

Impacts of fish predation on an Ohio River zooplankton community

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*Compared to lentic systems, much less is known about the factors that structure zooplankton communities in large river environments. In this study, we used an in situ mesocosm system, the potamocorrals, to assess the impact of larval fish on the zooplankton community in the Ohio River (USA). The responses of zooplankton to increasing biomasses of fish were taxon-dependent. The population growth rates of the most common zooplankton, *Diatylops thomasi*, varied inversely with fish biomass, while other crustacean zooplankton showed no significant responses to the fish treatment. The reverse pattern was seen for the rotifer *Polyarthra* sp. whose population growth rates increased with increasing fish biomass. This is the first in situ evaluation of fish predation on zooplankton in a large river system and demonstrates that predation as well as physical factors may influence riverine zooplankton densities and community structure.*

INTRODUCTION

Despite the recent increased interest in large river ecosystems, our knowledge of the zooplankton of these habitats remains fragmentary. With some notable exceptions [e.g. (Kofoid, 1903; Reinhard, 1931)] comparatively little early research was conducted on the phytoplankton and zooplankton of large rivers compared to the numerous studies on fish and freshwater mussels. This lack of research may have resulted from the impression that rivers were not suitable environments for zooplankton. Stream flow (velocity and turbulence) can have negative effects on zooplankton by transporting them into unfavourable environments, physically damaging them, diluting their food resources, and hindering reproduction (Rzsoka, 1978; Pace *et al.*, 1992).

The relationship between zooplankton biomass and water residence time has been recently examined in rivers of various sizes. In a comparison of 31 north temperate rivers, Basu and Pick (Basu and Pick, 1996) found that zooplankton biomass was directly proportional to water residence time ($r^2 = 0.33$) although a small positive relationship was also present with chlorophyll *a* (Chl *a*). In many other rivers that have been studied, zooplankton densities or species richness are generally lowest during high flow periods (Saunders and Lewis, 1989; Ferrari *et al.*, 1989; Vasquez and Rey, 1989; Thorp *et al.*, 1994; Van

Zanten and Van Dijk, 1994). Reynolds' observation that the river must be 'low or slow' for phytoplankton to reach appreciable biomass is probably also true for zooplankton in the main channel (Reynolds, 1988).

While such physical constraints are important, biotic interactions may also significantly influence zooplankton communities in rivers. While comparatively few experimental studies have analysed the effects of fish on riverine zooplankton, corollary evidence suggests that direct and indirect interactions with fish may influence riverine zooplankton communities. For example, zooplanktivorous fish compose 30% of the fish population numerically in the Rhine River (Van Dijk and Van Zanten, 1995) and these fish presumably remove some percentage of the zooplankton production in this system. Rotifers and other zooplankton are important in the diets of larval fish in the Great River Ouse (Bass *et al.*, 1997; Mann *et al.*, 1997). Adult paddlefish (*Polydon spathula*) in the rivers of the USA also feed on zooplankton (Rosen and Hales, 1981; Blackwell *et al.*, 1995). These large fish have historically been very abundant in the Mississippi River network, which suggests that the zooplankton have been common in rivers historically and are not just an artefact of river management practices by humans.

The importance of fish predation on zooplankton in rivers may seem obvious based on the wealth of observational and experimental evidence that fish planktivory

in lakes can significantly alter zooplankton behaviour, densities and community composition (Carpenter *et al.*, 1987; Bollens and Frost, 1989; Vanni and Layne, 1997). However, some important differences between lentic and lotic systems may make the ‘top-down’ effects of fish on zooplankton in rivers much less significant than in lakes. The zooplankton communities of many rivers are dominated by rotifers and small-bodied crustacean zooplankton, such as *Bosmina*, and zooplankton densities in the rivers are often lower than those commonly seen in lakes (Pace *et al.*, 1992; Thorp *et al.*, 1994). In addition, rivers like the Ohio are generally more turbid than many lakes, which may reduce the ability of visually foraging fish to locate zooplankton prey.

While manipulative approaches are needed to assess the impacts of fish predation on riverine zooplankton, little experimental work has been undertaken to date [but see (Richardson and Bartsch, 1997)]. One likely reason for this is that it is difficult to conduct the *in situ*, large-volume, controlled experiments in rivers that have been so successful in lentic environments. Traditional polyethylene enclosures (limnocorrals) anchored in position with their solid walls do not mimic riverine conditions very well. However, Thorp *et al.* developed limnocorral-like enclosures, the Nitex-net potamocorrals, which function well in large river environments and which enable investigators to conduct manipulative experiments under more realistic field conditions (Thorp *et al.*, 1996). This system has been used successfully to assess the impacts of benthic suspension feeders on zooplankton communities in the Ohio (Jack and Thorp, 2000) and St. Lawrence Rivers (Casper and Thorp, submitted for publication). In this paper, we describe an experiment in which this potamocorral system was used to assess predation by small zooplanktivorous fish on the summer zooplankton community in the Ohio River. We hypothesized that fish predation would reduce population growth rates and densities of the larger cladoceran and copepod taxa, while not affecting population growth rates of the smaller zooplankton, such as rotifers, over the course of the experiment.

METHOD

The potamocorrals were constructed and deployed as described in Jack and Thorp (Jack and Thorp, 2000). Potamocorrals are 3500 l, 83- μ m-mesh enclosures supported by a large floating raft of wood, PVC and rubber floats. Each corral is 1.5 m in diameter and 2.5 m deep. The lower 2 m of each corral is made primarily of Nitex mesh and is submerged in water; the upper 0.5 m consists of a cordura nylon collar which protrudes above water-level to reduce wash-over from waves. The mesh sides of

the corrals permit slow exchange of river water along with its pico- and nanoplankton to minimize ‘container effects’ from the corrals. The corrals are allowed to drift with the current during daylight hours, being steered by boats when necessary to avoid obstructions or river traffic. At night, the corrals and boats are anchored near shore for safety reasons. In previous trials corral movement was slower than average river current because of the large drag generated by the bags, but the environments within the corrals closely matched that of the river (Thorp *et al.*, 1996; Jack and Thorp, 2000).

For this experiment we used 12 potamocorrals and launched the raft at Vevay, Indiana at Ohio River Kilometer 866 in late July when the river had reached low pool level. The corrals were lowered closed into the water to prevent the accidental introduction of fish. Because the Nitex walls also excluded the larger zooplankton, we performed a series of vertical and horizontal net tows with 153 μ m and 25 μ m plankton nets to inoculate the bags with a representative zooplankton community. The volume filtered was estimated using the distance pulled or towed and assuming the plankton nets approximated a cylinder in shape during towing.

Larval fish were obtained by seine netting over cobble beds near the launching site for the experiment. Of the fish collected, only the larvae of two species, bluntnose minnows (*Pimephales notatus*) and emerald shiners (*Notropis atherinoides*), were numerous enough to be used in the experiment. The effectiveness of these species as predators of riverine zooplankton has not been assessed, but their congeners have been shown in previous experiments to be effective zooplanktivores (Hambright and Hall, 1992; Mueller-Solger *et al.*, 1997; Zimmer *et al.*, 2000) and they are thought to feed on zooplankton in the Ohio River during their early life stages (William Pearson, personal communication). These fish were held in an aerated bait well for transport to the corrals, and they were added to the corrals in densities of 0 (no fish) 10, and 20 fish per corral (four replicates each). These fish densities were considered representative of what zooplankton experience in the shallow cobble bed areas of the Ohio River (Richie Kessler, unpublished data). To minimize handling stress, fish were not measured or weighed before their introduction to the corrals, but we added a representative size range of fish and equal numbers of each species to each corral. Despite our efforts to minimize handling, we had significant mortality of these fish early in the experiment, but this is probably a conservative effect. The loss of fish or fish in poor condition would reduce predation pressure on the zooplankton and make it less likely that we would show a significant impact of fish predation on zooplankton population growth rates.

While previous experience with the system had shown

that most physical parameters in the corrals were very similar to those in the river (Jack and Thorp, 2000), we measured temperature, dissolved oxygen, pH, conductivity and turbidities on days 1 and 3 of the experiment using a Hydrolab Surveyor Sonde and a Hach turbidity meter. On day 7, whole water samples for Chl *a* and nutrients were taken and kept on ice in a cooler. Once at the laboratory, chlorophyll was extracted with correction for phaeophytin following the procedure of Wetzel and Likens (Wetzel and Likens, 1991). Sample absorbances were read using a Turner Model 10A fluorometer. Nutrient samples were analysed for nitrate, ammonia, soluble reactive phosphorous, and silica using a Skalar Sans Plus automated analysis system.

On days 1, 3, and 6 zooplankton samples were collected with a battery-driven pump system (Little Giant Potent). A clear tube attached to the pump was lowered into the corrals, and 5 l whole samples were taken at 0.5 m and 1.2 m depths in each corral. The samples were pooled in a bucket, and 8 l of the combined sample was poured through a 125 μm mesh to remove the macrozooplankton. The retained organisms were fixed in 95% ethanol and later stored in 70% ethanol. A 50 ml whole water sample was removed from the 2 l sample that remained in the bucket and fixed in ice-cold glutaraldehyde for bacteria counts. The rest of the sample was then poured through a 25 μm plankton net to capture rotifers and other small metazoan microzooplankton. The retentate from these samples was poured into a sample bottle and one-quarter of an Alka-Seltzer tablet was added to narcotize the rotifers and prevent distortion of the soft-bodied species. The samples were then preserved in 70% ethanol.

Macrozooplankton samples were counted in their entirety using an Olympus dissecting microscope. Lengths (excluding spines) and egg ratios were obtained for the first 50 individuals of each species. The microzooplankton samples were divided using a plankton splitter, and one of the subsamples was randomly selected, settled for at least 12 h using the \ddot{U} termohl technique, and counted with an Olympus inverted microscope. The zooplankton were identified using various keys (Pennak, 1987; Thorp and Covich, 1991; Coste, 1978; Stemberger, 1979). Population growth rates for common zooplankton taxa were calculated ($r = \ln N_t - \ln N_0 \text{ day}^{-1}$, where N_t is the final density and N_0 is the initial density) and used to compare the responses of individual taxa among treatments. Nauplii were not identified to species but their population growth rates were calculated as a group separately from the adults. Copepodids were not included in the growth rate calculations. The bacteria were counted with an Olympus epifluorescent compound microscope using acridine orange and the techniques described in Hobbie *et al.* (Hobbie *et al.*, 1977).

We performed a MANOVA and regression analysis of the data using the wet weight of fish in each corral at the end of the experiment as the independent variable in place of the zero, low and high fish density treatments because of unequal fish mortality during the experiment. These procedures were run in the GLM Module of SAS (SAS, 1996).

RESULTS

The physical environment in the potamocorrals was very similar to that in the river throughout the duration of the experiment (Table I). The wet weight of fish in the corrals at the end of the experiment was not correlated with temperature, dissolved oxygen, conductivity, turbidity, or pH ($P > 0.45$). These results were not surprising, as previous work has shown that the potamocorrals provide an environment that, except for current velocity, is very similar to that of the Ohio River (Jack and Thorp, 2000). There were no differences among corrals in the levels of Chl *a*, ammonia, nitrate/nitrite, soluble reactive phosphorus, or silica (Table II). The levels of nutrients were somewhat lower than often noted in the Ohio River in midsummer (Bukaveckas, unpublished data), but it is unlikely at these concentrations that nutrients were limiting to the phytoplankton communities (Reynolds, 1998). Bacterial densities were not correlated with fish wet weight either, but some samples had high levels of detritus that greatly interfered with the staining and the counting of these samples. In previous potamocorral experiments there was no significant bacterial response to treatments. This has been attributed to the porous walls of the corrals and the currents around these enclosures that introduce more bacteria into the corrals (Jack and Thorp, 2000).

The original design of this experiment was to subject the plankton communities to continuous predation from a group of planktivorous larval fish. However, there was considerable mortality (30–60%) of these young, easily damaged fish in the experiments. Most of the dead fish were retrieved during the experiment or at the end of the experiment but three fish in two of the replicates were not found; they may have been lost as the corrals were raised and cleaned at the end of the experiment. Mortality rates between the two species within each corral were usually very similar so ending ratios of shiners to minnows remained close to 1 in all but two replicates, where the ratios were 5 and 0.6. These lower fish densities would presumably lower predation pressure and make it more difficult to show significant effects, thus this is likely to be a conservative effect in this experiment.

The relationship of fish wet weight and population growth rates of individual zooplankton species varied

Table I: Ranges of physical parameters across all corrals during day 3 of the experiment. None of the regressions of these parameters with fish wet weight were significant ($P > 0.45$)

	Temperature (°C)	pH	Conductivity (µOhms)	O ₂ (mg l ⁻¹)	Turbidity (NTU)
Corrals (n = 12)	30.3–30.84	8.46–8.48	0.442–0.445	5.60–5.91	6.9–9.2
River (n = 2)	30.5, 30.77	8.46, 8.47	0.445, 0.446	5.57, 5.70	–

Turbidity readings were not taken in the river.

Table II: Ranges of chlorophyll a and nutrient samples taken in the corrals and the Ohio River on the final day of the experiment

	Chl a	NH ₄	NO ₃ -N	SRP	Silica
Corrals (n = 12)	4.17–5.1	26–40	1300–1958	36–47	3800–4101
River (n = 2)	3.27, 3.5	33, 48	1934, 2108	55, 64	3100, 3508

There were no significant correlations of these parameters with fish wet weights in the corrals ($P > 0.15$). All values are in µg l⁻¹. SRP, soluble reactive phosphorus.

with taxon. MANOVA indicated significant differences among treatments ($P = 0.0025$), and linear regression analysis with Bonferroni-adjusted critical values was used to identify significant effects (critical value = 0.007; Table III). This analysis indicated that the population growth rates of the cyclopoid copepod *Diacyclops thomasi*, nauplii and the rotifer *Polyarthra* were significantly correlated with the wet weight of fish present. Growth rates of *D. thomasi* dropped steeply while those of the nauplii and *Polyarthra* increased as the biomass of fish increased (Figure 1a–c).

Table III: Results of linear regression on population growth rates of dominant zooplankton species in potamocorrals (outliers included)

Taxa	R ²	P	Outliers
<i>Diacyclops</i>	0.82	< 0.0001	No
<i>Eurytemora</i>	0.29	< 0.07	Yes
Nauplii	0.56	0.005	No
<i>Sinobosmina</i>	0.25	0.09	Yes
<i>Diaphanosoma</i>	0.09	0.34	No
<i>Polyarthra</i>	0.80	< 0.0001	No
<i>Keratella</i>	0.59	0.007	Yes

Significant results are in bold type; Bonferroni adjusted critical value is 0.007.

This initial analysis indicated that there was no significant effect of the fish on the three other common zooplankton species, the calanoid copepod *Eurytemora affinis*, the cladoceran *Bosmina (Sinobosmina)* sp. and the rotifer *Keratella*. Plots of the residuals and graphical examination indicated that there were outliers present in the data for all these taxa. After these outliers were deleted from the data set, the identical analyses were run again. After the removal of outliers, the MANOVA was still significant ($P = 0.024$; Table III). The results of the regression analysis were identical to the first analysis with the exception that the growth rates of *Keratella* were positively and significantly correlated with increasing fish biomass ($P = 0.002$). Because this result was obtained from the removal of a point from a relatively small data set however, this result for *Keratella* should be interpreted with caution. *Eurytemora affinis* was present in all treatments but at very low densities (< 1.0 l⁻¹), so any response of this taxon to fish may not be ecologically meaningful.

There were no significant patterns in the egg ratio data. Very few of the copepods or cladocerans were carrying eggs. We have noted similar results from other collections late in the summer made from the river (< 5% carrying eggs, Guelda *et al.* unpublished data) and from a previous experiment [14% carrying eggs, (Jack and Thorp, 2000)]. This suggests that reproductive rates of zooplankton may be low in the river during the late summer period.

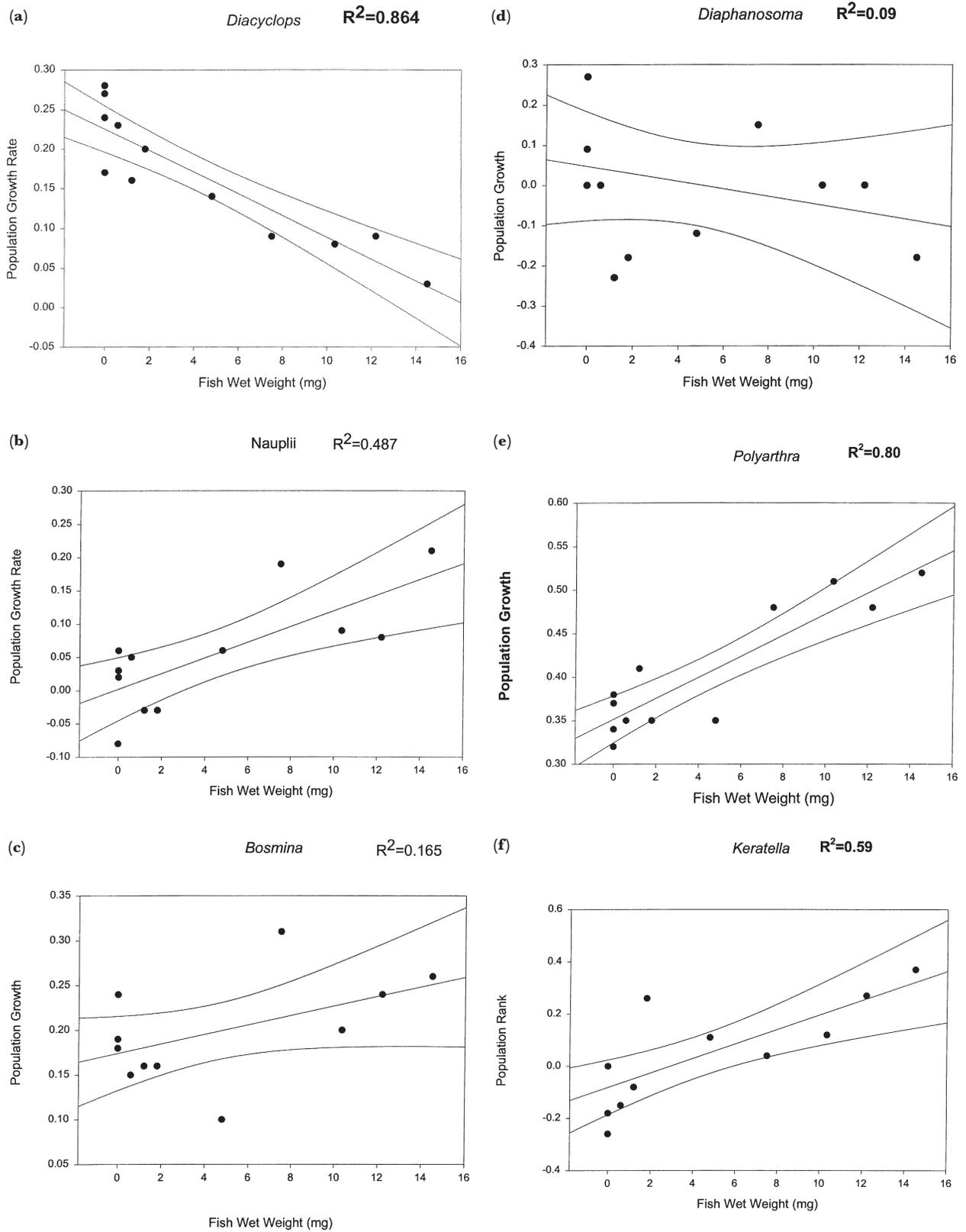


Fig. 1. Population growth rates of (a) *Diacyclops thomasi*, (b) Nauplii, (c) *Bosmina* (*Sinobosmina*), (d) *Diaphanosoma*, (e) *Polyarthra* and (f) *Keratella* vs. fish wet weight at the end of the experiment. Graphs show regression lines and 95% confidence intervals.

DISCUSSION

Knowledge of the role of biotic interactions in regulating potamoplankton is very limited. This is due in great part to the limited number of manipulative experiments that have been done on large rivers. This experiment is the first *in situ* pelagic enclosure experiment with fish in a large North American river. While downstream transport and water residence time are clearly important in plankton dynamics (Basu and Pick, 1996), our experiment suggests that fish planktivory may play a significant role. Given that food resources (as measured by bacterioplankton densities and Chl *a*) did not vary among treatments, we contend that the experimental effects on zooplankton resulted from direct interactions between fish and zooplankton.

Crustacean responses

The population growth rate of *D. thomasi*, the numerically dominant macrozooplankton species in the Ohio River during the period of this experiment, declined progressively as fish biomass increased. This cyclopoid is common in the Ohio during the summer months (Thorp *et al.*, 1994; Jack and Thorp, 2000) and it is the second largest common member of the zooplankton (0.70–0.95 mm compared to *E. affinis* at 0.80–1.2 mm). With its high density and relatively large size, it is not surprising that the zooplanktivorous fish negatively affected it. This conclusion is consistent with research in other rivers and in estuarine habitats showing that larval fish readily feed on copepods [(Meng and Orsi, 1991; Limburg *et al.*, 1997); freshwater studies reviewed in (Mehner and Thiel, 1999)]. However, while even the population growth rate of *D. thomasi* declined as fish wet weight increased, the densities of this copepod were still up to 10 times higher than other crustacean zooplankton species even in the high fish density corrals.

The positive correlation between population growth rates of nauplii and fish wet weights in this experiment may be the result of a release from *Diacyclops* predation, as cyclopoids prey on nauplii (Brandl and Fernando, 1979). An alternative explanation is that the presence of fish was linked to an increase in the copepod's production of nauplii. This latter explanation is unlikely, however, for few female copepods we examined were carrying eggs. Also, the relatively short time-frame of this experiment would limit a numerical response by the copepods, even though the high river water temperatures at this time (Table I) would have accelerated this response. In a tank study using Black River zooplankton, it was also reported that nauplii densities rose in the presence of bluegill sunfish (*Lepomis macrochirus*) concurrently with decreased densities of larger predaceous zooplankton such as *Tropocyclops* (Richardson and Bartsch, 1997).

We had expected that the calanoid *Eurytemora affinis*, the largest common zooplankton in the Ohio River (Thorp *et al.*, 1994), would be especially vulnerable to fish predation. While our results did not support this hypothesis, we suspect the unusually low ambient density of this copepod may have obscured a possible relationship between its population growth rate and fish predation.

While *Bosmina* (*Sinobosmina*) and *Diaphanosoma* are somewhat smaller than *D. thomasi* (around 0.40 and 0.80 mm respectively), they do not have the escape responses common to copepods; thus, we expected their vulnerability to predation by fish would be high. However, the fish did not have any significant effects on the population growth rates of either of these species. Richardson and Bartsch (Richardson and Bartsch, 1997) also saw no changes in *Bosmina* densities in response to fish treatments in their tank experiments. Thorp and Casper (Thorp and Casper, 2001) used a similar potamocorral system on the St Lawrence River with juvenile yellow perch (*Perca flavescens*) as one of the treatments. Densities of *Bosmina* (*Sinobosmina*) increased more than 100% in the fish treatments. These studies suggest that this species is generally not negatively affected by fish predation in riverine systems, although it was reported that *Bosmina* in the estuarine reaches of the Hudson River were heavily preyed upon by the larvae of striped bass (*Morone saxatilis*) and white perch (*Morone americana*) (Limburg *et al.*, 1997).

The low vulnerability of these cladocerans to fish may reflect low encounter rates, low predator foraging behaviour or both. *Bosmina* and *Diaphanosoma* were uncommon in this experiment compared to densities recorded in previous years in the Ohio River. The predator's low encounter rate with this zooplankton and the relatively high densities of copepods may have resulted in the fish focusing their foraging efforts on the more abundant copepod prey.

Rotifer responses

With increased fish predation, densities of the cyclopoid *Diacyclops* dropped and those of the rotifer *Polyarthra* rose. Copepods are known to be effective predators on rotifers (Williamson and Butler, 1986) and *Polyarthra* has been shown to be vulnerable to *Mesocyclops edax* (Williamson, 1980). The strong positive response of *Polyarthra* to lowered densities of *Diacyclops* was somewhat unexpected, however, because the *Diacyclops* is much smaller than *Mesocyclops* (0.70–0.95 mm versus 1.5 mm) and we had assumed that the escape response of *Polyarthra* would be more effective against this smaller copepod. Nonetheless, *Polyarthra*, like most rotifers, has a high intrinsic growth rate compared to many other metazoan zooplankton, so its rapid numerical response to reduced predation pressure is not surprising. In an earlier lake study, rotifer

densities were found to be increased in enclosures where fish had reduced numbers of competing cladocerans (Romare *et al.*, 1999).

We expected the rotifer *Keratella* to respond positively to fish, as it is vulnerable to a wide assortment of invertebrate predators including copepods. While not statistically significant, the pattern of response seen for *Keratella* was very similar to that of *Polyarthra*. In contrast, Richardson and Bartsch (Richardson and Bartsch, 1997) found that *Keratella* densities were significantly suppressed in the presence of fish. Thus, we can draw no clear conclusions at this time about the effects of fish predation on *Keratella* growth rates.

Experimental constraints

While these results indicate an important role for fish predation in riverine foodwebs, there are potential problems with the experiment that need to be addressed. One of the challenges in the design of any experiment assessing the impact of fish on invertebrate prey is choosing reasonable densities of fish and reproducing the fish community that the prey is likely to encounter. It is very difficult to get reliable estimates of fish densities in large river systems such as the Ohio River. We chose to add fish at densities we considered moderate based on the extensive seining and electrofishing work done in this area by colleagues at the University of Louisville (Kessler, unpublished data). The densities used were 25–50% of those used by Richardson and Bartsch (Richardson and Bartsch, 1997) in their tank experiments but higher than those by Thorp and Casper (Thorp and Casper, 2001) in an experiment in the St Lawrence River using a similar potamocorral system. Using two fish species in treatment corrals provided a more representative predator community for the zooplankton in the corrals as these fish species often occur together in the Ohio River (Kessler, personal communication).

Another set of potential problems can arise from ‘container effects’ confounding experimental treatments. Limiting the experiment to 6 days was one way in which we attempted to control such effects (see above). Another potential problem is the possibility that the zooplankton in the enclosures were prevented from using spatial or temporal refuges which may have reduced predation pressure on some of these groups. Recent work [(Reckendorfer *et al.*, 1999); Thorp and Casper, in press] has indicated that zooplankton may be capable of vertical or horizontal positional adjustments within the water column of rivers. We do not think this is a major concern in this case because of the depth of the corrals (2.5 m). Secchi disk depths were often less than 2.0 m in the corrals so the lower portions of the corrals were probably dark enough to provide a refuge from visually feeding fish for the zooplankton during the day.

While our data indicate that the pelagic habitat in the corrals was very similar to that which the fish experience in the Ohio River, the benthic habitat as it existed in the corrals was not. The fish we used in this experiment are capable of switching to larger macroinvertebrates when such prey are available, although such switching behaviour usually occurs when the fish are larger than the individuals we used (William Pearson, personal communication). It is possible that the lack of alternative benthic prey resulted in higher predation pressure on the zooplankton in the corrals than might otherwise have been the case. In contrast to the other predation effects outlined above, this may result in an over-estimate of the impact of fish predation on riverine zooplankton. We believe the small size of the fish we used in this experiment probably minimized the importance of this effect but we cannot rule out the possibility that predation rates were influenced by the lack of alternative prey.

The results of our experiment are consistent with a growing body of evidence that biotic interactions in rivers may be more important in structuring zooplankton communities than was previously thought. Previous work in large rivers has established how important both biological and hydrological mechanisms can be in structuring the zooplankton communities in these systems. In a comparative study of the Rivers Moselle and Meuse, Viroux (Viroux, 1997) noted that there was often no correlation between phytoplankton and zooplankton densities in the Moselle while phytoplankton and zooplankton blooms tended to alternate in the Meuse. Viroux identified several factors, such as degree of regulation and water residence time, as likely factors that would influence species composition in large rivers. In a later study in the same rivers, Viroux (Viroux, 1999) noted that zooplankton had patchy distributions in these rivers which also may be related to the different morphology of these systems. In their study of 31 Canadian rivers, Basu and Pick (Basu and Pick, 1996) showed that zooplankton biomass was positively related to Chl *a* levels as well as to water residence time. Although the correlation with Chl *a* was much weaker than for residence time, their data suggest that food resources may have some influence on the development of zooplankton communities in rivers. In fact, recent evidence suggests that zooplankton may remove a significant portion of the primary production from some rivers, at least during parts of the year (Gosselain *et al.*, 1998a,b). It is also clear that the range of vertebrate and invertebrate predators may affect the densities and species structure of the zooplankton in these systems. In the Hudson River (USA), the invasion of the zebra mussel (*Dreissena polymorpha*) has resulted in significant declines in many zooplankton groups, particularly the microzooplankton such as nauplii, rotifers and ciliates (Pace *et al.*, 1998). Jack and

Thorp (Jack and Thorp, 2000) saw similar impacts of zebra mussels on Ohio River zooplankton in a potamocorral experiment, while Welker and Walz found that unionid mussels in the River Spree could have significant negative effects on the zooplankton over a 21 km stretch of the river (Welker and Walz, 1998).

It is clear that river ecologists should thus consider biological as well as physical loss factors when assessing zooplankton populations in large rivers. Experimental techniques such as the potamocorrals may be helpful in separating biological impacts from physical ones and improving our understanding of the factors influencing zooplankton structure in these dynamic and important aquatic habitats.

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