

## Effects of gizzard shad on benthic communities in reservoirs

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*(Received 20 November 2002, Accepted 14 April 2003)*

Effects of gizzard shad *Dorosoma cepedianum* on benthic communities in a large southern reservoir (Lake Texoma, U.S.A.) were examined during two field enclosure and enclosure experiments in which enclosures were stocked at high and low densities in 1998 and 1999, respectively. In both years, chironomid abundance significantly increased in treatments that excluded large fishes from foraging on sediments. Mean abundance of chironomids and ostracods were significantly higher ( $P < 0.05$ ) in enclosures than enclosures stocked with gizzard shad at 1140–1210 kg ha<sup>-1</sup>. In 1999, benthic invertebrate abundances did not differ ( $P > 0.08$ ) between enclosure and enclosures stocked at 175–213 kg ha<sup>-1</sup>. Per cent organic matter, algal abundance and abundance of other macroinvertebrates in sediments did not differ significantly among treatments in either year. Although chironomid abundance was reduced in gizzard shad enclosures in 1998, food habits from this and other studies showed that adult gizzard shad in Lake Texoma only consumed detritus and algae. It is likely that high sedimentation rates in Lake Texoma limit the ability of gizzard shad to regulate algae and detritus in benthic sediments. Thus, it is concluded that disturbance of benthic sediments by gizzard shad caused the observed reduction in chironomid abundance, rather than through consumption or competition for resources.

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Key words: algae; benthic organisms; chironomids; detritus; omnivorous fishes; reservoirs.

### INTRODUCTION

The ability of benthic fishes to regulate ecosystem processes in reservoirs has important management implications because these fishes may indirectly influence other economically important species (*e.g.* sport fishes) by altering the prey base or productivity in those systems. For example, benthic foraging by large-bodied omnivorous fishes stirs up benthic sediments, increases water-column nutrient concentrations and increases rates of nutrient regeneration (Lamarra, 1975; Shormann & Conter, 1997). Moreover, planktivory and benthic foraging by gizzard shad *Dorosoma cepedianum* (Lesueur) allows them to regulate zooplankton abundance through both top-down and bottom-up processes (Vanni, 1996; Schaus & Vanni, 2000). Because the general effects of benthic fishes are thought

to negatively influence predatory sport fishes, a common management objective is to eliminate or reduce their abundance (Wydoski & Wiley, 1999; Tomlinson *et al.*, 2002).

In addition to changes in water chemistry and nutrient dynamics, benthic fishes can also reduce the abundance of benthic invertebrates. In general, most studies in lentic systems that have excluded fishes from foraging on sediments reported an increase in invertebrate abundance in the absence of fishes (Gerking, 1994). One exception was Thorp & Bergey (1981) who concluded that environmental heterogeneity and food web complexity limit the ability of vertebrates (fishes and turtles) to control benthic invertebrate populations, and that other factors such as temperature and habitat were more important regulators of these organisms. Several other studies using field enclosures or exclosures have reported minimal effects of fish on benthic invertebrates in streams with coarse substrata (Allan, 1982; Reice & Edwards, 1986) and ponds with high densities of macrophytes (Gilinsky, 1984; Batzer *et al.*, 2000). Field cage experiments, however, have indicated a strong effect of fishes on benthic invertebrate communities in farm ponds (Morin, 1984) and warm-water, soft-sediment streams (Gilliam *et al.*, 1989). Moreover, the exclusion of fishes in streams has been shown to directly or indirectly affect invertebrates, algae and detritus (Power *et al.*, 1985; Flecker, 1996). Indeed, the relative importance of fishes varies across habitats and it is necessary to perform experiments across a broad range of systems and species groups to predict the conditions under which fishes are important regulators of benthic community composition.

The ability of a species to regulate properties of an ecosystem may depend on its abundance (Power *et al.*, 1996; Power, 1997), population size structure (Mehner *et al.*, 1998), trophic level (Carpenter *et al.*, 1992; Schindler *et al.*, 1993) or mode of feeding (Matthews, 1998). Large-bodied benthic fishes that can process large amounts of sediments (*e.g.* *Prochilodus*, Flecker, 1996) are likely to disrupt sediment processes more than disturbances by smaller fishes. North American reservoirs often have high densities of large-bodied benthic omnivorous fishes, including gizzard shad. Because adult gizzard shad are large enough to escape predation by most predators, their populations have expanded and they are typically the numerically dominant fish species in many North American reservoirs (Stein *et al.*, 1995).

Recent studies indicate gizzard shad can potentially have strong effects on ecosystem functioning of reservoirs. Gizzard shad are facultative detritivores, but primarily consume detritus and algae as adults (Dalquest & Peters, 1966; Gido, 2001). Mundahl (1991) estimated that dry mass of sediments processed daily by gizzard shad was equivalent to 13% of their wet body mass. Because of high sedimentation rates, however, he suggested gizzard shad were unlikely to affect benthic community dynamics. By foraging on sediments, gizzard shad also transport nutrients into the water column of reservoirs through excretion; this flux of nutrients can contribute substantially to the total nutrient budget of the reservoir during periods of low inflow from tributaries (Vanni, 1996; Schaus *et al.*, 1997; Schaus & Vanni, 2000; Gido, 2002). As far as is known, only one study has examined the effects of gizzard shad foraging on benthic invertebrate abundance. Using 900 l mesocosms stocked with gizzard shad at *c.* 1000 kg ha<sup>-1</sup>, Cline *et al.* (1994) found no significant effect of gizzard shad on the density of

benthic invertebrates. Because these were closed systems, however, indirect effects of the fish (*e.g.* increased nutrient levels) may have obscured the effects on the benthos.

In this study, field enclosure and enclosure experiments were conducted to evaluate the effects of gizzard shad on benthic processes in Lake Texoma (33°49' N; 96°33' E), a large impoundment on the Oklahoma–Texas border, U.S.A. Gizzard shad are abundant in this system and comprised *c.* 14% of the offshore fish biomass captured during gillnet surveys (Gido & Matthews, 2000; Gido *et al.*, 2000). Thus, gizzard shad are probably an important component of the benthic food web that, based on their feeding ecology, are hypothesized to either directly or indirectly affect benthic invertebrates, algae and detritus. Direct effects should occur through consumption or mechanical disturbance of the sediments and indirect effects would probably occur through exploitative competition. It is predicted that the exclusion of gizzard shad from feeding on sediments will cause an increase in algae, detritus and benthic invertebrate abundance.

## MATERIALS AND METHODS

### STUDY AREA

Lake Texoma is a 36 000 ha impoundment of the Washita and Red Rivers. Reservoir releases and resulting fluctuations in water level are primarily for hydropower and flood control. Secchi disk depth transparency typically ranges from 100 to 125 cm, but can decrease to 15 cm during turbid inflow episodes (Matthews, 1984). Locations of fish collections and the field experiment were *c.* 35 km upstream 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 (Patten, 1975). This silt- and sand-bottomed cove is typical of other coves in the transitional zone of the reservoir (Kimmel & Groeger, 1986).

Catches from benthic-set gillnets in this cove during summer and autumn of 1997 and 1998 (Gido & Matthews, 2000) showed that gizzard shad numerically dominated the assemblage (44%). Striped bass *Morone saxatilis* (Walbaum 16%), threadfin shad *Dorosoma petenense* (Günther 14%) and smallmouth buffalo *Ictiobus bubalus* (Rafinesque) (6%) were commonly collected.

### EXPERIMENTAL DESIGN

Experimental cages were constructed with 2.54 cm mesh plastic netting to allow rapid exchange of water through the cage walls. Although cages were sheltered from direct exposure to wind-waves, there were sufficient currents (*i.e.* 'fetch' within the cove) to inhibit the accumulation of excreted nutrients and potentially faeces within the cages. This mesh-size also allowed smaller fishes [*e.g.* juvenile *Lepomis* and *Morone* spp., *Menidia beryllina* (Cope) and *Pimephales vigilax* (Baird & Girard)] to pass through while retaining or excluding the large-bodied (>100 mm total length,  $L_T$ ) focal species. Cages were open at the top and bottom and edges were secured to the substratum with metal posts and rocks. All cages were carefully placed in *c.* 1.5 m water with minimal disturbance to the enclosed sediments. Fish were captured with a 40 m × 1.5 m beach seine and immediately placed in cages. Two separate experiments were conducted during July 1998 and May 1999. In the first experiment, the effects of gizzard shad were tested at relatively high densities (1140–1210 kg ha<sup>-1</sup>). For this experiment, eight cylindrical cages, each 1.94 m in diameter, were used to either enclose or exclude fish from foraging on

benthic sediments. The experiment was a factorial design with three treatments and four replicates each. As a measure of ambient conditions, one treatment included samples taken in a haphazardly chosen location in close proximity (<1.5 m) to the cages. By taking these ambient samples close to cages, this controlled for a potential effect of cage walls. In a second enclosure treatment no fish were added. The third treatment enclosed three gizzard shad (211–241 mm standard length,  $L_S$ ).

Cove rotenone surveys of North American reservoirs by the National Reservoir Research Program (unpubl. data) estimated that the mean  $\pm$  s.d. standing crop of gizzard shad was  $119 \pm 176 \text{ kg ha}^{-1}$  and ranged from 0 to  $2232 \text{ kg ha}^{-1}$  for 360 reservoirs. Average standing crop estimates for gizzard shad in Oklahoma reservoirs based on cove rotenone surveys was  $118 \text{ kg ha}^{-1}$  (Jenkins, 1976). Thus, densities used in the above experiment probably represent an upper limit for Lake Texoma and a second experiment was conducted in 1999, using larger cages (3.88 m diameter) stocked with four individuals per cage (225–240 mm  $L_S$ ,  $175\text{--}213 \text{ kg ha}^{-1}$ ). The 1999 experiment was the same factorial design with three treatments (fish enclosure, ambient and fish enclosure), but had three replicates per treatment. At the end of each experiment, a  $3 \text{ m} \times 1.5 \text{ m}$  seine with 5 mm bar mesh was used to collect all fishes (including those fishes that could passively move into cages). The entire intestinal tract of gizzard shad was dissected and per cent composition of diet by volume was estimated in the laboratory under  $\times 40$  magnification following methods of Gido (2001).

## RESPONSE VARIABLES

To examine changes in sediment biota, core samples (8 cm diameter) were taken from a haphazardly selected position within each cage and at locations outside of cages at the beginning of the experiment and every 4 days thereafter. To minimize the disturbance of substrata, only one core sample was taken per sampling interval in the 1.94 m diameter cages in 1998 and three cores (pooled for each cage) were taken in the 3.88 m diameter cages in 1999. A previous study (Gido, 2001) indicated invertebrate abundance in replicate sediment cores are very homogeneous throughout this and two other coves in this region of the reservoir (CV of replicate samples averaged 21%), probably because of the even distribution of fine sediments in these sheltered coves. Thus, this appeared to be an adequate sample to characterize the benthic communities in these cages. 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 & 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 four, 4 ml aliquots were drawn from this homogenate. The remainder of the sample was passed through a  $210 \mu\text{m}$  sieve to retain macroinvertebrates and large zooplankton. One of the 4 ml aliquots was placed in an aluminium tray, dried at  $60^\circ \text{C}$  for 24 h and then ashed at  $550^\circ \text{C}$  for 1 h to determine per cent organic matter, a composite for algae and detritus. Algal abundance was determined from the other three aliquots (*i.e.* three replicates per core sample). A 0.1 ml sub-sample from each aliquot was placed in a Palmer counting cell and algal cells were counted in 50 fields of view at  $\times 400$  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 experiments were assessed with a repeated measures ANOVA with time as the repeated factor. Because core samples were taken prior to the addition of fish on day 0, this date was excluded from the analysis, but the data are plotted for reference. If significant differences were found among treatments, *post-hoc* comparisons were made with Ryan's multiple comparison procedure (Toothaker, 1991).

## RESULTS

Core samples were overall, numerically dominated by several genera of chironomids (primarily *Dicotendipes* spp. and *Glyptotendipes* spp.), which accounted for 67% of the individuals averaged across years and treatments. Ostracods (16% of total individuals) and oligochaetes (15% of individuals) were commonly found. Less abundant taxa in core samples included copepods, water mites (Hydracarina) and phantom midges (*Chaoborus* spp.). These less abundant taxa were excluded from the analysis. Algal counts were dominated by diatoms with few filamentous green algae and cyanobacteria (67, 19 and 14% of total biovolume averaged across years and treatments).

In 1998, mean chironomid densities differed significantly among treatments ( $F_{2,8} = 7.90$ ,  $P = 0.013$ ; Fig. 1). Because the effects of time and the interaction between time and treatment were not significant, *post-hoc* comparisons were only made among the three treatments. In this analysis, densities of chironomids in ambient and enclosure treatments were lower than in core samples from

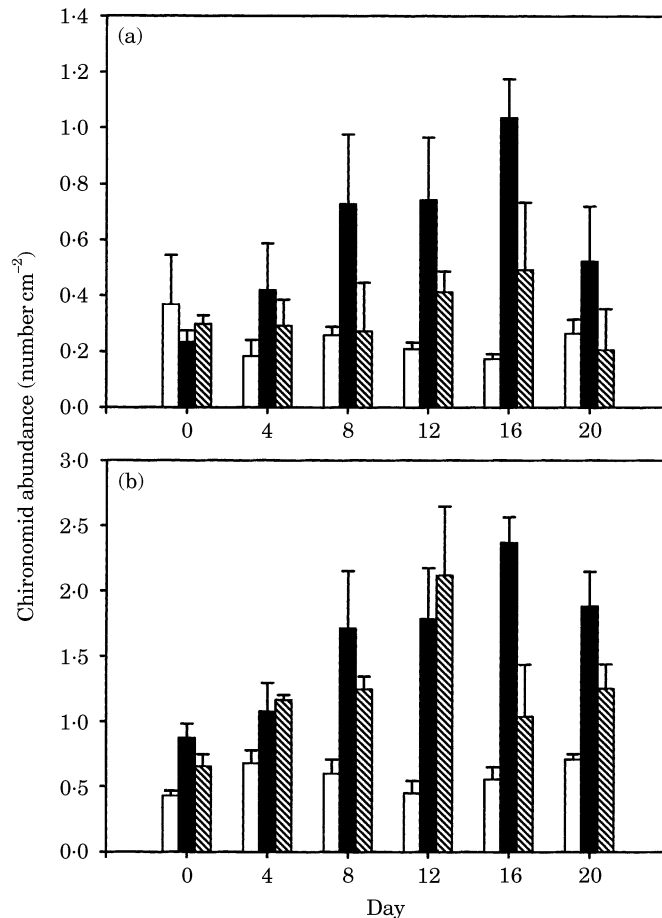


FIG. 1. Mean + s.e. chironomid densities in benthic core samples taken from experimental treatments in (a) 1998 and (b) 1999. □, Ambient; ■, enclosure; ▨, *Dorosoma cepedianum*.

enclosures; there was no difference between ambient and enclosure treatments. Ostracod density differed across time ( $F_{4,32}=2.970$ ,  $P=0.034$ ) and among treatments ( $F_{2,8}=1.311$ ,  $P=0.019$ ), but the interaction of these variables was not significant (Fig. 2). As with chironomid densities, *post-hoc* comparisons among treatments indicated that ostracod densities were greater in the enclosure than ambient or enclosure treatments, but not different between ambient and enclosures. Although there was a significant effect of time on oligochaete density ( $F_{4,32}=3.77$ ,  $P=0.013$ ), there was no treatment or time  $\times$  treatment interaction (Fig. 3). Algal biovolume (not shown) and per cent organic matter (Fig. 4) did not differ across time or among treatments (all  $P$ -values  $> 0.1$ ).

Chironomid densities in the 1999 experiment were significantly different among treatments ( $F_{2,6}=33.9$ ,  $P<0.001$ ; Fig. 1). The effect of time and the time  $\times$  treatment interaction were not significant. *Post-hoc* comparisons among treatments revealed that chironomid abundance was significantly lower in ambient treatments than gizzard shad enclosures and enclosures. Although

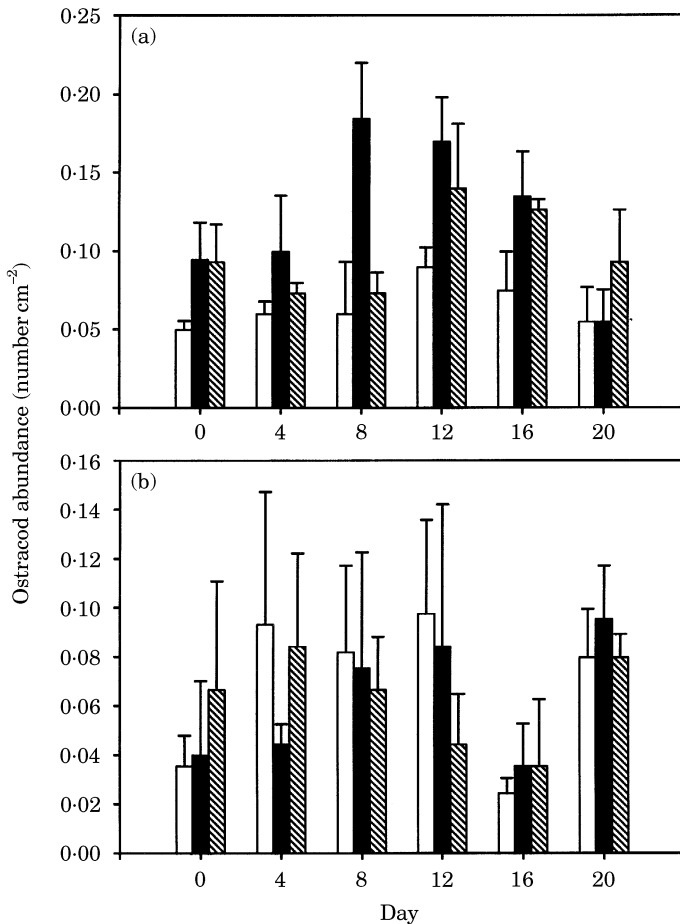


FIG. 2. Mean  $\pm$  s.e. ostracod densities in benthic core samples taken from experimental treatments in (a) 1998 and (b) 1999.  $\square$ , Ambient;  $\blacksquare$ , enclosure;  $\square$  (hatched), *Dorosoma cepedianum*.

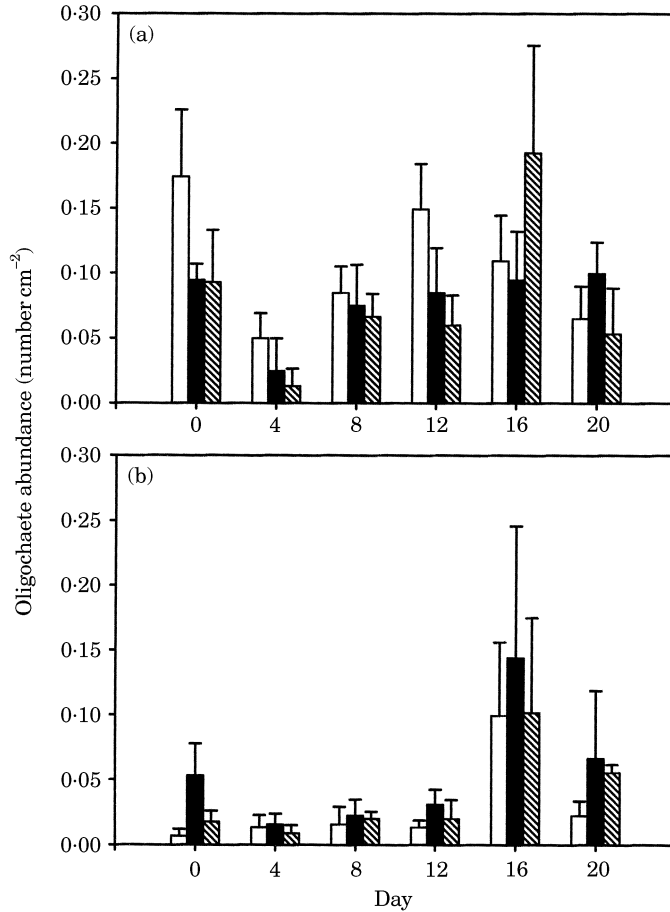


FIG. 3. Mean + s.e. oligochaete densities in benthic core samples taken from experimental treatments in (a) 1998 and (b) 1999. □, Ambient; ■, enclosure; ▨, *Dorosoma cepedianum*.

mean chironomid densities in enclosures were *c.* 60% lower in enclosures than enclosures on day 16 and 30% lower on day 20; these differences were not significant ( $P = 0.081$ ), possibly because of the low power of this experiment ( $1 - \beta = 0.237$ ). Ostracod density did not differ across time or among treatments (all  $P$ -values  $> 0.1$ ; Fig. 2) nor did algal biovolume (all  $P$ -values  $> 0.25$ ). Oligochaeta density ( $F_{4,24} = 9.14$ ,  $P < 0.001$ ; Fig. 3) and per cent organic matter ( $F_{4,24} = 5.22$ ,  $P = 0.009$ ; Fig. 4) both showed a significant decrease across sample dates but no treatment effect.

Food habits of gizzard shad taken from enclosures at the end of the experiment consisted primarily of detritus and algae (98.2% by volume) with a few ostracods (1.6%) and no chironomids. Gizzard shad appeared to consume primarily vegetative detritus and diatoms rather than filamentous algae.

The presence of small fishes that could pass through the cage mesh could have affected the abundance of benthic organisms and organic content of sediments inside cages. Although there was no significant difference between

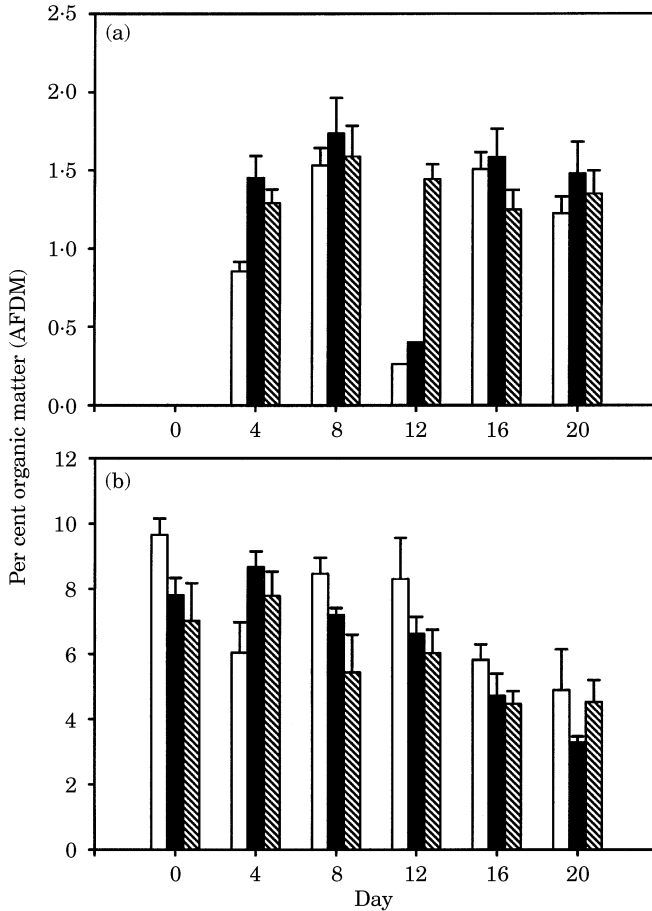


FIG. 4. Mean  $\pm$  s.e. per cent organic matter in benthic core samples taken from experimental treatments in (a) 1998 and (b) 1999.  $\square$ , Ambient;  $\blacksquare$ , enclosure;  $\square$  (hatched), *Dorosoma cepedianum*.

enclosures and enclosures or between years in mean total density of smaller fishes (ANOVA,  $P < 0.3$ ), there were relatively high densities in all cages; bluegill *Lepomis macrochirus* Rafinesque, *Morone* spp. and bullhead minnow *P. vigilax* mean  $\pm$  s.d. densities were  $14.4 \pm 9.5$ ,  $4.4 \pm 3.1$  and  $1.1 \pm 0.6$  individuals  $m^{-2}$ , respectively.

## DISCUSSION

Chironomid abundance was strongly affected by experimental treatments in this study, but these effects varied between the two years. In both 1998 and 1999 experiments, ambient chironomid densities were approximately three times lower than in fish enclosures by day 12, probably because of the exclusion of large-bodied fishes that prey on chironomids or disturb sediments. In addition, ostracods were shown to increase in enclosures in the 1998 experiment, however, this effect was strongest on day 8 and was absent by day 20. These differences

suggest that either a single species or a combination of species are affecting benthic invertebrate abundance. Moreover, data from the fish enclosures suggest that gizzard shad are at least partially responsible for this pattern, but there are clearly other large-bodied species, *e.g.* channel catfish *Ictalurus punctatus* (Rafinesque) and smallmouth buffalo in the system that, when excluded from the sediments, allowed chironomid densities to increase.

Treatment effects in this study may have been obscured because of temporal differences in chironomid abundance and sediment organic content between years; chironomid densities were approximately twice as high and organic content was more than three times higher in May 1999 than in July 1998. Differences in chironomid densities probably represent a seasonal pattern, as a decline in chironomid abundance from May to August is typical in Lake Texoma (Gido, 2001). Rising water levels in 1999 and dropping water levels in 1998 may have been partly responsible for differences in organic content of sediments between years. Although it is unclear what effect these factors had on the experimental results, relative difference between enclosures and ambient conditions were similar between years. Thus, the interannual differences were probably minimal.

Results from this study contrast with those by Cline *et al.* (1994) who found no difference in benthic invertebrate densities between control and gizzard shad-stocked mesocosms. Because the current study was conducted in larger field cages, it is possible that processes differed among these experiments. For example, nutrients or faeces released by gizzard shad, which could have indirectly increased benthic invertebrate abundance, might be expected to positively affect benthic invertebrate abundance in mesocosms. In open field cages, however, any effect of nutrient or faecal accumulation would be diluted by high exchange rates with surrounding water.

A number of other studies in which the abundance of benthic fishes in lentic environments has been manipulated also reported increased densities of benthic invertebrates in the absence of fishes (Gerking, 1994). Perhaps this is a general pattern for reservoirs as well (Wetzel, 2001). For example, removal of *Catostomus commersoni* (Lacépède) from a Michigan lake was associated with a 13–18-fold increase in abundance of chironomid larvae (Hayes *et al.*, 1992). Moreover, a fish kill of *Abramis brama* (L.) in Lake Ringsjon resulted in an increase in the benthic invertebrate fauna of this lake (Bergman *et al.*, 1999). The strong negative effect of benthic fishes on sediment-dwelling invertebrates is probably because of several processes including direct predation and mechanical disturbance of substrata.

Examination of gut contents at the end of the experiment, in addition to other published reports, suggests that adult gizzard shad primarily forage on detritus and algae (Dalquest & Peters, 1966; Mundahl & Wissing, 1987; Gido, 2001). Thus, the reduction in chironomid abundance in gizzard shad enclosures did not appear to be caused by direct predation. Because the dominant species of chironomids in Lake Texoma are collector-gatherers that feed on detritus and algae (Vaughn, 1982), it is possible that gizzard shad may compete for resources (*e.g.* diatoms and detritus) with chironomid larvae. This would require that resources are limited, however, which does not appear to be the case in Lake Texoma as organic matter and algal biovolume (volumetric quantity of

algae in or attached to benthic sediments) did not differ among treatments in either year. Because there was no apparent reduction of detritus or algae in enclosures, resources did not appear to be limited and competition for resources does not appear to explain the observed effect. The lack of decline in algae or organic matter in the gizzard shad enclosures relative to exclosures was surprising because this species foraged almost exclusively on these items. Several factors could have contributed to a weak association between the presence of fishes and abundance of benthic algae and organic matter. Foremost, is that high sedimentation rates of silt, detritus and algae may have dampened the effects of fishes. For example, Mundahl (1991) predicted that gizzard shad processed <4% of the deposited sediments in Acton Lake, Ohio. Typical of many reservoirs, Lake Texoma is very turbid and sedimentation rates were estimated as between 150 and 550 g dry mass m<sup>-2</sup> day<sup>-1</sup> in the region of the reservoir where this study was conducted (Gido, 2001). The continuous 'rain' of organic matter from the water column would probably buffer the removal of these materials by fishes. Thus, it can be hypothesized that reduced densities of chironomids in gizzard shad enclosures was caused by mechanical disturbance of substrata.

Whereas foraging by stream fishes is known to reduce structural habitat (*e.g.* filamentous algae and detritus) for invertebrates (Gelwick & Matthews, 1992; Flecker, 1996), foraging by benthic fishes in soft sediments did not appear to influence the physical structure of the sediments. The mechanical mixing of the sediments, however, probably alters the chemical exchange equilibria at the sediment-water interface and changes the microhabitat for these small benthic organisms. Several studies of marine fishes and spawning salmonids have reported the effects of foraging-related disturbances on benthos (Virnstein, 1977; McCormick, 1995; Peterson & Foote, 2000). Palmer (1988) found that disturbance by predatory marine fishes accounted for virtually all the nematode mortality in laboratory experiments. Experiments in freshwater lentic systems report strong effects of common carp *Cyprinus carpio* (L.) and small mouth buffalo on resuspension of sediments and changes in nitrification rates (Richardson *et al.*, 1990; Shormann & Conter, 1997). In addition, the stirring of sediments during feeding may reduce chironomid abundance by dislodging individuals which are then either swept away by currents or consumed by other fishes. Although direct experimental evidence is lacking to show that mechanical disturbance of sediments was responsible for the reduced densities of chironomids in fish enclosures relative to exclosures, this appears to be the most parsimonious explanation for the observed treatment effects.

Based on this and other studies (Andersson *et al.*, 1978; Hayes *et al.*, 1992; Bergman *et al.*, 1999), benthic fishes appear to have a capacity to influence benthic invertebrate composition in soft-bottomed littoral habitats of reservoirs. The effect of these fishes, however, is highly dependent on density. In this study chironomid and ostracod densities in gizzard shad enclosures stocked at 175–213 kg ha<sup>-1</sup> were not significantly different than exclosures. Although the statistical power of this comparison was low and the treatment effect was only marginally insignificant, gizzard shad appeared to have a weaker effect on the benthos at lower densities. Assuming that these results apply to other reservoirs

and that standing crop estimates for North American reservoirs averages  $119 \text{ kg ha}^{-1}$  (National Reservoir Research Program, unpubl. data), it would appear that most reservoirs do not have sufficient gizzard shad densities to significantly reduce chironomid abundance. There is, however, much variation in abundance across years and longitudinally within reservoirs and, as reported here, gizzard shad can have rapid effects (<20 days) on the benthos. Thus, it is likely that benthic invertebrates in reservoirs that experience high gizzard shad densities, even temporarily, may be limited by their feeding activities.

Benthic invertebrates can be affected by top-down processes such as predation and bioturbation (disturbance of sediment layers by biological activity) as well as bottom-up processes such as sedimentation of algae and detritus. In Lake Texoma, high sedimentation rates provide adequate resources to allow benthic invertebrates to increase when fishes are excluded from feeding on sediments. Thus, reduction or removal of gizzard shad in this and other reservoirs would probably result in an increase in abundance of benthic invertebrates, at least over short time scales. An increase in the biomass of benthic invertebrates resulting from the removal of benthic fishes, however, may not be transmitted to higher trophic levels (Hayes *et al.*, 1992). Future studies should consider the net effect of these fishes in the ecosystem based on a variety of pathways (*e.g.* trophic and nutrient dynamics) before fish removal is considered as a means to increase sportfish production.

This would not have been possible without field and laboratory assistance from D. Cobb, A. Gido, R. Gido, A. Marsh, D. Lutterschmit and J. Schaefer. I extend special thanks to W. Matthews for thoughtful discussions and his critical review of this manuscript. This manuscript further benefited by critical reviews from L. Canter, C. Hargrave, M. Kaspari, N. Mundahl, J. Schaefer, W. Shelton, D. Spooner, C. Vaughn, M. Weiser and two anonymous reviewers. The University of Oklahoma Biological Station provided logistic and financial support. Thoughtful discussions concerning design and analysis were provided by E. Marsh-Matthews, G. Wellborn and T. Wissing.

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