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## Ecosystem effects of water column minnows in experimental streams

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**Abstract** We used red shiner (*Cyprinella lutrensis*) as a model to examine ecosystem effects of water column stream minnows (Cyprinidae) in experimental streams. Benthic primary productivity, benthic invertebrate abundance, water column nutrient concentrations, size distribution of benthic particulate organic matter (BPOM), and sedimentation rates were measured across a range of fish densities (0–26.6 fish m<sup>-2</sup>) over a 35-day period. In addition, effects of fish density on algal standing crop and benthic invertebrates in experimental streams were examined over a longer time span (156 and 203 days). After 35 days, benthic primary productivity was positively associated with fish density, with an approximate three-fold increase in productivity between experimental streams stocked with no fish and those with 26.6 fish m<sup>-2</sup>. No effects on other ecosystem properties were detected after 35 days. Additionally, there was no effect on algal standing crop after 156 or 203 days and no effect on benthic invertebrates after 203 days. Because red shiners fed primarily on terrestrial insects, this experiment suggests that water column minnows can affect primary productivity in streams by transporting nutrients from terrestrial sources to the benthic compartment of the ecosystem. However, this effect may only be important in streams or during periods when nutrients are limiting.

**Keywords** Ecosystem effects · Stream fishes · Primary productivity · Experimental streams · Nutrient excretion

### Introduction

Ecosystem properties such as productivity, stability, and resistance to invaders can depend not only on species richness, but also on qualitative (species-level) composition of biotic communities (Tilman 1999). Thus, the removal or addition of a particular species in a community might cause dramatic changes to the ecosystem. Strongly interacting species have been termed “keystone” if their effect is large in comparison to their relative biomass (Power et al. 1996) or “ecological engineers” if they modulate the availability of resources by causing physical state change in biotic or abiotic materials (Lawton and Brown 1993). Given the variety of ways that species can function in ecosystems, identification of the roles of particular species is an important requisite to understanding the importance of biodiversity. However, in many ecosystems little is known about the functional roles of most species.

Stream fishes can have diverse effects on ecosystem properties that vary greatly among species (Power et al. 1985; Grimm 1988; Gilliam et al. 1989; Power 1990a; Gelwick and Matthews 1992; Flecker 1996). For example, Matthews (1998) proposed 17 functional groups of North American fishes based on their interactions within the ecosystem. Studies of fishes with different modes of feeding (i.e., different functional groups) can improve understanding of and facilitate generalizations about the roles fishes play in stream ecosystems. Such studies might, for example, ask if fishes play a significant role in the processing of organic matter or in regulating primary productivity.

Ecosystem effects of fishes vary with their feeding strategies and the abiotic conditions of the habitat (e.g., Gilliam et al. 1989; Dahl 1998; Dahl and Greenberg 1998). Benthic, algivorous minnows (*Campostoma anomalum* and *Agosia chrysogaster*) can change the structure of algal assemblages or have strong effects on nitrogen cycling (Power and Matthews 1983; Grimm 1988; Gelwick and Matthews 1992, 1997; Gelwick et al. 1997). In general, bottom-feeding fishes also can affect

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the distribution and size fractions of benthic organic material (Gelwick and Matthews 1992; Gardner 1993; Flecker 1996; Pringle and Hamazaki 1998). As predators, fishes can affect abundance of grazing invertebrates and algal standing crops through trophic cascades (Power and Matthews 1983; Power 1990b; McIntosh and Townsend 1996; Dahl 1998). Of particular interest in the present study are water column omnivorous minnows that could affect ecosystem properties through both top-down (e.g., trophic cascades) and bottom-up (e.g., nutrient recycling) processes.

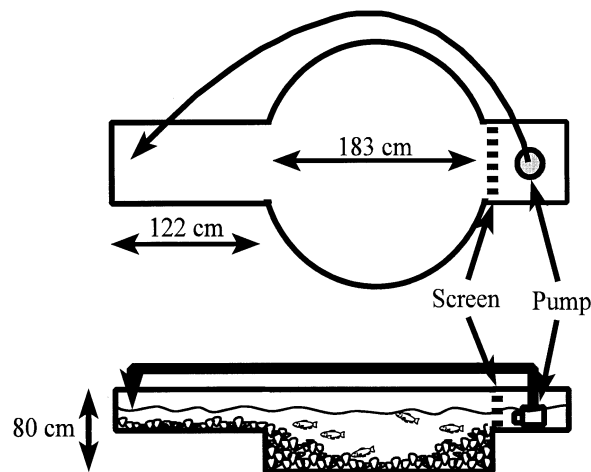
We tested the effect of water column minnows on benthic processes in stream ecosystems. Despite their high abundances across North America, little is known about the effects of water column omnivorous minnows (e.g., *Notropis* and *Cyprinella*; Cyprinidae) in streams. We used red shiner (*Cyprinella lutrensis*) as a model for this large guild of fishes. Red shiner is widespread and reaches high densities in many stream habitats across the mid-western United States (Matthews and Hill 1979; Matthews 1985; Cross and Collins 1995). This species also is a very successful invader and can be abundant (>50 individuals  $m^{-2}$ ) where it has been introduced (e.g., Gido and Propst 1999). The success of red shiner is likely due to its broad ecological tolerances that suit the harsh environments where it occurs (Matthews and Hill 1977), and its ability to rapidly produce large numbers of young. Like other species of water column minnows they are opportunistic foragers, typically relying on drifting insects and microcrustaceans, but are known to ingest vegetative debris and algae (Hale 1962; Cross and Collins 1995).

To examine the effect of water column minnows on benthic processes in stream ecosystems, we measured ecosystem level properties in experimental streams across a range of fish densities at three time periods (35, 156, and 203 days). Based on results from previous studies of benthic fishes already cited and recent literature on ecosystem effects of drift-feeding fishes (Dahl and Greenberg 1996; Dahl 1998), we predicted that increasing density of red shiner would (1) increase primary productivity through either a trophic cascade effect or nutrient enrichment, (2) decrease macroinvertebrate abundance by predation, and (3) shift the size fractions of benthic particulate organic matter (BPOM) from large to smaller sizes due to mechanical breakdown of ingested organic matter. We additionally asked if the relationship of any effects had a linear or non-linear (e.g., threshold) relationship with fish density.

## Methods

### Experimental streams and fish stocking

Large experimental streams located outdoors at the University of Oklahoma Biological Station (Marshall County, Oklahoma, USA) included 16 independent riffle-pool units (Fig. 1). These streams had been used previously with red shiners, and this species behaves and reproduces normally in these systems (Gido et al.



**Fig. 1** Design and dimensions of experimental streams located at the University of Oklahoma Biological Station

1999). Each unit was filled with natural sand, gravel, and cobble substrate that was sculptured to form a concave stream bottom (Fig. 1). Because the streams were used in prior experiments, substrates were washed with a high power hose, drained, and allowed to dry for 1 week prior to the beginning of this experiment. In addition, approximately 10 kg of substrate from each stream was removed and thoroughly mixed with substrate from other streams. Equal portions of this mixture were then returned to each stream to help homogenize any carryover of senescent algae among stream units.

In each unit, water was continuously pumped from a downstream collection box to the riffle with a 1/8 hp (93 W, 2500  $l\ h^{-1}$ ) submersible pump (Fig. 1). Downstream collection boxes were screened with 0.5-cm plastic mesh to exclude fish. Stream units were filled on 18 October 1998, at which time they were inoculated with an algal slurry and associated invertebrates (mostly *Spyrogyra* and *Rhizoclonium* and associated snails; Power and Stewart 1987; Power et al. 1985; Gelwick and Matthews 1992) from nearby Brier Creek. Liquid fertilizer (10 ml; 20:3:3, N:P:K) was added to each unit to stimulate growth and colonization of algae (Stewart 1987; Vaughn et al. 1993). Streams were not covered and thus were freely colonized by winged insects and their larvae (mostly dipterans). In addition, some allochthonous materials (primarily leaves and insects) entered stream units and likely provided an external source of nutrients.

Red shiners for the experiment were collected by seining the Washita River, Carter County, Oklahoma, on 29 October 1998. Fish were transported directly to experimental streams in coolers and randomly assigned to stream units. A sub-sample of these fish was preserved in 10% formalin for estimation of mean length and weight of fish at the onset of the experiment.

### Experimental design

Red shiners were stocked in stream units across a range of densities to examine their effects on ecosystem properties and to examine how these effects varied with density (e.g., linear vs. non-linear). Two replicates at each density of 0, 7, 14, 21, 28, 42, 56, and 70 fish per unit (0–26.6 fish  $m^{-2}$ ) were established in the 16 units. Natural population densities of red shiner have been reported to average 12.9 fish  $m^{-2}$  in the Canadian River, Oklahoma, but can exceed 100 fish  $m^{-2}$  in some habitats (e.g., backwaters; Matthews 1977). Fish of similar sizes were chosen from a large collection of fish (>1,000 individuals; mean standard length 21 mm) and randomly assigned to treatments. Our primary goal was to examine effects of these varying densities of fish on ecosystem properties over a 1-month period (35 days); however, as a secondary goal we

extended the experiment another 6 months to test for long-term effects on algal standing crop and benthic invertebrate densities.

Response variables for short-term effects of red shiner (35 days) were benthic primary productivity, benthic macroinvertebrate abundance, organic fraction in sediments, phosphate and ammonia concentration in the water column, and sedimentation rates. Benthic primary productivity was estimated from periphyton growth on unglazed clay tiles (Stewart 1987; Gelwick and Matthews 1992; Gelwick et al. 1997). Eight 15.2×15.2 cm tiles were placed in each stream on 23 October 1998, 6 days before the introduction of fish. On two occasions (day 14 and day 35) tiles were removed to measure primary productivity and accumulation of organic matter. On each sampling date, two tiles from each stream were placed in individual plastic Ziplock bags and placed on the stream bottom in direct sunlight for approximately 2 h during midday. Initial and final dissolved oxygen concentrations were measured with an oxygen meter (YSI model 54), and the volume of water in each bag was measured to estimate total oxygen production following Stewart (1987) and Gelwick and Matthews (1992). Tiles were then brought to the laboratory where periphyton was scraped from tiles with a razor blade and toothbrush. Scrapings were filtered through a pre-weighed and pre-ashed Whatman GF/F filter. Filters and scrapings were oven-dried at 60°C for 24 h, combusted at 550°C for 1 h, placed in a dessicator, and reweighed to estimate ash-free dry mass (AFDM).

Water temperature, dissolved oxygen, and conductivity were measured periodically throughout the experiment with YSI meters. Water samples taken on day 35 were analyzed for dissolved reactive phosphorous using the ascorbic acid method and ammonia-nitrogen using the phenate method (American Public Health Association 1995). Although nutrient enrichment by fishes may result in increased levels of nutrients, there are several limitations to these analyses. Rapid uptake of nutrients by algae, or nitrification of ammonia to nitrate could mask any differences among treatments due to nutrient enrichment by fish. Additionally, these methods may not be sensitive enough to detect slight differences in or low levels of nutrient concentrations (i.e., these measurements were only intended as a measure of gross differences in water column nutrient concentrations).

Macroinvertebrates were sampled on day 35 with a Hess sampler (0.087 m<sup>2</sup>, 0.5 mm mesh collection net). Because of low current velocities in the experimental streams, substrates were agitated to dislodge invertebrates and then the suspended materials were forced into the net with a paddle. Only one sample was taken per stream unit because of the relatively large area covered by the Hess sampler in comparison to the stream bottom (surface area of Hess sampler 3.3% of total stream bottom). Invertebrate samples were only taken from pools because the fish were typically associated with pools and rarely entered riffles. Samples were preserved in 70% ethanol and returned to the laboratory where they were identified and counted.

Percent organic fraction of various sized particles were based on the AFDM of random grab samples of BPOM following the methods of Gelwick and Matthews (1992). A 19-l bucket with the bottom removed was pushed into the substrate to enclose a 0.053-m<sup>2</sup> area. Substrates were agitated by hand and a suction pump was used to collect 2.2 l of this slurry. Samples were preserved with 40 ml of concentrated formalin and returned to the laboratory. The total sample was drawn through a stacked series of sieves with mesh sizes of 925 µm (coarse), 508 µm (large), 157 µm (medium), and 41 µm (fine). Materials retained by the various sieves were backwashed through pre-ashed GF/F filters. The filtrate that passed through all sieves was also passed through a pre-ashed Whatman GF/F filter to estimate the ultrafine (0.70–40 µm) proportion of the samples. All size fractions were oven-dried at 60°C for 24 h, weighed, and materials were combusted at 550°C for 1 h as described above.

At the beginning of the experiment two 450-ml glass jars (60 mm diameter) were placed in the center of each stream to measure sediment deposition. The rim of each jar was coated with petroleum jelly to deter snails from entering the jars. At the end of the experiment, jars were capped in place and then 10 ml of formalin was added to preserve the contents. In the laboratory, con-

tents were filtered through a pre-ashed, pre-weighed Whatman GF/F filters. The filter was dried at 60°C for 24 h and re-weighed.

Effects of red shiner density on primary productivity also was assessed by examination of total algal standing crop after 156 and 203 days and invertebrate densities after 203 days. To estimate total algal standing crop in each unit, floating algal mats were harvested from the streams by hand. In addition, the substrate was agitated to dislodge attached algae and then scooped into a dip net (2 mm mesh). This procedure was repeated until little additional algal material was removed by dip net passes. Algae were air-dried and weighed to give total dry weight. Benthic invertebrates were sampled using a 10.2-cm-diameter PVC pipe sampler (Palmer and Strayer 1996). In each stream, three cores were removed from downstream, middle, and upstream portions of each pool and combined into a bucket. The three samples were stirred vigorously and all loose materials were elutriated off into a 0.5 mm mesh sieve and preserved in 70% ethanol.

On day 37, seven fish were removed from units with densities of 70 individuals (high density) and five fish were removed from units with densities of 14 individuals (low density) to assess growth and examine stomach contents. These fish were replaced with Washita River fish of similar sizes from a holding tank.

#### Statistical methods

For all statistics, each experimental stream unit was considered a single variate, with a single mean value (if there were subsamples within a stream) used for each stream unit. Measurements from all response variables were examined for normality and appropriate transformations were applied to better approximate normal distributions. Percent organic fraction was arcsine-square-root-transformed. We used regression analysis to examine the relationship between fish density and the various response variables. To test for non-linear relationships between fish density and response variables, we tested if polynomial regressions were able to remove a significant portion of the residual sum of squares from linear regression (Sokal and Rohlf 1995).

## Results

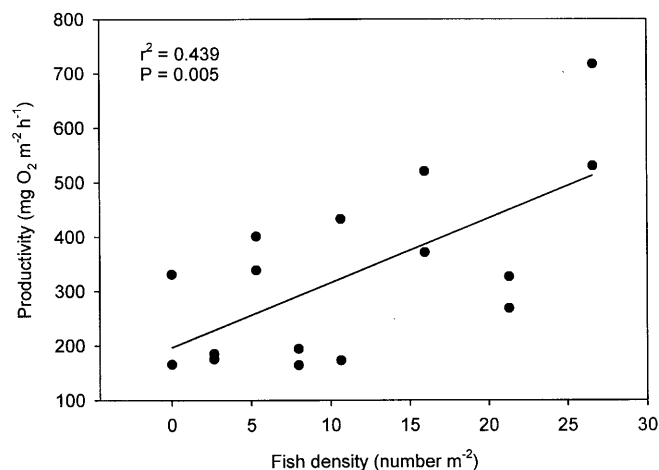
During the initial experiment (35 days; 29 October–2 December) midday water temperature ranged from 13 to 21°C and conductivity ranged from 298 to 460 mho cm<sup>-1</sup>. Only trace amounts of phosphate were found in water samples (<20 µg l<sup>-1</sup>) thus no statistical comparisons of phosphate were made among treatments. Ammonia concentrations were low (<50 µg l<sup>-1</sup>) and unrelated to fish density ( $r^2=0.021$ ,  $P=0.733$ ). We found no evidence of fish mortalities throughout the first phase of the experiment and all fish appeared to be feeding and in good health. Mean length of red shiners at the beginning of the experiment was 20.3 (±3.0 SD) mm standard length (SL) (mean estimated weight 0.194±0.09 g) and on day 35 averaged 23.0 (±2.3) mm SL. Because no response variable appeared to vary with fish density in a non-linear fashion ( $P$ -values decreased and coefficients of correlation did not notably improve with higher order equations), simple linear regressions were used to examine relationships between fish density and response variables.

On day 35 there was a significant positive relationship between fish density and primary productivity on tiles, as measured by O<sub>2</sub> production (Table 1). At least 3 times more primary productivity was measured in

**Table 1** Range of values for response variables measured across different levels of red shiner densities in experimental streams. Coefficients of correlation and *P*-values were derived from regression analysis of each response variable and fish density (*BPOM* benthic particulate organic matter)

Response variable	Range of values	<i>r</i>	<i>P</i>
Primary productivity			
O <sub>2</sub> production day 15 (g C h <sup>-1</sup> m <sup>-2</sup> )	20–75	0.290	0.276
O <sub>2</sub> production day 35 (g C h <sup>-1</sup> m <sup>-2</sup> )	51–224	0.663	0.005*
AFDM day 15 (g m <sup>-2</sup> )	1.4–9.3	0.287	0.281
AFDM day 35 (g m <sup>-2</sup> )	10.5–100.2	0.391	0.134
Standing crop day 156 (g m <sup>-2</sup> )	60–238	0.303	0.254
Standing crop day 203 (g m <sup>-2</sup> )	43–145	0.364	0.165
Invertebrates (day 35)			
Gastropoda (snails) (number m <sup>-2</sup> )	23–298	0.028	0.976
Oligochaeta (number m <sup>-2</sup> )	0–214	–0.422	0.104
Diptera (number m <sup>-2</sup> )	299–2816	–0.185	0.492
Plecoptera (number m <sup>-2</sup> )	0–92	0.232	0.387
Invertebrates (6 months)			
Diptera (number m <sup>-2</sup> )	1973–23,176	0.194	0.468
BPOM (day 35)			
Coarse (%)	17.2–44.4	0.118	0.662
Large (%)	2.6–34.9	–0.362	0.169
Medium (%)	1.8–35.5	–0.130	0.629
Fine (%)	1.8–30.7	0.405	0.120
Ultrafine (%)	22.5–51.2	0.307	0.248
Sediment trap			
Day 35 (g m <sup>-2</sup> )	9.1–36.6	0.056	0.838

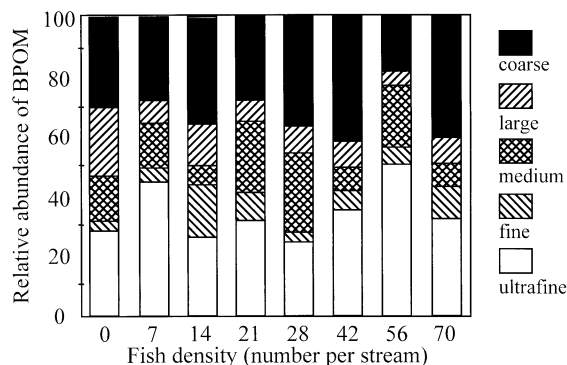
\*Significant association with fish density (*P*≤0.05)



**Fig. 2** Relationship between fish density (number of individuals per stream) and net primary productivity on clay tiles measured on day 35 of the experiment

streams stocked at highest densities (70 fish) than in streams with no fish (Fig. 2). Percent organic matter (AFDM) on tiles was not significantly associated with fish density.

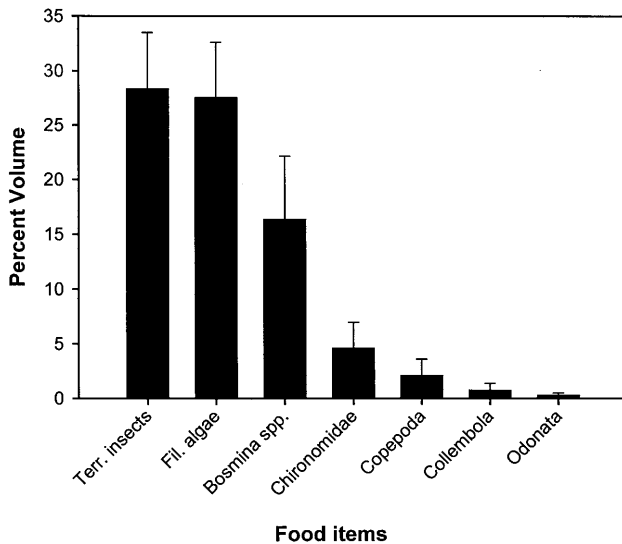
We found no relationship between fish density and the other response variables (Table 1). Total density of benthic invertebrates in Hess samples ranged from 517 to 3582 individuals m<sup>-2</sup> and were dominated by dipterans (primarily chironomids; 82.2% of total individuals). There was no indication that increased fish density caused a decrease in BPOM size fragments (Fig. 3, Table 1). Accumulation of sediments was minimal ( $\bar{x}$  = 17.7 gm<sup>-2</sup>, SD=1.8 g m<sup>-2</sup>) and not related to fish density.



**Fig. 3** Relationship between fish density and the various size fractions of benthic particulate organic matter (BPOM). Proportions of BPOM for each density are based on the mean values of the two replicates for each fish density

Based on stomach contents from a limited number of fish taken from two densities on 4 December 1999, red shiners primarily consumed terrestrial insects, algae, and *Bosmina* spp. (Fig. 4). Other invertebrates (e.g., chironomids) represented only a small proportion of their diet.

After 156 and 203 days, there was no significant relationship between fish density and algal standing crop (Table 1). On day 203, benthic invertebrate densities ranged from 1,973 to 23,177 individuals m<sup>-2</sup> and consisted almost entirely of chironomids (98% of total individuals). We found no relationship between fish density and chironomid abundance (Table 1). Because other invertebrates were in low abundance, no statistical tests were used to examine their relationships with fish density.



**Fig. 4** Food habits of red shiner taken from experimental streams on day 35 of the experiment. Vertical bars represent 1 SD

## Discussion

We observed strong effects of a water column minnow on benthic primary productivity in experimental streams after one month. Such an increase of algal production in the presence of stream fishes could occur indirectly because of suppression of herbivorous invertebrates (i.e., trophic cascade), directly by nutrient enrichment through excretion, or by removal of dead or senescent algae. Most studies of stream fishes have shown strong cascading effects of predatory stream fishes on primary productivity mediated through consumption (e.g., Power 1990b; Dahl 1998) or by changing behavior (e.g., McIntosh and Townsend 1996) of grazing invertebrates. In this study, because red shiner tended to consume more terrestrial insects and zooplankton, and because red shiner caused no significant reduction in number of benthic invertebrates, we suggest that red shiner enhanced primary productivity by increasing nutrient inputs to the benthic compartments of these systems. This demonstration of a strong link between a water column species and benthic processes thus expands our concepts about the potential importance of more generalized (in contrast to strictly benthic) fish species in stream ecosystems. In the case of red shiner, we see a species not typically in direct physical contact with the substrate, but nevertheless having strong effects on an important ecosystem property, benthic primary productivity.

Although our measurements of nutrients showed no significant relationship with fish density, this could have been due to rapid uptake by algae or nitrification of ammonia to nitrate (see Methods). However, lacking a direct link between fish density and nutrient concentrations leaves the possibility of other mechanisms responsible for the observed increase in primary productivity. For example, because red shiner were shown to consume

some algae (Fig. 4), they may have increased primary productivity on tiles by removing senescent algae. Lamberti et al. (1989) showed that low to moderate levels of grazing by invertebrates can stimulate primary production by removal of dead or senescent algal cells or by shifting the assemblage to more photosynthetically active species. Gelwick and Matthews (1992) also showed that *C. anomalum* reduced standing crop of algae but increased algal productivity per unit biomass (Gelwick and Matthews 1992). Unlike for *C. anomalum*, red shiner density was not related to algal productivity per unit biomass ( $P > 0.15$ ) nor did standing crop of algae on tiles (AFDM) decline with increased fish density. Thus, because it did not appear red shiners removed noticeable amounts of algae from tiles, we doubt that grazing by red shiner was the primary factor responsible for stimulating primary productivity.

Effects of increased nutrient availability or enrichment by red shiner over longer time periods (156–203 days) appeared to be attenuated by other sources of nutrients, presumably leaves and terrestrial insects. The lack of relationship between fish density and standing crop at this time scale suggests that other sources of nutrients (e.g., from leaf litter) were more important than fishes during longer time periods. Because allochthonous pulses of nutrients are common in stream ecosystems (Mason and MacDonald 1982; Vannote et al. 1980), fishes may only regulate primary productivity during periods of low nutrient input from the surrounding watershed. For example, stream pools often become partially or entirely isolated during periods of low precipitation. During these conditions, changes in internal nutrient dynamics by water column minnows could be an important factor in structuring algal assemblages in stream pools.

Field experiments designed to determine the effects of stream fishes rarely have suggested nutrient excretion or recycling as a mechanism responsible for increased primary productivity (e.g., Dahl 1998). However, because field enclosures or exclusions are permeable to surrounding, flowing water, effects of nutrients might be diluted or transferred downstream and hard to detect in field cage experiments. Although experimental streams likely overestimate effects of nutrient enrichment because they lack inputs from ground or surface waters, this may be typical of what might occur in a small stream that was populated throughout by a water column minnow. Thus, the relative importance of nutrient enrichment by fishes should depend on the distribution of fishes throughout the stream and dilution by external sources of water and nutrients (e.g., ground water).

Because nutrients strongly limit primary production in streams (Grimm and Fisher 1986; Hecky and Kilham 1988; Allan 1995; Steinman and Mulholland 1996) it follows that stream fishes should play important roles in the nutrient budget of these ecosystems by providing nutrients in a form that is readily available for uptake by primary producers. Grimm (1988) showed that nutrient recycling by *A. chrysogaster* may be an important com-

ponent in the nitrogen budget of a nitrogen-limited Sonoran stream. Presumably these fish increase recycling rates of nutrients and decrease turnover time (i.e., spiraling length). This may have important implications for the resilience of producer assemblages, by decreasing the time it takes for these assemblages to rebound from disturbance events (DeAngelis 1992).

Contrary to our predictions, red shiner had little effect on ecosystem properties in our experimental streams other than primary productivity. This is in contrast to recent studies of benthic stream fishes. For example, in a series of field experiments Gelwick and Matthews (1992, 1997) and Gelwick et al. (1997) showed that the algivorous *C. anomalum* affected organic matter processing, primary productivity, and community composition and density of invertebrates. Studies of tropical fishes also showed that foraging by fishes reduced sediment accrual on the stream bottom that altered species composition of algae and macroinvertebrates (Flecker 1996; Pringle and Hamazaki 1998). However, these studies have focused on mostly benthic-feeding fish species. Although red shiner will forage on benthic macroinvertebrates, they are primarily water column foragers and rarely or only moderately disturb the substrate. If red shiner caused substantial disturbance to benthic surfaces we would have expected greater amounts of sediment accumulation in sediment traps in high fish density treatments due to the resuspension of organic materials.

The lack of effect of red shiner on benthic macroinvertebrates (particularly chironomids) may have been because of structural complexity (e.g., Flecker and Allan 1984; Power 1992), drift from upstream habitats (i.e., the riffle in our experimental units; Flecker 1984; Culp 1986; Reice and Edwards 1986), or a preference for other food items (Dahl and Greenberg 1996). Although we cannot exclude any of these possibilities, we suggest that the lack of effect on benthic invertebrates was because red shiner tended to forage on terrestrial insects and zooplankton. A similar pattern was reported by Dahl (1998), who showed brown trout, *Salmo trutta*, to have relatively little effect on benthic invertebrate abundance because they relied primarily on terrestrial insects. Based on food habitats reported in this study (Fig. 4) and in natural systems (Hale 1962; Cross and Collins 1995), it appears that red shiners eat more terrestrial invertebrates and zooplankton than benthic invertebrates. Thus, red shiner, as a mostly water column invertivore may play a major role in moving nutrients from surface or water column prey into benthic compartments, which subsequently increases algal productivity.

Individual species can affect ecosystems in different ways depending on their modes of feeding, habitat use, and behavior (Dahl and Greenberg 1998; Dahl 1998; Matthews 1998). We have shown that a water column minnow that is very abundant in mid-western United States streams can affect benthic primary productivity. However, the magnitude of this effect on other ecosystem properties appears less than that reported for benthic foraging species such as *Camptostoma* spp. (Gelwick and

Matthews 1992) and *Prochilodus* spp. (Flecker 1996). Regardless, the presence of red shiner potentially can affect the stability of the producer community by increasing the turnover rate of nutrients, thus allowing algae to rebound more rapidly from disturbance events (e.g., DeAngelis 1992). Because many fish species in North America are at least in large part water column rather than benthic feeders (e.g., *Notropis* spp.), the finding that red shiner can effect ecosystem properties may have important implications for many stream ecosystems. Additional detailed experiments comparing species with different modes of feeding (e.g., Dahl 1998) are needed to evaluate the generality of these results, and their connectance to stability of stream systems.

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