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The algivorous minnow, *Campostoma anomalum*, strongly influences the distribution and standing crop of periphyton in north temperate streams. We conducted a 5 wk experiment in large, recirculating artificial streams to examine the effects of *Campostoma* on secondary production of two invertebrate grazers, the crayfish *Orconectes virilis* and the pulmonate snail *Physella virgata*. Treatments included experimental streams with snails alone, crayfish alone, snails and fish together, crayfish and fish together, and a non-grazed control. In this study, algivorous fish had significant impacts on production of co-occurring invertebrates. Crayfish were negatively impacted, apparently through resource monopolization by fish. Snail production was indirectly enhanced through fish grazing activities that reduced the algal overstory and may have made nonfilamentous algae more available to snails. Additionally, in the presence of *Campostoma*, snails exhibited a phenotypically-plastic shift in life-history traits. Our results show that these abundant, widespread freshwater fish can influence not only the secondary production of co-occurring invertebrate grazers, but life histories as well, and confirm the conclusions of other recent studies in assigning periphyton-grazing fish an important role in temperate stream ecosystems.

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Invertebrates are important grazers in temperate streams (Lamberti and Moore 1984). They can markedly alter primary productivity and algal assemblages (Steinman et al. 1987, Hill and Knight 1988, Brönmark 1989, Feminella et al. 1989, Lamberti et al. 1989, DeNicola et al. 1990) and are often limited by their food supply (Vaughn 1986, Hart 1987, Hill and Knight 1987, 1988, Lamberti et al. 1987, Hart and Robinson 1990, DeNicola and McIntire 1991). Fish are also important grazers in streams (Matthews et al. 1987, Power 1990, Power and Matthews 1983, Power et al. 1985, 1988a, Stewart 1987). Dominant invertebrate grazers can significantly impact co-occurring invertebrate grazers (Cuker 1983, McAuliffe 1984, Hawkins and Furnish 1987, Feminella and Resh 1991), but effects of grazing fish on grazing stream invertebrates have not been tested until now.

Algivory by fish might influence grazing stream invertebrates in several ways. Fish could inhibit grazing of invertebrates through exploitation of algal resources or through interference (e.g., by physically displacing invertebrates from a food patch as a school moves across the substrate). Periphyton communities are refugia for many invertebrates (Hynes 1970, Cuker 1983), thus periphyton removal by grazing fish may displace invertebrates or expose them to predators. *Campostoma anomalum* (central stoneroller minnow) grazing alters standing crop and growth forms of algae (Matthews et al. 1986, Stewart 1987, Power et al. 1988a). Such alterations should affect the types, quantity and quality of food and/or shelter available to invertebrates. Any or all such effects might affect overall success or well-being of invertebrates.

One powerful way to document effects of consumer activity at the ecosystem level is through measurement of secondary production (Fisher and Gray 1983, Benke

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1984). In contrast to the routine measurement of primary production/community metabolism in studies of stream grazers, comparable estimates of secondary production have been rare (Benke et al. 1988, Minshall 1988). We tested the null hypothesis that *Campostoma* have no effect on secondary production of co-occurring invertebrate grazers (snails and crayfish). During the experiment we also found a major, unexpected shift in reproductive schedules of snails in treatments with fish, suggesting phenotypic plasticity (Crowl and Covich 1990) in snail life history.

Methods

Grazers

Invertebrate herbivores were chosen to represent contrasting sizes, trophic morphology and methods of food acquisition typical in midwestern streams. The grazers were a physid snail, *Physella virgata,* and a crayfish, *Orconectes virilis.* Both exist with *Campostoma* in many streams in the central United States. Both can be marked and measured alive. Although *Physella* are mobile grazers that actively aggregate on periphyton patches, they are much smaller and less mobile than *Campostoma. Physella* feed with a radula equipped with many fine teeth to scrape substrates for adherent algae (Kesler et al. 1986, Barnese et al. 1990). *Orconectes* graze by picking up tufts of algae with their walking legs (A. P. Covich, pers. comm.). All organisms used in the experiment were collected from local streams and maintained for two wk at a daily average temperature of 25°C before the experiment. During the holding period, fish were fed periphyton on natural rock substrates, and crayfish and snails were fed lettuce.

Experimental units

The experiment was conducted in artificial experimental stream units that allowed us to minimize the heterogeneity typical of natural streams. The artificial streams reduced the variability in the animals' test environment with respect to substrate, water, nutrients, flow, and initial algal community composition. They allowed algal growth typical for regional streams and were of sufficient size to allow normal grazing behavior (pers. obs.). We used a total of 10 artificial, recirculating streams (described in detail in Matthews et al. 1990) in a climate controlled greenhouse at the Univ. of Oklahoma Biological Station, Marshall County, Oklahoma, USA. Each stream consisted of a 760 l, circular, black polypropylene tank with a 27 cm diameter plastic center post, and had a bottom area of 2.58 m^2. The resulting streams had a 4.4 m outer circumference and were 50 cm wide. Submersible pumps (1/15 H.P., 2000 lph @25 cm) were used to drive a unidirectional current in the streams. Water depth was maintained at about 26 cm, and velocity (6 – 16 cm s^{-1}) was in the range of that in many natural stream pools where our study organisms occur. Stream tanks were treated with sodium hypochlorite and thoroughly rinsed before filling. Stream bottoms were covered with about 3 cm of washed, commercially obtained, non-calcareous gravel. Streams were filled with water pumped directly from an adjacent reservoir (Lake Texoma) and filtered through an 80 μm plankton net. Streams were exposed to ambient sunlight reduced 60% by a shade cloth.

Six wk before the experiment, unglazed ceramic tiles (532 cm^2 total area including sides and bottom) were placed in outdoor troughs filled with lake water which had been filtered through 80 μm mesh. Equal aliquots of periphyton from Brier Creek (Power and Stewart 1987), along with 25 ml of 20:3:3 N:P:K fertilizer (Stewart 1987), were added to each trough. Ten days before beginning the experiment, each artificial stream was filled with filtered lake water, lined with the precolonized tiles, and continuous flow initiated. Nutrients (fertilizer, as previously stated) were added to the streams twice before starting the experiment to promote initial algal growth. Because we wanted treatments to be similar with respect to olfactory cues and potential water column nutrients, we circulated water between streams weekly to homogenize water column features. Water was circulated by pumping water from tank to tank at a rate of 2000 l h^{-1} for one h. Water temperature, dissolved oxygen concentration, and pH were recorded daily, and turbidity, conductivity, and alkalinity were measured every 3 d to insure that none of the streams drifted toward aberrant or unique water quality conditions between weekly periods of inter-tank circulation.

Treatments

Five treatments (two replicate streams each) were randomly assigned to the 10 streams : (1) *Campostoma* and *Orconectes,* (2) *Orconectes* alone, (3) *Campostoma* and *Physella,* (4) *Physella* alone, and (5) no grazers. The experiment lasted five wk, from 19 June (Day 1) to 24 July 1989 (Day 35). At the beginning of the experiment, 20 medium-sized *Campostoma* (40 – 75 mm standard length) were added to each fish treatment. Initial total fish biomass ranged from 31 to 37 g per stream. Fish numbers per stream were kept constant throughout the experiment. Initial densities of crayfish were 20 per stream. Crayfish ranged from 1.59 to 8.71 g, and each stream was given an equal number of small and medium crayfish so that starting biomass was as similar as possible. All crayfish treatments were assigned equal numbers of males and females. During the first week of the experiment dissolved oxygen concentrations fell at night to low (3 ppm) levels in the treatments containing both fish and crayfish. For this reason, we reduced all cray-

fish densities to 10 per stream at that time and maintained this level to the end of the experiment. Because *Campostoma* are less likely to behave normally at smaller school sizes their numbers were not reduced. Starting densities of *Physella* were 77 snails m^{-2} (200 per stream). All snails were initially between 4 and 6 mm in total shell length. The densities of the three taxa in this experiment were chosen to approximate their densities in local streams.

Density estimates – snails

After snails began to reproduce in the streams we also estimated densities of juveniles and egg masses. Five tiles on Day 23 and Day 29, and 10 tiles on Day 35, were sampled randomly in each stream. All snails < 4 mm long on each tile were counted without removal. These snails were considered juveniles, as they were smaller than and a result of reproduction by the original individuals. Snail egg masses on each tile also were counted, and tiles were returned to the streams. Mean juvenile and egg mass densities (per stream) were tested by a repeated measures ANOVA (SAS 1985) for differences between fish and no-fish treatments and for interactions. Snail densities were estimated at the end of the experiment by counting and removing all the snails on the tiles in each experimental stream. These snails were assigned to 2 mm increment size classes (Richardson and Brown 1989) from < 2 to 10 mm total shell length.

Biomass and production estimates – snails and crayfish

Physella that were collected from local streams and held in the laboratory, but not used in the experiment, were used to calculate a wet mass-ash free dry mass regression line following Brown et al. (1989) and Richardson and Brown (1989). Ten snails from each size class were frozen for 24 h, defrosted until ice crystals were no longer visible, and blotted. Each individual was measured to the nearest 0.1 mm and wet weighed to the nearest 0.01 mg. Soft parts were then removed from the shell with the visual aid of a dissecting microscope. Snail soft tissue was then dried at 60°C for 24 h, reweighed, ashed at 500°C, and weighed again. Weights were log transformed. The resulting regression equation for AFDM on wet mass was $Y = (0.07)X - 0.0015$ ($n = 50$, $R^2 = 0.93$, $P < 0.0001$). The regression equation for log wet mass on log shell length was $Y = (3.01)X - 0.93$ ($n = 50$, $R^2 = 0.97$, $P < 0.0001$).

Fifty snails were randomly captured from each experimental stream weekly, measured (total length) to the nearest 0.1 mm using digital calipers, and returned to the streams. Also, at the beginning of the experiment 50 snails were individually marked with colored, pre-numbered plastic queen bee tags (available from Königinzucht, Stuttgart, Germany) attached with superglue. Marked snails recaptured weekly also were measured. Changes in mean weekly shell length of both marked and unmarked snails were used to estimate growth in mm wk^{-1}, but only growth rates of marked snails were used in calculating secondary production.

All snails collected at the end of the experiment were frozen and sorted into 2-mm size classes. For each experimental stream, if a size class contained < 20 individuals, length of each individual was measured and a wet mass taken as described above. If the size class contained more than 20 individuals, 20 were randomly subsampled, weighed, and measured. Wet masses were used to predict ash free dry masses using the regression equation derived above. Mean ash free dry mass was calculated for each size class and multiplied by the final density of that size class to calculate biomass per area. The regression equations were also used to predict growth in mg from growth in mm of marked snails. These data were used to estimate standing crop biomass and production by the instantaneous growth method (Waters 1977, Benke 1984, Richardson et al. 1988). Differences in mean standing crop biomass and production estimates for snails were compared between fish and no-fish treatments by a t-test, with N = 2 (streams per treatment) as true replicates. With such a small N, power to reject a false null hypothesis is very low. However, such an application of a t-test for N = 2 is valid (Sokal and Rohlf 1981) and any finding of significant differences with our power limitations would indicate a strong effect.

Individual crayfish were marked on the dorsal surface of the carapace using queen bee tags attached with superglue. We recorded the length from the tip of the rostrum to the end of the cephalothorax for each individual. Individuals were wet weighed at the beginning of the experiment and each week thereafter. Experimental streams were checked daily for molting crayfish. Crayfish that had molted were measured and retagged. Crayfish densities were held constant throughout the experiment, by replacing dead individuals with new, tagged individuals. However, only crayfish that were added at the beginning of the experiment and thus had been subject to treatment effects for the entire period were used in biomass and production calculations. Crayfish secondary production was calculated using the instantaneous growth method. Crayfish growth as change in wet mass was converted to ash free dry mass using the regression equation $Y = 0.078(X) - 0.048$ ($n = 34$, $R^2 = 0.83$, $P < 0.0001$). Means for crayfish growth and secondary production between treatments were compared with t-tests (N = 2) as above.

To assess the potential effects of fish grazing on foraging frequency of crayfish we took scan samples of the number of crayfish in each stream exposed and foraging at 10.00 and 22.00 on 4 separate days.

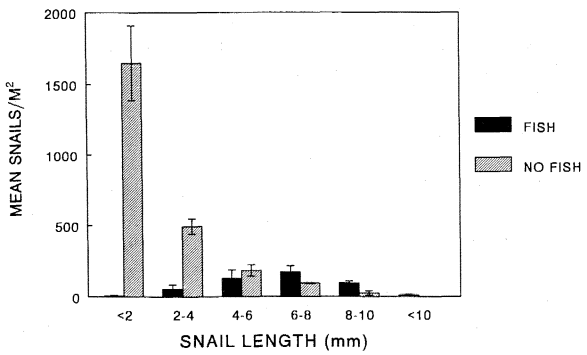

Fig. 1. Mean size distribution of the *Physella* populations in fish and nonfish streams at the end of the experiment. Error bars are the standard deviation from the mean. N = 2 streams per treatment.

Primary productivity and AFDM

We determined net primary productivity (NPPR) of algae on three randomly selected tiles weekly from each experimental stream. Each tile was placed into an individual 3.8 l (Ziploc™) freezer bag (2.7 mm thick), following procedures of Stewart (1987). Bags were filled underwater to eliminate air bubbles, sealed, and incubated in the experimental stream for one h. A fourth bag containing water but without a tile was used as a control for production by phytoplankton or any periphyton suspended in the water column. Initial and final dissolved oxygen concentrations were measured using a Yellow Springs Instrument model 54 oxygen meter. While we recognize that static chambers may underestimate actual production, in this study only relative comparisons between streams were made. The volume of water in each bag was measured and the tile scraped and brushed to remove all algae. The algal scrapings were diluted to 180 ml with water and homogenized with a hand held blender. A 10 ml algal subsample was preserved in 2% borate buffered formalin for algal and bacterial counts. Algal biomass was determined as ash free dry mass (AFDM) by drying algae at 60°C, weighing, ashing at 550°C and reweighing. NPPR was calculated per unit biomass (mg O_2 g AFDM^{-1} h^{-1}) and per unit area (mg O_2 m^{-2} h^{-1}).

Bacteria and periphyton community composition

Two subsamples of algal homogenate from each scraped tile were used to determine periphyton community composition and bacterial abundance for Days 1, 17 and 35. Two slides from each subsample were examined for algal composition using the point quadrat method with a Whipple grid at 400 × (Jones 1968). Fifty fields per slide were examined and 100 points (grid intersections) were searched per field. Each grid intersection within the area of an alga was scored as green algae, blue-green algae, or diatom. Thus, quantification included a measure of cell size, i.e. a large cell intersecting more than one grid would have a higher score. Empty cells were not scored. The percentage of points for each algal category was calculated for each tile. These percentages were then multiplied by the AFDM of algae on an individual tile to estimate a surrogate for biovolume as g m^{-2} for each algal category.

For bacterial counts, three subsamples per stream (one from each tile) were stained in duplicate following Porter and Feig (1980). One ml of subsample was stained with 0.1 ml of DAPI stain (0.01 mg ml^{-1} of 4, 6-diamidino-2-phenylindole), filtered onto Nuclepore filters (25-mm diameter, 0.2 µm pore size) which had been blackened in a solution of Irgalan Black (Baker). The damp filters were immediately mounted on microscope slides; at least 10 fields were counted on each filter. All bacterial cells fluorescing within the area of a Whipple grid were counted. A Nikon Labophot microscope equipped with objectives for use with epifluorescence and an episcopic fluorescent lamp with filters for ultraviolet excitation were used.

Treatment means for AFDM, NPPR, bacterial den-

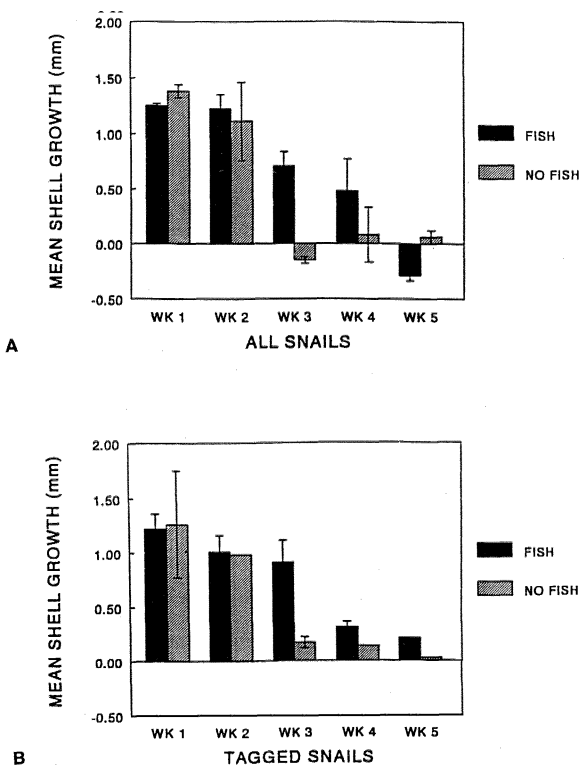

Fig. 2. Mean weekly growth of *Physella* as total shell length. Error bars represent the standard deviation from the mean. The top graph (A) (all snails) is the weekly change in shell length calculated for the entire snail population. Data shown on the lower graph (B) are the means of weekly changes in length of individual, tagged snails. N = 2 streams per treatment.

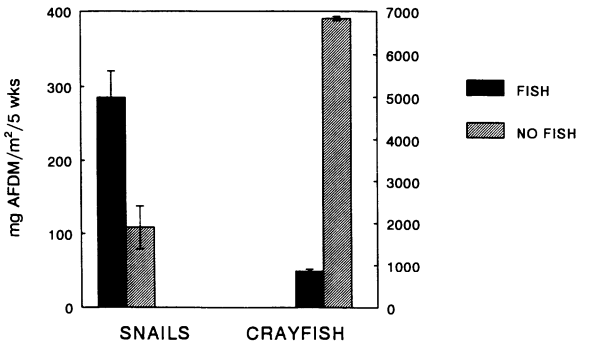

Fig. 3. Mean secondary production and standard deviation of snails (left y axis) and crayfish (right y axis) in fish and no-fish treatments. N = 2 streams per treatment.

sity and periphyton biovolume were compared using a repeated measures ANOVA (SAS 1985) testing for main effects of grazing treatments, time, and treatment × time interactions. Planned comparisons between fish and no-fish treatments were made for variables that had significant main effects. Variables were log-transformed (Sokal and Rohlf 1981) before performing ANOVA.

Results

Secondary production

Snails

Physella numbers increased in both fish and no-fish treatments over the course of the experiment, but increases were much greater in the absence of *Campostoma*. Mean final density in treatments with fish was 458.5 ± 2.12 (S.D.) snails m^{-2}. Mean final density in the fishless treatments was 2439.5±251.02 snails m^{-2}. These densities were significantly different ($t = 11.16$, $df = 1$, $P < 0.01$) Most snails collected at the end of the experiment from fishless treatments were <2 mm long (Fig. 1).

Snails in treatments with and without fish grew at approximately the same rate for the first two wk of the experiment, averaging 0.17–0.18 mm d^{-1}. In the third week, snails in the no-fish treatments stopped growing and began reproducing (Fig. 2A). Snails in the fish treatments continued to grow, and did so at a reduced rate until the last week (Fig. 2A). Growth rates of tagged snails closely paralleled growth rates of all snails (Fig. 2B) ($R^2 = 0.71$, $P < 0.05$). Survival of tagged snails retrieved at the end of the experiment was 13% ± 1% (S.D.) in no-fish treatments and 45% ± 5% in treatments with fish. Standing crop biomass of snails increased almost twice as much in fish treatments (+ 480 mg m^{-2}) as in no-fish treatments (+ 247 mg m^{-2}) ($t = 4.78$, $df = 1$, $P < 0.05$). Secondary production of snails was greater in fish-grazed treatments than in no-fish streams ($t = 5.43$, $df = 1$, $P < 0.05$) (Fig. 3).

When we began censuses of juvenile *Physella* on Day 23, their densities were already quite high in the no-fish treatments, and at a nearly constant low level in the treatments with fish (Fig. 4A). Fish versus no-fish treatment juvenile densities were significantly different overall ($F = 153.14$, $p < 0.01$) and there was no significant time effect or treatment × time interaction. Snail egg mass densities were not significantly different between fish and no-fish treatments ($F = 9.26$) because most eggs had hatched in no-fish treatments before we began censuses (Fig. 4B). Although locations of egg masses were not quantified in this study, we observed the majority of egg masses on the undersides of tiles in both fish and no-fish treatments containing snails. Egg masses were never found on the tops of tiles.

Crayfish

The increase in crayfish wet mass during the experiment was greater in streams where there were no fish (X =

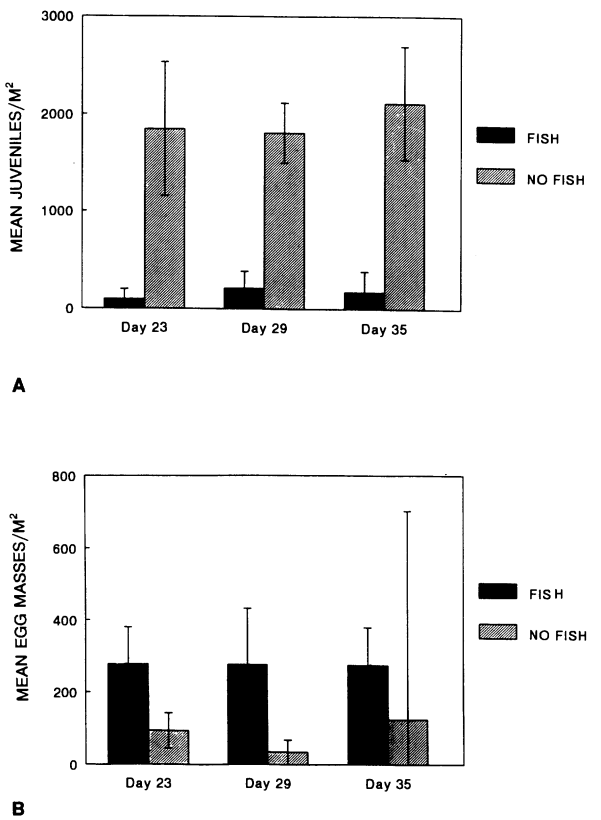

Fig. 4. (A) Mean densities and standard deviations of juvenile snails (< 4 mm total length) in fish and nonfish streams during the last three weeks of the experiment. (B) Mean snail egg mass densities and standard deviations during the last three weeks of the experiment. N = 2 streams per treatment.

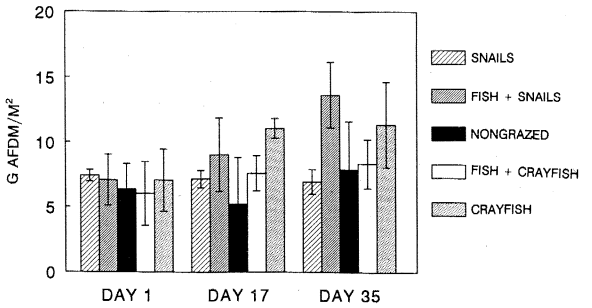

Fig. 5. Mean AFDM and standard errors by treatment on Days 1, 17, and 35.

590 ± 610 mg) than in streams with fish (X = 80 ± 520 mg) (t = 13.87, df = 1, P < 0.01). Crayfish secondary production was less in fish treatments than in no-fish treatments (t = 18.54, df = 1, P < 0.01) (Fig. 3). Crayfish survival was 85% ± 5% (S.D.) in all treatments. In experimental streams without fish, crayfish had a tendency to graze in day and night, but in streams with fish crayfish remained hidden during the day and only grazed at night. Scan samples of the number of crayfish observed feeding during the day (no fish = 18, fish = 6) were tested against a null hypothesis of 50:50. There were significant differences in the numbers of crayfish observed foraging in treatments without fish versus with fish ($\chi^2 = 5.04$, $P < 0.02$, one-tailed test with Yates correction).

Algal and bacterial resources

AFDM on tiles increased over time in most treatments (Fig. 5), but there were no significant grazing or grazing × time effects (Table 1). There were no significant grazing or grazing × time effects (Table 1) on area-specific NPPR (mg O_2 m^{-2} h^{-1}) or biomass-specific NPPR (mg O_2 g $AFDM^{-1}$ h^{-1}) (Fig. 6).

Table 1. Results of repeated measures analysis of variance for main effects of grazing treatments in the experiment. Grazing treatments were: crayfish alone, crayfish + fish, snails alone, snails + fish, and no grazers. F values are in the table. All tests had the following degrees of freedom: Grazing (4, 5); Time (2, 10); Grazing × Time (8, 10). Levels of significance are * = P < 0.05, ** = P < 0.01, and *** = P < 0.001.

Variable	Grazing treatment	Time	Grazing × time
AFDM	1.15	4.45*	1.32
NPPR – area	0.19	0.72	0.97
NPPR – biomass	0.96	0.01	0.42
Bacteria	1.05	38.11***	2.17
Green algae	1.72	15.81***	1.11
Blue-green algae	9.62**(*)[1]	1.80	3.29*
Diatoms	2.69	9.68**	2.61

[1] Significance level with Bonferroni correction to protect elevated alpha's.

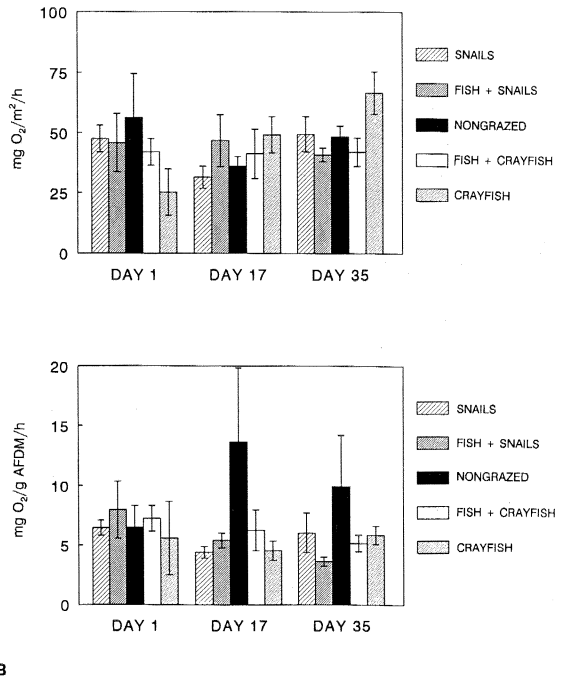

Fig. 6. Mean NPPR and standard errors by treatment on Days 1, 17 and 35. The upper graph (A) is area-specific NPPR, and the lower graph (B) is biomass-specific NPPR.

Bacterial numbers increased significantly in all treatments over time (Fig. 7; Table 1), but there were no significant grazing or grazing × time effects. Amounts of green algae and diatoms changed during the experiment (Fig. 8), but there were no significant treatment effects (Table 1).

There were significant grazing treatment and grazing × time effects on blue-green algal abundance (Table 1). Biovolume of blue-green algae (mostly *Oscillatoria* and *Lyngbya*) was greater in grazer treatments with fish than in comparable treatments without fish (Fig. 7). At

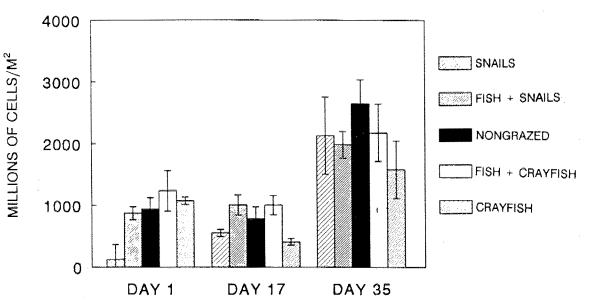

Fig. 7. Mean numbers of bacteria and standard errors by treatment on Days 1, 17 and 35.

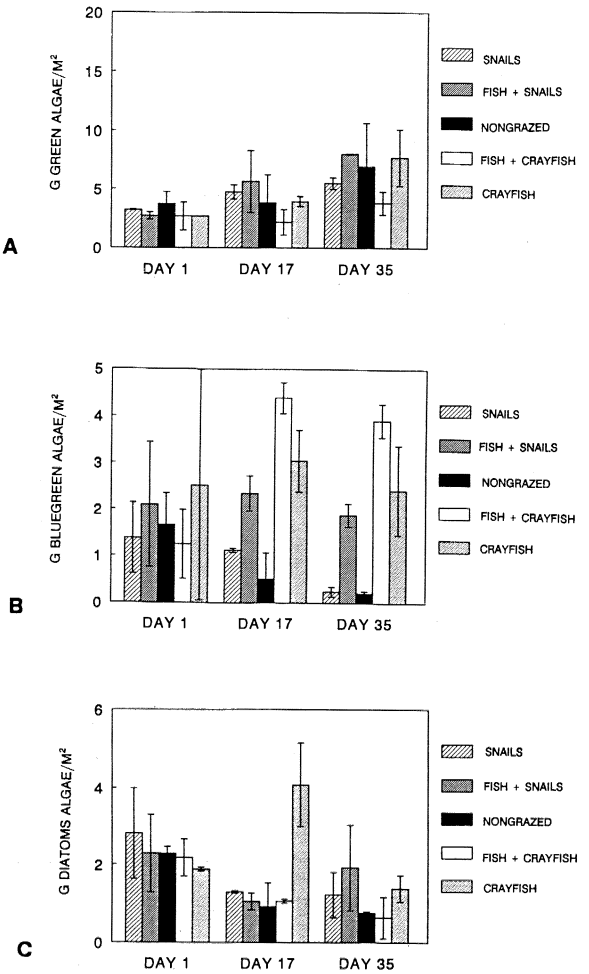

Fig. 8. Mean biovolumes in g m^{-2} and standard deviations of algae (A = green algae, B = bluegreen algae, and C = diatoms) on Days 1, 17 and 35.

the end of the experiment (Day 35), there was significantly lower blue-green algal biovolume in snails alone vs fish + snails treatments (F test for planned comparisons; $F = 59.19$, $p < 0.001$) (Fig. 7). Biovolume of green algae was dominated by filamentous forms (*Rhizoclonium, Spirogyra,* and *Oedogonium*).

Discussion

Grazing fish effects on periphyton available to other grazers

AFDM and algal biovolumes alone do not reflect the large physical differences in algal physiognomy and patchiness that developed between treatments with large grazers (fish and crayfish) and treatments with small grazers (snails) or no grazers. In treatments containing either snails or no grazers, long, loosely-attached algal filaments developed which subsequently sloughed from the substratum, leaving tiles denuded of most algae (and thus with low biomass). Additionally, in these no grazer or small grazer treatments algae was patchily distributed among tiles within a stream. At any one time within such a stream, some tiles had long algal filaments, whereas others were almost bare. In contrast, tiles in streams with fish and/or crayfish grazers were covered with dense, tightly-adhering, relatively uniform "lawns" of cropped filamentous algae (mainly the green alga *Rhizoclonium*) with bluegreen algae and diatoms intermixed.

Our results support previous observations and experiments that demonstrate *Campostoma* grazing activities promote bluegreen algal development (Power et al. 1988a). Comparison of streams with fish + crayfish vs crayfish alone suggest that streams with fish had less AFDM, more bluegreen algae, and less green algae, although these differences were not statistically significant. However, we recognize that with limits of power due to N = 2 streams per treatment, a biologically important difference in AFDM, bluegreen algae or green algae might have gone undetected.

Crayfish production

Crayfish gained less weight and their production was lower in the presence of *Campostoma.* Although crayfish are known for their ability to control macrophytes (Carpenter and Lodge 1986, Lodge and Lorman 1987, Feminella and Resh 1989), most crayfish, including *O. virilis,* are opportunistic, switching from herbivory to carnivory to detritivory depending on food availability (Hobbs 1991). In the largely autotrophic streams in southern Oklahoma, periphyton is an important food resource for crayfish (Vaughn, pers. obs.). Lower production of crayfish in the presence of fish in this experiment likely is related to decreased food availability to the crayfish. The presence of grazing fish probably decreased food availability to crayfish by decreasing algal abundance, changing the proportion of algal types (green algae to bluegreen algae) and thus potential food quality, and by restricting the use of algal resources by the crayfish by decreasing their foraging in daylight hours. Behavioral observations made during this experiment indicate that fish limit the time spent grazing by crayfish.

Snail production

Snail production and life history were altered in the presence of grazing fish, with significantly higher standing crop biomass and secondary production and delayed reproduction. Increased production is likely related to the phenomenon that grazing fish actually increase food available to snails. Algae are a major food source for

most freshwater snails (Calow 1970, Brönmark 1989). Algae are consumed through scraping movements of the radula (Brown 1991), thus small cells are preferred over and are easier to consume than filamentous growth forms (Kraft 1988, Dillon and Davis 1991). Fish grazing may facilitate *Physella* grazing by removing the filamentous green (*Rhizoclonium*) algal overstory and thereby increase accessibility to small, adnate cells. Other studies have shown that when herbivores reduce the algal overstory, there is a resultant increase in the proportion of small, adnate species (Gregory 1980, Kesler 1981, Sumner and McIntire 1982, Hunter and Russell-Hunter 1983, Steinman et al. 1987, Feminella and Resh 1991). Basal cells of the filaments are not grazed by *Campostoma* (Power et al. 1988a), and their presence could provide a refuge for small cells from fish grazing but not snail grazing. Such a refuge would result in an increased availability of small cells to snails.

Bacteria are an important nutritional source for many snails (Calow 1974, Prejs 1984, Brown 1991). Grazing schools of *Campostoma* produce large amounts of fecal material that quickly accumulates in artificial streams, as in natural stream pools. Snails probably feed on bacteria that colonize feces.

Snail production has been linked directly to food availability (Aldridge 1982, Russell-Hunter and Buckley 1983, Richardson and Brown 1989, Bosnia et al. 1990). In a reciprocal exchange experiment using the pulmonate snail *Lymnaea* and a series of ponds, Brown (1985) determined that snails from more productive ponds had longer life cycles and reproduced at a larger size. Gebhardt and Ribi (1987), in a comparative study of prosobranch snails in two Swiss lakes, found that snails from the less productive lake had shorter life spans and reproduced at an earlier age. Snails may compensate for low food levels (and thus future loss in reproductive output) by increasing or initiating earlier egg laying.

Phenotypic plasticity is the ability of organisms from the same gene pool to modify phenotypes according to external environmental cues (Stearns 1989). We found clear evidence of phenotypic plasticity in that snails grew larger and delayed reproduction in the presence of *Campostoma*. Stream species often exhibit regional differences in life-history traits such as age and size at first reproduction or numbers of generations per year (Butler 1984, Power et al. 1988b). Historically, such differences have been assumed to be genetic. However, recent studies indicate that phenotypically plastic responses are frequently important in nature (Dobson and Murie 1987, Reznik 1990, Trexler and Travis 1990). Environmental factors which may cue phenotypic changes in life history traits include nutrient and food levels, photoperiod, disturbance frequency and intensity, conspecific crowding and social structure, and predation (Brown 1983, Brown et al. 1985, Bailey and Mackie 1986, Dodson 1989, Stearns 1989, Crowl and Covich 1990).

Physella also show phenotypic plasticity in life history traits in response to predation. Crayfish are voracious snail predators, consuming a higher proportion of small, thin-shelled individuals (Covich 1977, 1981, Alexander and Covich 1991a,b). Crowl (1989, 1990) showed that predation by *Orconectes virilis* on *Physella virgata* indirectly governed the population dynamics of these snails in small, stable Oklahoma streams, with snails delaying reproduction, growing to a larger size, and only producing one generation per year if predators were present. These changes in *Physella* life-history characteristics were initiated by a water-borne cue released when crayfish actively feed on *Physella* (Crowl and Covich 1990). Although not experimentally tested, gut analyses of *Campostoma* from our experiment indicate that these fish did not feed on snails. Videotapes of fish and snail grazing during this experiment (Vaughn and Gelwick, unpubl.) gave no indication that fish consume snails or disturb snails by their grazing. Furthermore, in our experiment any chemical cues caused by fish feeding on snails would have been ameliorated by regular circulation of water among streams. For this reason, it is more likely that the shift in life-history characteristics we observed is related to food availability and quality than predation.

Previous studies of *Campostoma* in Oklahoma streams showed that these grazing minnows have strong effects on distributions and kinds of attached algae (Power and Matthews 1983, Power et al. 1985, 1988a, Matthews et al 1986, Stewart 1987, Harvey et al. 1988). We have now shown that these abundant, widespread fishes also can substantially influence secondary production and life-history traits of co-occurring invertebrate grazers.

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