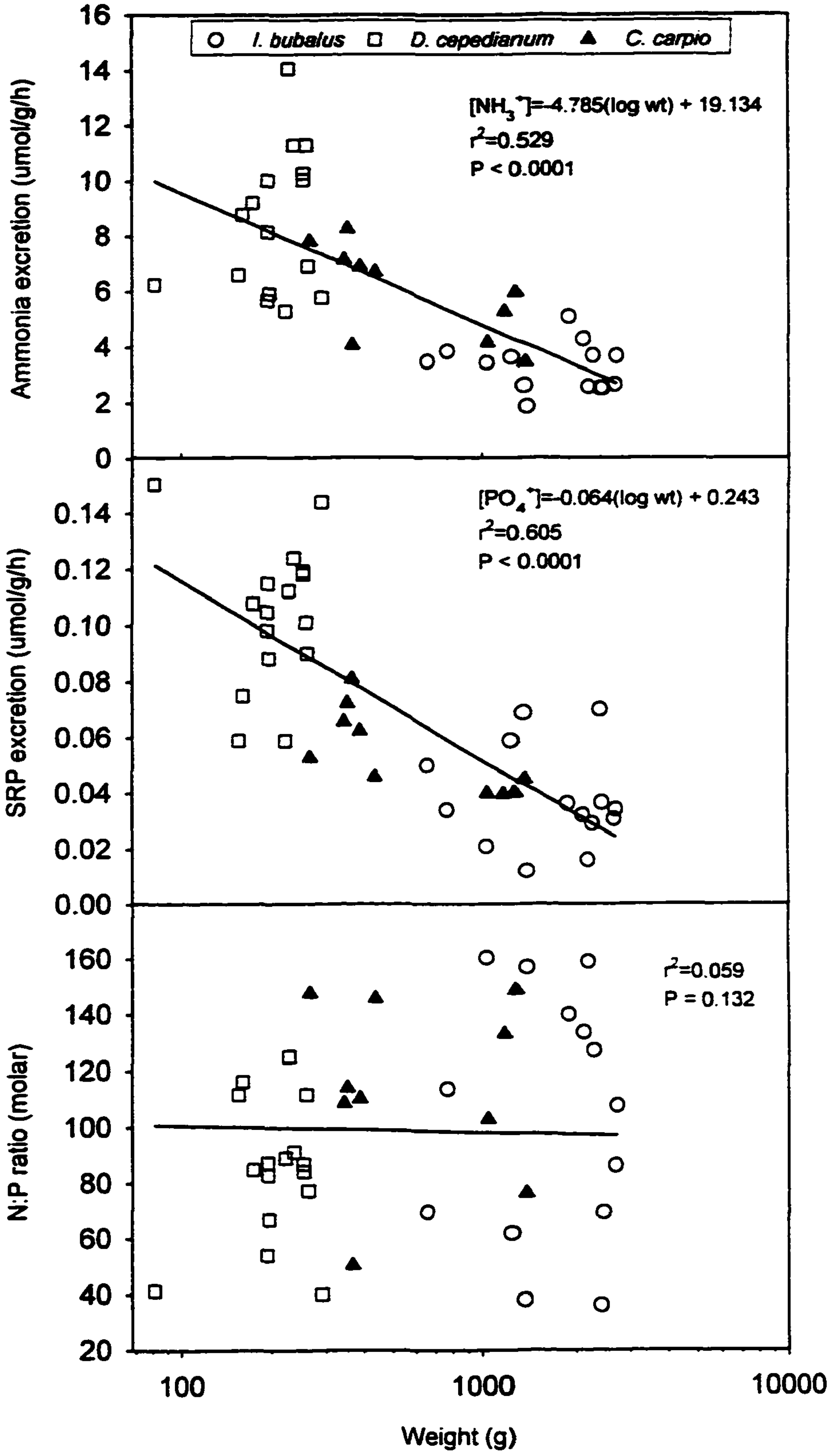
Figure 1. Nutrient excretion rates and N:P ratio for three omnivorous fishes in Lake Texoma. Regression lines and statistics are based on all species combined.

Figure 2. Mean gut fullness for three omnivorous fishes during three time periods. Gut fullness is represented as dry weight of gut contents as a percentage of body weight of each fish (wet weight). Vertical bars represent one standard error.

Figure 3. Predicted loading rates by fish excretion from three omnivorous fishes on Lake Texoma (solid line). Predictions are based on mean excretions rates given in Figure 1 and relative densities of *D. cepedianum*, *I. bubalus*, and *C. carpio* at 61.1 %, 27.5 %, and 11.1 %, respectively. Shaded area represents range of values for predicted external loading rates based on inflow from tributaries during summers of 1995 - 1998.

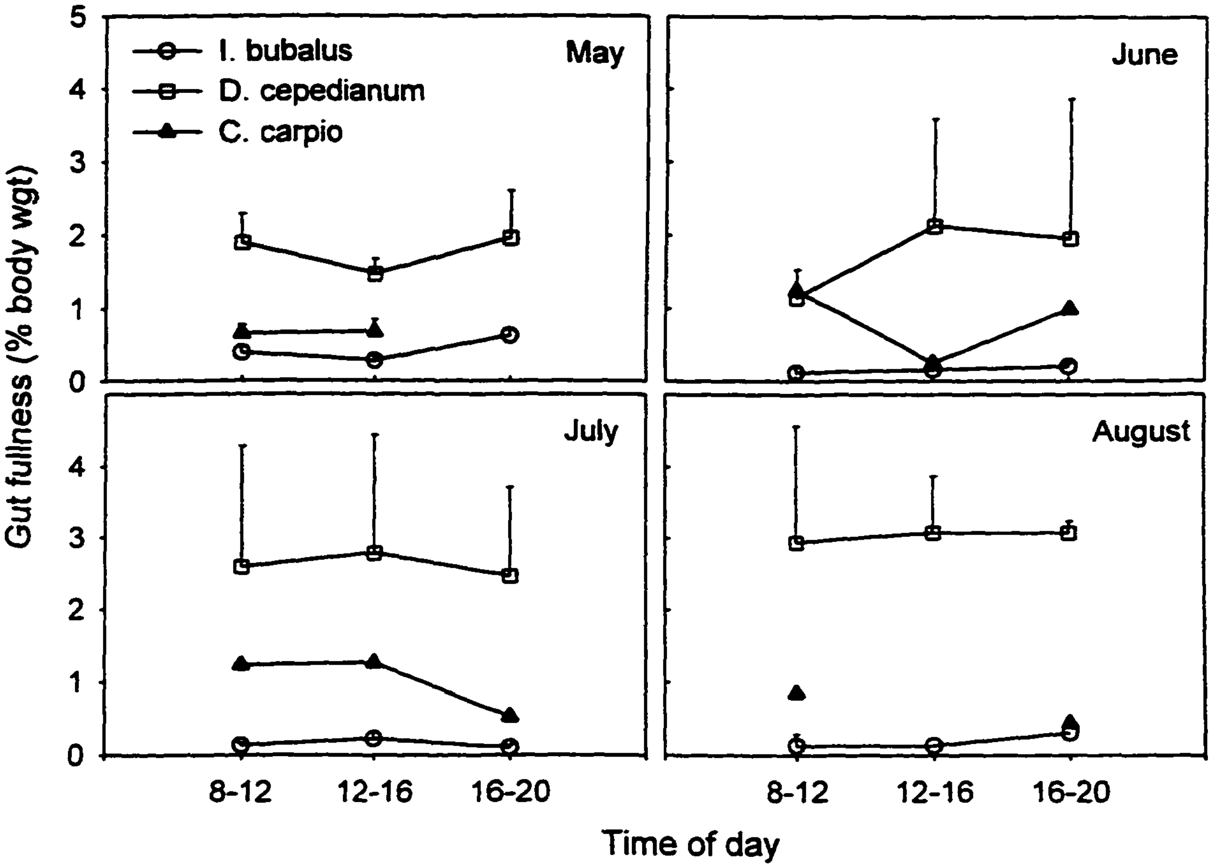
Figure 4. Mean values for six response variables measured in field enclosure/exclosure experiments. Significant P-value indicates differences among treatments detected by a repeated measures ANOVA with time as the repeated factor.

Figure 1



I. bubalus
D. cepedianum
C. carpio
Ammonia excretion (umol/g/h)
16
14
12
10
8
6
4
2
0
[NH$_3^+$]=-4.785(log wt) + 19.134
r^2=0.529
P < 0.0001
SRP excretion (umol/g/h)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
[PO$_4^-$]=-0.064(log wt) + 0.243
r^2=0.605
P < 0.0001
N:P ratio (molar)
160
140
120
100
80
60
40
20
r^2=0.059
P = 0.132
100
1000
10000
Weight (g)

Figure 2



5
4
3
2
1
0
I. bubalus
D. cepedianum
C. carpio
May
June
July
August
Gut fullness (% body wgt)
8-12
12-16
16-20
Time of day

Figure 3

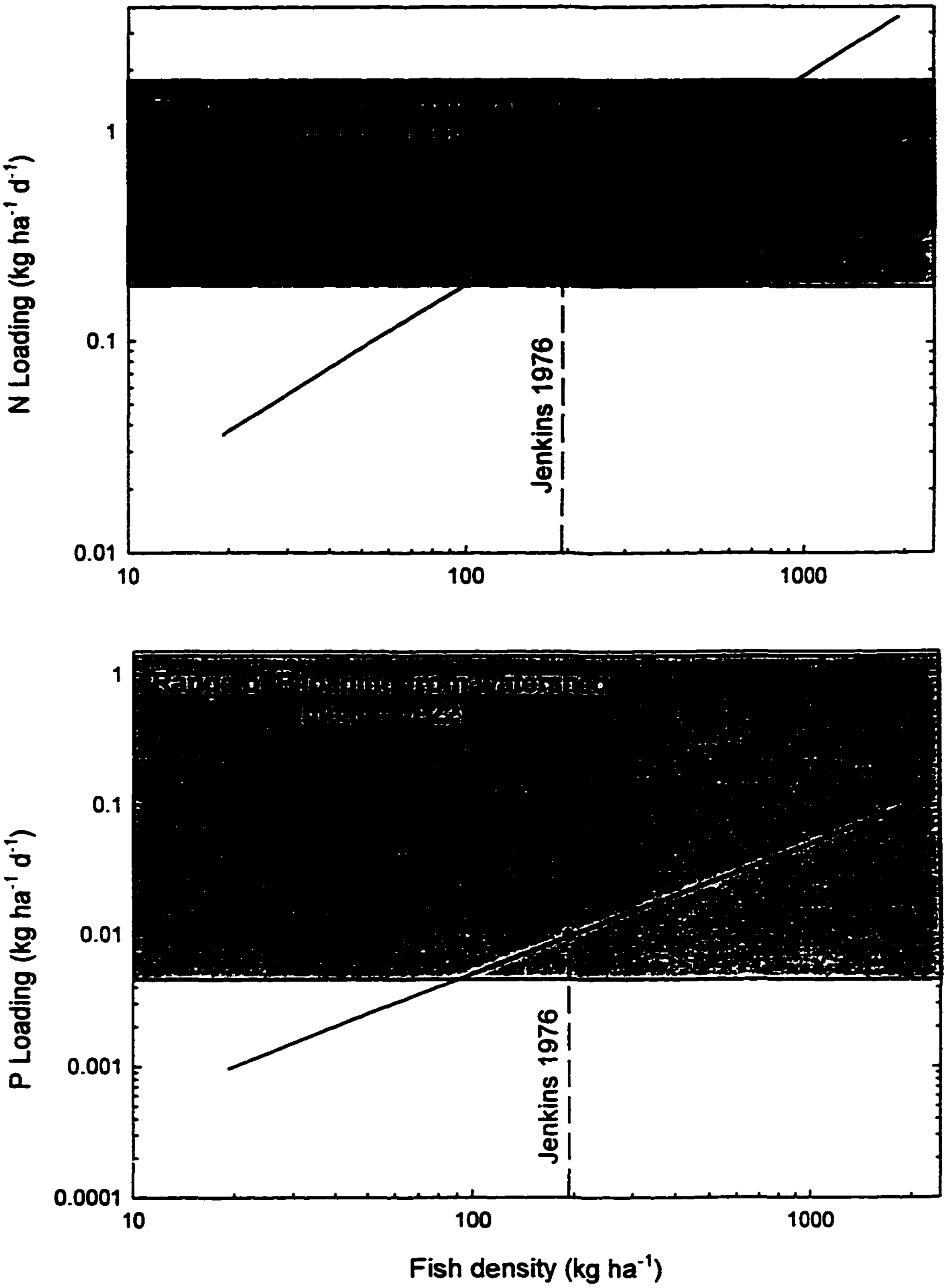

N Loading (kg ha^{-1} d^{-1})
0.01
0.1
1
Jenkins 1976
10
100
1000
P Loading (kg ha^{-1} d^{-1})
0.0001
0.001
0.01
0.1
1
Range of
Jenkins 1976
10
100
1000
Fish density (kg ha^{-1})

Figure 4

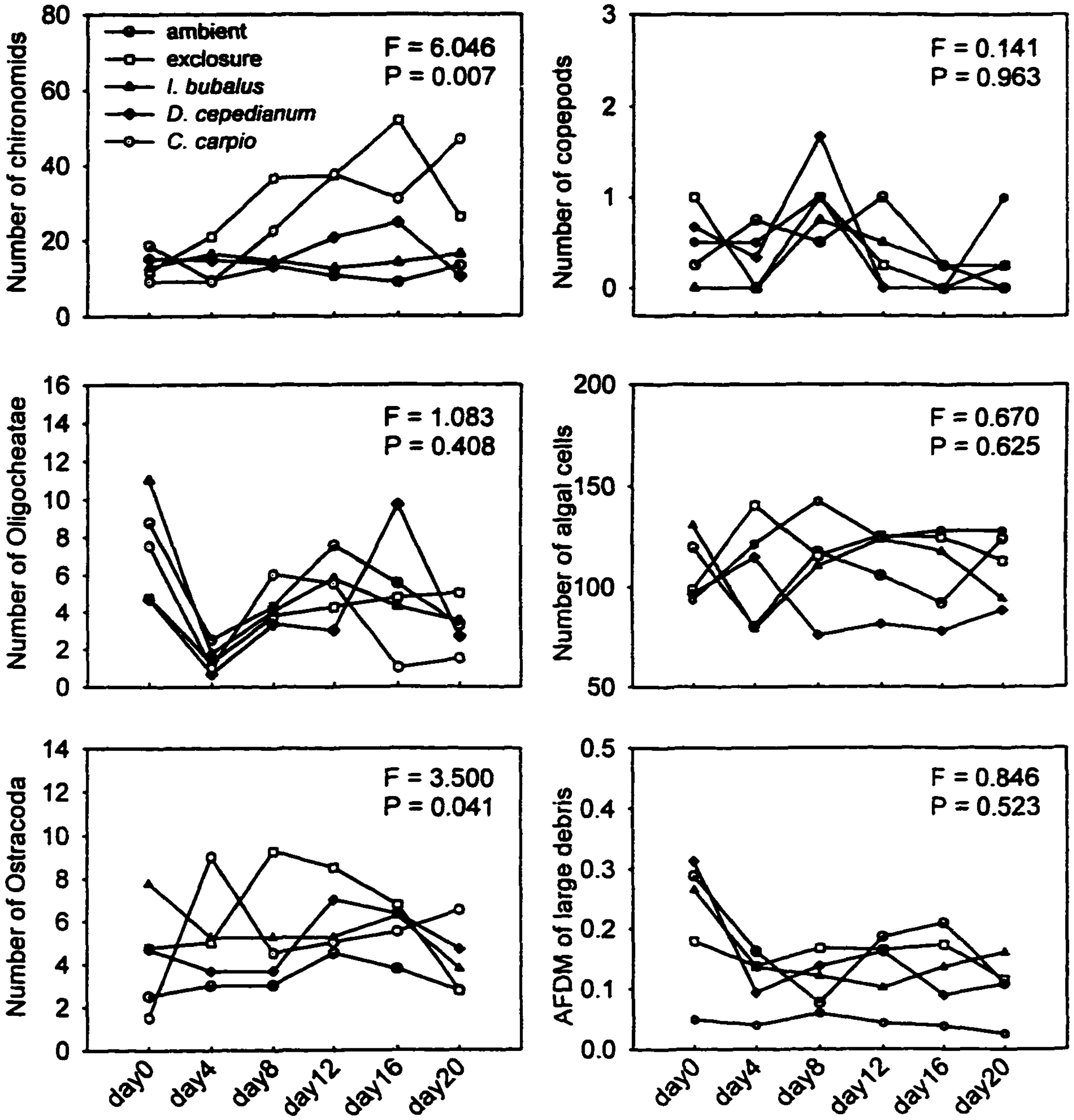
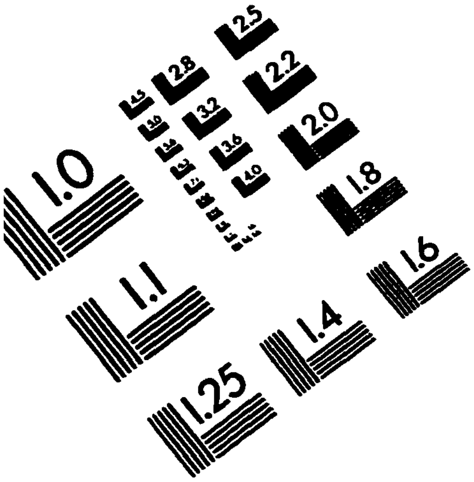
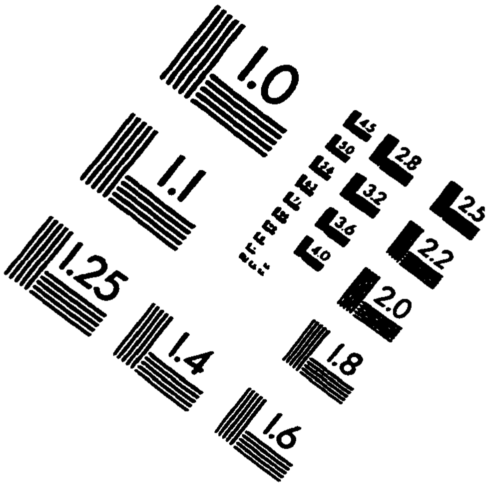
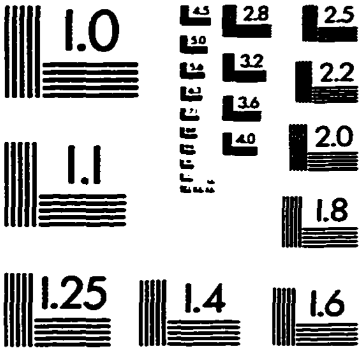
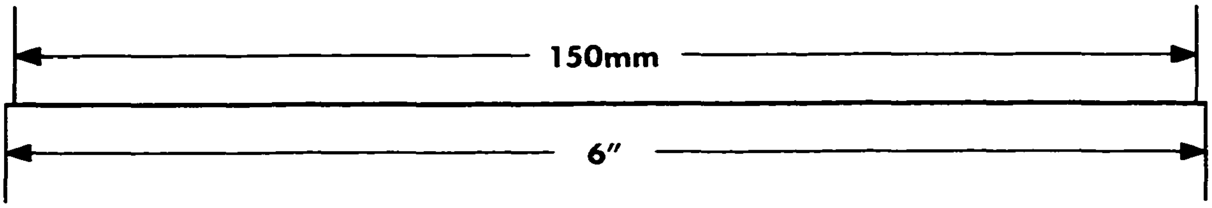

Number of chironomids
80
60
40
20
0
ambient
exclosure
I. bubalus
D. cepedianum
C. carpio
F = 6.046
P = 0.007
Number of copepods
3
2
1
0
F = 0.141
P = 0.963
Number of Oligocheatae
16
14
12
10
8
6
4
2
0
F = 1.083
P = 0.408
Number of algal cells
200
150
100
50
F = 0.670
P = 0.625
Number of Ostracoda
14
12
10
8
6
4
2
0
F = 3.500
P = 0.041
AFDM of large debris
0.5
0.4
0.3
0.2
0.1
0.0
F = 0.846
P = 0.523
day0
day4
day8
day12
day16
day20
day0
day4
day8
day12
day16
day20

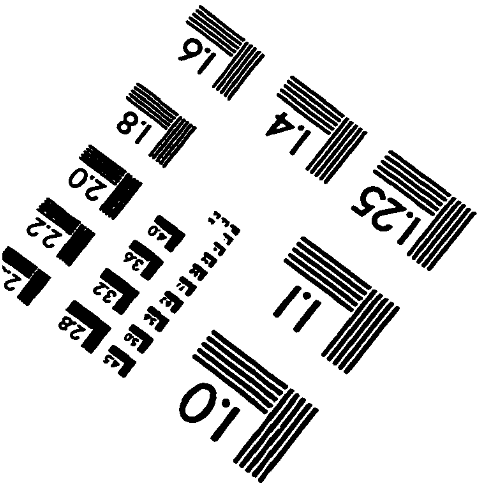
IMAGE EVALUATION TEST TARGET (QA-3)











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