GRAZING MINNOWS, PISCIVOROUS BASS, AND STREAM ALGAE: DYNAMICS OF A STRONG INTERACTION[1]

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Abstract. Striking differences in pool-to-pool distributions of an algae-grazing minnow (*Campostoma anomalum*), attached algae (predominantly *Spirogyra* sp. and *Rhizoclonium* sp.), and bass (*Micropterus salmoides* and *M. punctulatus*) are known to occur in some small Oklahoma streams. This study evaluates the complementarity of bass, *Campostoma*, and algae at different seasons, and uses in-stream experimental manipulations of bass and *Campostoma* to determine if the patterns resulted from strong interactions between predators, herbivores, and algae. In a 1-km reach of Brier Creek (south-central Oklahoma), bass and *Campostoma* distributions in 14 consecutive pools were inversely related in six of seven censuses conducted from 8 November 1982 to 5 September 1983. Bass and *Campostoma* co-occurred in more than two pools only on two occasions, following the largest floods of the year. *Campostoma* and algal abundances were inversely related during late summer and in both autumns of this study. This relationship did not hold during the spring, when floods strongly affected algal distributions.

During autumn of 1983, we removed bass from a pool, fenced it longitudinally, and added *Campostoma* to one side (1.4 individuals/m²). Over the next 5 wk, standing crop of algae decreased significantly on the *Campostoma* side but increased on the control side. In a nearby unmanipulated *Campostoma* pool, standing crop of algae was consistently low. We added three free-swimming bass to a *Campostoma* pool to evaluate presumptive predator-prey interactions. Within 3 h, the *Campostoma* moved from the deepest part of the pool to shallow areas. Over the next 5 wk, numbers of grazing *Campostoma* declined due to behavioral changes, emigration, and (presumably) predation. The standing crop of algae increased significantly 10–13 d after bass addition. In a second bass-addition experiment in June 1984, *Campostoma* responses were almost identical, and algal standing crop in deeper areas increased significantly after 1 wk. Collectively, our censuses and the experiments indicate that in Brier Creek, biotic interactions strongly influence the pool-to-pool distributions of *Campostoma* and algae, particularly during long periods of constant low discharge.

Key words: algivorous minnows; bass; Campostoma; *floods; freshwater herbivory; grazing; predator-prey interactions; streams.*

INTRODUCTION

Grazers, and predators that control their numbers or constrain their behavior, can strongly affect community patterns (Harper 1969, Paine 1980). In benthic communities, grazers in the absence of predators can denude substrates of attached algae which would otherwise provide food and cover essential to many aquatic organisms (Estes and Palmisano 1974, Mann 1977, Duggins 1980). Herbivorous fishes are typically larger, more mobile, and have higher feeding rates than invertebrate grazers. The importance of herbivorous fish in marine reef communities has been documented extensively (John and Pople 1973, Lassuy 1980, Lobel 1980, Montgomery 1980, Hixon and Brostoff 1983, Hay 1984 and references therein). Much less is known about the roles of herbivorous fishes in freshwater communities, particularly in streams (but see Power 1983, 1984*a, b*). At least 45 species of minnows, suckers, killifish, or pupfish in North America are partially algivorous, and of these, 21 species are primarily herbivorous (Lee et al. 1980). While some of these species have limited distributions (e.g., locally isolated pupfish), others such as *Phoxinus* spp., *Notropis nubilis,*

Pimephales promelas, and *Campostoma* spp. are widely distributed and abundant (Pflieger 1975, Burr 1980).

In some Midwestern streams where pools are separated by shallow riffles, striking patterns of complementarity occur in the distributions of algivorous minnows (*Campostoma anomalum*) and piscivorous bass (*Micropterus salmoides* and *M. punctulatus* >7 cm SL [standard length]) (e.g., Power and Matthews 1983). In late summer and autumn, pools in these streams that contained schools of *Campostoma* lacked bass, and had substrates that were barren or covered with detritus (largely *Campostoma* feces). Pools with bass lacked *Campostoma* and contained large quantities of algae. In simple field experiments, *Campostoma* grazed voraciously on algae transferred into their pools, but did not (over a 3-d period) feed on algae placed within 0.5 m of a tethered bass (Power and Matthews 1983). These results suggest that in small streams, *Campostoma* and bass are "strong interactors" as defined by Paine (1980: 668): "in their absence, pronounced changes ensue" (MacArthur 1972).

Predators may alter feeding impacts of their prey in various ways: by reducing their numbers; by constraining their feeding in space or time (e.g., Stein and Magnuson 1976, Garrity and Levings 1981, Sih 1982, Wer-

ner et al. 1983, Cooper 1984); or by preventing their colonization of habitats or causing prey to emigrate (Peckarsky 1980, Peckarsky and Dodson 1980, Fraser and Cerri 1982). The study of Power and Matthews (1983) did not reveal the mechanism of bass–*Campostoma* segregation, which could have been predation by the bass, predator avoidance (emigration or habitat selection) by the minnows, or both.

To study processes underlying the distribution pattern of bass, *Campostoma,* and algae, we examined this pattern at seven times during the year in the 14 consecutive pools of Brier Creek (south-central Oklahoma) used as a study site by Power and Matthews (1983). In autumn 1983 and June 1984, we carried out experimental transfers of bass and *Campostoma* in stream pools. Here we report results from these observations and experiments, which indicate that grazing, predation, and predator avoidance, superimposed on seasonal and successional events, exert rapid, strong effects on the distribution patterns of bass, algae and *Campostoma* in this small, prairie-margin stream.

STUDY SITE DESCRIPTION

Censuses and experiments were carried out within a 1-km reach of Brier Creek in Marshall County, Oklahoma (34°0'N, 97°2'W). The fish assemblage of pools in this reach of the creek is dominated numerically by minnows (*Campostoma anomalum, Notropis boops,* and *N. lutrensis*), a topminnow (*Fundulus notatus*), green sunfish (*Lepomis cyanellus*), longear sunfish (*L. megalotis*), and largemouth bass (*Micropterus salmoides*). Seven snorkeling censuses of the 14 pools in this reach (see below) showed 24 species of fish present, of which 35% were *Campostoma* (6117 of 17 415 individuals counted in all censuses) (W. J. Matthews, *personal observation*). The invertebrate fauna is relatively depauperate. In stream pools, larvae of biting midges (Ceratopogonidae) and true midges (Chironominae) are present in moderate numbers, while mayfly (Ephemeroptera), dragonfly and damselfly larvae (Odonata) are less common. Other grazing invertebrates such as caddisflies and snails are sparse except in very shallow riffles. Crayfish are also rare.

A general description of the Brier Creek watershed and fish assemblages is in Smith and Powell (1971). The study reach is also mapped and described in Power and Matthews (1983). The stream remains free-flowing in all but very dry summers. Pools do not exceed 2 m in depth at normal flow, and most have maximum depths of 30–70 cm. Pools tend to be well isolated from one another by shallow riffles, many of which are only 2–3 cm deep.

METHODS

Seasonal censuses

Fishes in the 14 pools were counted on seven dates from 8 November 1982 to 5 September 1983 (Fig. 1).

A snorkeler (W. J. Matthews) swam slowly upstream, counting *Campostoma* and bass, and estimating the lengths of bass in each pool.

The standing crop of algae in pools was evaluated along three cross-stream transects, in downstream, middle, and upstream areas of each pool. Successive measurements of total transect widths varied by only 1–2 cm. We therefore assume that our error in relocating specific sampling sites on the streambed under the transects was ±4 cm. At intervals along each transect, usually 0.5 or 1.0 m apart, we measured depth of water and described the substrate according to a modified Wentworth scale (Hynes 1970). This procedure resulted in 15 sites for evaluation in each pool (five sites per transect, three transects per pool). We recorded the dominant and subdominant alga at each site. Algal condition (1 = senescent, 3 = fresh) and density (1 = sparse, 3 = 100% cover) was scored, and we noted whether or not algae were attached to the substrate. At each site, we also measured the height (or length, if algae were unattached) of typical algal strands (those visually estimated to represent the average). For the types of algae dominant in Brier Creek, measured algal height was strongly correlated with ash-free dry mass per square centimetre ($r = 0.91$, $n = 23$, $P < .001$). Algal height was also correlated with density indices for all algae sampled during this study ($r_s = 0.16$, $n = 953$, $P < .001$). Censuses of algae were conducted in all 14 pools on 8 and 19 November, and in Pools 1–7 on 13 June, 18 June, and 5 September.

Records of stream stage were kept by noting stream level on staff gauges when these were available, observation during floods, and by inferring crests of floods from debris lines.

Field experiments

Field experiments were conducted in Brier Creek from 9 September to 17 November 1983 and in June 1984, to study within-pool dynamics of processes leading to the pool-to-pool variation in abundances of algae, *Campostoma,* and bass. We added *Campostoma* to a bass pool after the bass had been removed to assess the effect of *Campostoma* on the pool's well-developed algal standing crop. To a second pool containing *Campostoma,* we added bass. A third pool containing *Campostoma* was monitored as an unmanipulated control. Pools were selected on the basis of logistical requirements of manipulations, including ease of observation of fish in pools, barriers to fish emigration, feasibility of capturing bass, and the need for a straight, bilaterally symmetric pool for a split-pool experiment.

Algae were sampled along three to five permanent cross-stream transects in each experimental pool at 3- or 7-d intervals, by methods described above. Data on depth and substrate were also collected on each sampling date, using methods described above. These physical features did not change appreciably in any of the study pools over the 2-mo duration of our study.
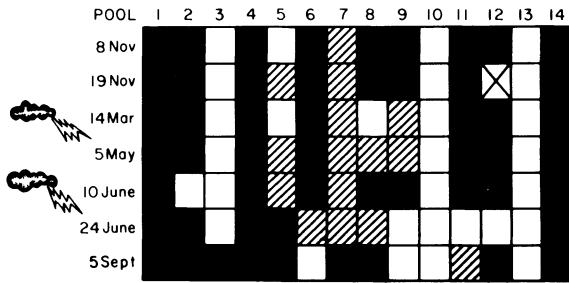
FIG. 1. Distribution of bass and *Campostoma* among 14 consecutive stream pools at seven dates throughout the year. ■ bass, no *Campostoma*; ▨ bass, *Campostoma*; □ *Campostoma*, no bass. Pool no. 1 is downstream, pool no 14 upstream. Thundercloud symbols indicate dates of the two major floods that occurred during the year (17 March and 13 June 1983). On 19 November 1982, a census was not taken in Pool 12.

Care was taken to minimize disruption to sampled sites, as these were monitored repeatedly throughout the 2 mo of the experiments.

Campostoma additions

Immediately before manipulation, Pool 5 (Power and Matthews 1983) was a bass pool that lacked *Campostoma* but had a well-developed standing crop of algae (53% of all sampled points contained algae ≥2 cm in height), two largemouth bass (15 and 20 cm SL), and several green and longear sunfish >15 cm SL. These potential predators were removed by electroshocking, which disrupts stream substrate less than seining. A 67 cm high fence of flexible plastic sheeting (Visqueen) was then installed, splitting the pool longitudinally. The base of the fence was buried in gravel and flow of water was equalized through each side of the pool. The two sides of the split pool were similar in area (89.6 vs. 92.6 m², respectively), and maximum depth (36 vs. 37 cm). Algal composition on both sides appeared similar, although one side had a higher standing crop.

After baseline sampling of algae and invertebrates, we added 121 *Campostoma* (captured elsewhere in Brier Creek) to one side of Pool 5 (determined by a coin toss). The resulting density (1.4 individuals/m²) was lower than those typically found in Brier Creek *Campostoma* pools (2–3 individuals/m²). The introduced *Campostoma* remained on the experimental side of the pool except for two occasions. Following small spates, we found 14 and 12 *Campostoma* on the control side on 26 September and 3 October, respectively. They were recaptured by electroshocking, and returned to the experimental side within 2 and 10 d, respectively, of the two dates.

Bass additions

Before this experiment was started on 9 September, Pool 9 (Power and Matthews 1983) had 70 *Campostoma* (0.82 individuals/m²) and no bass. To study interactions between these minnows and their preda-

tors and effects on algae, we added three largemouth bass (18, 25, and 28 cm SL) to this pool. Before adding bass we dug a shallow trench, 2 m long and <10 cm deep, from the downstream end of Pool 9 to the upstream end of Pool 8. This upper end of Pool 8 was blocked with a 5-mm mesh net so that fish emigrating downstream from experimental Pool 9 could be recovered. Emigration upstream from Pool 9 was prevented by a natural rock dam (38 cm high), over which the flow of water was only 2–3 cm deep.

We repeated this experiment in June 1984, using two largemouth bass, 17.5 and 23 cm SL. Over the winter, the natural dam had been broken, and riffles connected Pool 9 to Pools 8 and 10. We therefore blocked portions of Pools 8 and 10 adjacent to Pool 9 with 5-mm mesh Vexar screen so that fish emigrating in either direction from Pool 9 could be recovered. We also constructed a detailed map of Pool 9 with 10-cm bathymetric contour intervals, and installed a grid of 92 m² on the pool substrate to obtain quantitative data on use of space by bass and *Campostoma*. Small flags were used to mark the corners of each square metre cell of the grid. On 6 d during the week before the bass addition, and on 7 d in the following week, positions of *Campostoma* over the gridded pool substrate were mapped during 20 and 26 "scan samples" (Altmann 1974). Scan samples were taken at intervals ≥15 min apart, and 1–16 samples were taken per day. Between scans, per capita feeding rates were estimated by counting bites per minute for individual *Campostoma* during 0.5–5.0 min observations. Total observation time of *Campostoma* in Pool 9 was 235 min before bass addition, and 340 min after bass addition. Before and after bass addition, behavioral observations were made at various times on different days, from 0920 to 1900.

The standing crop of algae in Pool 9 was assessed at five fixed sites along each of eight cross-stream transects, 4 d before and 1 wk after bass were added to the pool using methods described earlier.

RESULTS

Seasonal censuses

Throughout most of the year, bass and *Campostoma* were spatially segregated among the 14 pools despite eight instances in which particular pools switched from "bass" to "*Campostoma*" pools, or vice-versa (Fig. 1). This complementarity was significant (.03 > P > .001, Fisher's Exact Test) in six of seven censuses. In the pools where bass and *Campostoma* co-occurred, bass occupied deep areas and *Campostoma* were found in shallow areas (see also Power and Matthews 1983). The two census dates on which bass and *Campostoma* co-occurred in >2 of the 14 pools followed the only major floods of the year. During these floods, the stream crested at 1.7 m (17 March 1983) and 2.7 m (14 June 1983) above base flow. All other stage fluctuations that occurred during the year were <0.5 m.
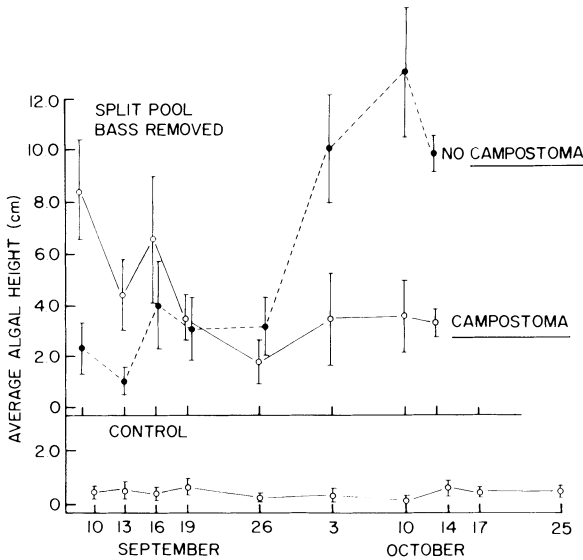
FIG. 2. Algal standing crops in the two sides of Pool 5, where bass were removed and *Campostoma* added to one side, and in a control pool, which contained a *Campostoma* school and was not manipulated. Points are means from 18–21 measurements (Pool 5, *Campostoma* side); 20–21 measurements (Pool 5, control side); and 11–21 measurements (Control Pool). Vertical bars indicate ±2 SE.

During late summer 1983 and in autumns of 1982 and 1983, algal standing crops were conspicuously low in *Campostoma* pools, but were high in pools that lacked *Campostoma* and contained bass. Complementarity for *Campostoma* and algae could not be defined on a strict presence-absence basis as it was for *Campostoma* and bass, for even the most barren pools contained some algae, particularly along pool margins <10 cm deep where *Campostoma* did not graze frequently. We imposed an arbitrary rule on algal survey data, calling algae in pools "absent" if >80% of the sites sampled within a given pool had algae <2 cm high. Using this criterion, algal standing crops and *Campostoma* were significantly complementary on 8 and 19 November 1982 and on 5 September 1983 ($P = .025$, .05, and .002, respectively; Fisher's Exact Test). On the two June dates, algae and *Campostoma* were not complementary. On 13 June, just before a large flood, four pools that contained *Campostoma* also had well-developed standing crops of algae, with 27, 53, 67, and 93% of their sampled sites bearing algae >2 cm high. On 18 June, 4 d after the flood, none of the 14 pools had conspicuous algae.

Campostoma addition

The side of Pool 5 to which *Campostoma* were added initially had more algae than the side lacking *Campostoma* ($P < .00003$, Mann-Whitney U test; Fig. 2). Within 3 d the standing crop of algae on the side with *Campostoma* was significantly reduced ($P = .025$, Wil-

coxon Matched Pairs Signed Ranks Test). Because our experimental treatments were not independently replicated in different pools, we cannot infer that changes in algal standing crops were caused solely by the presence or absence of *Campostoma*. We give statistical comparisons to show that despite spatial heterogeneity with pools or pool halves, detectable differences in algal standing crops did arise over the course of our experiments. Differences were not detected in algal standing crop on the side without *Campostoma* over this period. Over the next 6 d, algae on the side with *Campostoma* declined in average height (Fig. 2). Average height then remained similar until the experiment was terminated on 13 October. In the half of the pool lacking *Campostoma,* average algal height increased (Fig. 2). By 3 October, the algae on the side lacking *Campostoma* was significantly higher than it had been on all previous dates ($P < .001$, Wilcoxon Test), and was also significantly higher than average algal height on the side with *Campostoma* ($P < .05$, Mann-Whitney U test). Increase in algae on the side without *Campostoma* may
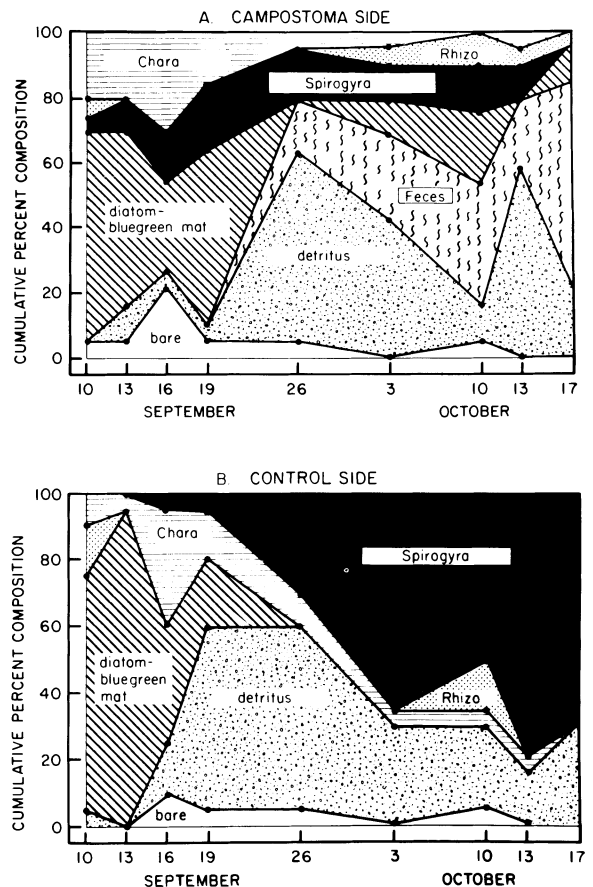

FIG. 3. Cumulative percentage of sample points with given cover in the divided Pool 5 over the course of the bass removal–*Campostoma* addition experiment. Rhizo = *Rhizoclonium.* Bass were removed from the entire pool and minnows added to one side.
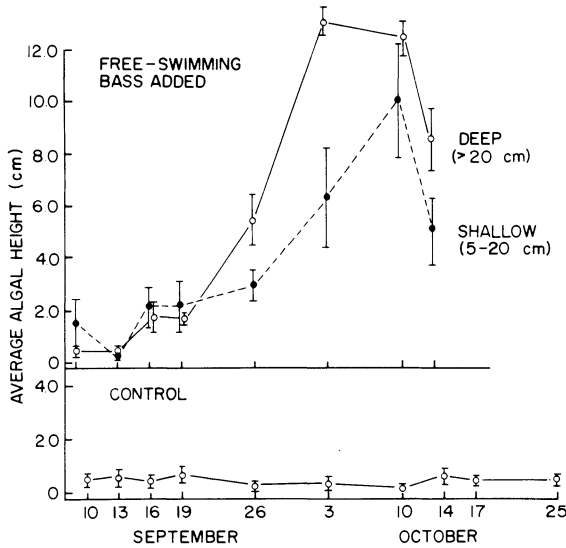
FIG. 4. Algal standing crops in Pool 9 over the course of the experimental addition of bass to this *Campostoma* pool. Points are means from 12–14 measurements from shallow sites (5–20 cm deep) and from 23–29 measurements from deep sites (21–60 cm). Vertical bars indicate ± 2 SE.

have occurred in response to an increase in availability of nutrients following mid-September rains.

On both sides of Pool 5, composition of algae changed during the course of the experiment (Fig. 3A, B). When the experiment started on 10 September, the predominant algal assemblage on most pool substrates was a thick, yellow-olive mat that sometimes sloughed from the substrate and floated on the water surface. This mat was a mixture of bluegreen filaments (predominantly *Oscillatoria*), with diatoms second in abundance (*Cymbella, Fragilaria, Synedra, Achnanthes, Navicula,* and *Gomphonema* were the most abundant genera), and senescent filaments of *Spirogyra* and *Rhizoclonium.* As Fisher (1983) noted for algae in an Arizona stream, such algal mats contain various species that appear elsewhere in the stream community, but the relative proportions of species and the gross, macroscopic features of the assemblages are characteristic and repeatable, so that treating them as ecological units is justified. *Spirogyra* and *Rhizoclonium,* the dominant algae in Brier Creek at other times of year, had died back when we started the experiments in September 1983. Where present, they were largely senescent: faded in color, with fragile filaments. *Spirogyra and Chara* had produced zygotes and fruiting bodies, respectively. Much of the *Chara* and *Rhizoclonium* that was present was covered with epiphytes. As these substrate algae decayed and collapsed, their epiphytes appeared to become incorporated into the mat.

Over time, the diatom-bluegreen mat senesced and was the source of much of the detritus that accumulated in pools from 19 September to 3 October (Fig. 3A, B). Spates (minor floods) in mid-September may have re-

leased nutrients to the water column and triggered regrowth of *Spirogyra.* In addition to local growth of *Spirogyra* intertwined within the decomposing mat, clumps of *Spirogyra* (and to a lesser extent, *Rhizoclonium*) became detached from upstream substrates and were carried into the pool during small spates. On the side of Pool 5 lacking *Campostoma, Spirogyra* increased markedly and by 3 October covered most of the pool substrate. On the side with *Campostoma,* however, the bloom of *Spirogyra* did not occur. As evidence that *Spirogyra* on the experimental side of Pool 5 was controlled by *Campostoma* grazing, green *Campostoma* feces composed mainly of intact filaments of *Spirogyra* appeared on and after 26 September. By 3 October, the side of Pool 5 lacking *Campostoma* was largely covered with a dense growth of *Spirogyra.* On this date, the proportion of sampling sites with *Spirogyra* was greater on the side without *Campostoma* than on the side with *Campostoma* ($P <$ .005 from a t test on arcsine square-root transformed data), and it remained so ($P <$ .025) until the end of the experiment. On and after 3 October, the side lacking *Campostoma* appeared similar to other stream pools that contained bass and lacked *Campostoma,* while the *Campostoma* side was relatively devoid of algae, contained large amounts of detritus, and appeared grossly similar to unmanipulated *Campostoma* pools.

Unmanipulated Campostoma *pool*

Although regrowth of *Spirogyra* occurred in stream pools lacking *Campostoma,* no increase in *Spirogyra* or other alage was observed in the unmanipulated *Campostoma* pool (6B) over the 2-mo experiments (Figs. 2 and 4). This constancy suggests that in control Pool 6B, as on the side of Pool 5 containing *Campostoma,* grazing pressure exerted by the minnows was sufficient to forestall autumn algal blooms that might otherwise have occurred. The density of *Campostoma* present in unmanipulated Pool 6B (3.1 individuals/ m²) was greater than that on the experimental side of Pool 5 (1.4 individuals/m²) and in Pool 9 (0.8 minnows/m²). This density difference and the shorter exposure of the experimental pools to *Campostoma* grazing may account for the lower standing crop of algae in the control vs. the experimental pools.

Bass addition (September–October 1983)

Before bass were added to Pool 9, the *Campostoma* spent most of their time over a bedrock platform in the deepest part of the pool (60–70 cm deep; Table 1). Within 2.7 h after the three bass were added, the *Campostoma* had moved from deep areas in the pool and the bass took positions over the bedrock platform. After the 1st d, bass were observed either hovering over the bedrock platform, or patrolling shoals, oriented toward the minnow school and making occasional drives at it. During a spate that elevated stream stage 17 cm on 15–16 September, the bass escaped

from Pool 9. Within 24 h we replaced them with bass of identical size (probably the same individuals), captured in Pool 8 by seining.

After bass addition on 9 September, *Campostoma* moved first to a pocket 20 to 30 cm deep near the upstream end of the pool. By the next day, the *Campostoma* had left the upstream pocket, perhaps because of a water snake (*Nerodia* sp. ≈70 cm long) that we observed under a nearby boulder. On one occasion, we also sighted one of the bass in the pocket. After moving out of the pocket, the *Campostoma* school settled in very shallow shoals (5–20 cm deep) near the pool's downstream end, where they had not formerly been seen. Over the 5 wk of the experiment, the numbers of *Campostoma* we sighted in Pool 9 dwindled. Bass are known predators of *Campostoma* (Gunning and Lewis 1956, Lennon and Parker 1960, Funk and Fleener 1974, Scalet 1977). In addition, as harrassment by bass continued, *Campostoma* spent less time grazing, and more time hiding under cobbles. When Pool 9 was censused by snorkeling at the end of the experiment, we found 11 *Campostoma* hiding under cobbles that we had not seen during bankside observations made the last few weeks of the experiment. This behavior was never observed in *Campostoma* in pools that lacked bass. (We would have detected minnows under cobbles during snorkeling censuses.)

In addition to changing their microhabitat and behavior in response to bass, *Campostoma* emigrated. On 24 September 1983, we recovered seven *Campostoma* from the blocked upstream portion of Pool 8. This number may underrepresent the amount of emigration that actually occurred, as the block net was displaced during the spate on 15 September, and *Campostoma* emigrating at that time would have escaped our detection.

Overall, attached algae in Pool 9 increased after we added the three bass (Fig. 4). The standing crop of algae in shallow water (5–20 cm deep, Fig. 4) initially decreased from 9 to 13 September, when *Campostoma* were first sighted in shallow areas following their displacement from deeper areas by bass. Over this 4-d period, the reduction in algal standing crop in these shallow areas was significant ($P = .05$, Wilcoxon Paired-samples Signed-ranks Test). On the deeper substrates occupied by bass, algae increased; standing crop in the deeper areas was significantly higher by 26 September ($P < .025$, Wilcoxon Test). As numbers of grazing *Campostoma* in shallow water dwindled, algal standing crop there also recovered. By 26 September, algal standing crop in the 5–20 cm depth stratum was significantly greater than it had been on 13 September ($P = .025$, Wilcoxon Test). Algal standing crop in shallow water was significantly lower than standing crop in deeper water on 26 September and 3 October ($P < .005$, Mann-Whitney U test), but by 10 October the difference was no longer significant ($P = .12$, Mann-Whitney U).

TABLE 1. Depth distributions of *Campostoma* before and after bass addition in June 1984. Numbers are scan samples in which *Campostoma* were sighted in depth interval.*

	Depth interval (cm)			
	<20	20–30	30–40	>40
Adult *Campostoma* (4–8 cm SL)				
Before bass	0	2	2	16
After bass	9	15	2	0
Small *Campostoma* (2–3 cm SL)				
Before bass	4	2	1	7
After bass	17	3	0	0

* When *Campostoma* occurred in different depth intervals during a single scan, a weighted average depth was computed. For adult *Campostoma* this occurred during two scans before and one scan after bass addition. For juveniles, weighted average depths were computed for three scans before and one scan after bass addition.

Bass addition (June 1984)

Before the second bass-addition experiment, a snorkeling census of Pool 9 revealed 74 adult *Campostoma* (4–8 cm SL) and 35 juveniles (2–3 cm SL). Juveniles were assumed to be young of the year, as no *Campostoma* this small had been seen the previous autumn. The two "escape ports" (adjacent, netted-off sections of Pools 8 and 10) initially contained no large *Campostoma*, although 30 and 25 juveniles were observed in the upstream and downstream ports, respectively.

Behavior of bass and adult *Campostoma* in this experiment was similar to that observed in the autumn 1983 experiment. Before bass were added, large *Campostoma* were sighted most frequently in loose aggregations, feeding on cobble and bedrock substrates in deeper parts of the pool (>40 cm, Table 1). Juvenile *Campostoma* were sighted in deep and shallow water with about equal frequency (Table 1). Two largemouth bass were added at 1030 on 11 June. Within 1 h, *Campostoma* had moved to shallow areas of the pool, and avoided deep water for the duration of the experiment (Table 1). Shifts to shallower areas of the pool were highly significant for both large and small *Campostoma* ($P < .0005$ and $< .005$, respectively, Kolmogorov-Smirnov Test; Siegel 1956: 135).

Average per capita feeding rates of large *Campostoma* declined significantly after bass addition, from 10.8 bites/min (SE = 2.3, $n = 35$) to 3.2 bites/min (SE = 1.3, $n = 34$) ($t = 3.22$, $P < .005$). The reduction in individual feeding rate coincided with a group shift from feeding in loose aggregations to tight schooling and milling. Differences in feeding rates for juvenile *Campostoma* before (31.1 bites/min) and after (20.5 bites/min) bass addition were not significant.

On 11 June at 1645, 6 h after the bass were added, 40 adult *Campostoma* were in the upstream escape port. Over the following week, numbers of large "emigrants" in this escape port varied between 25 and 40, as individuals moved between Pools 9 and 10. The blocked portion of Pool 10 was shallow (maximum

depth 22 cm) and lacked cover. Large *Campostoma* in this port milled and pushed against the upstream fence, and were easily frightened back into the riffle and the deeper waters of upstream regions of Pool 9. Three large *Campostoma* were in the downstream escape port at 1120 on 16 June, 5 d after bass addition. The lower rate of emigration of large *Campostoma* via riffles leading to the downstream port was possibly due to the shallowness of the riffle; the thalweg (deepest part of the channel cross-section) of the downstream riffle was in places only 3 cm. The minimum thalweg of the upstream riffle was 4 cm, and it contained more cover (rock rubble) than the downstream riffle.

When the experiment was terminated by removing the two bass at 1206 on 17 June, 31 large *Campostoma* and 23 small *Campostoma* were found in Pool 10, 33 large *Campostoma* and 20 juveniles in the upstream escape port, and 40 juveniles in the downstream escape port. Ten large *Campostoma* and 13 juveniles were unaccounted for, and were presumed to have been eaten by the bass. At the end of the experiment, algal standing crop in shallow areas of Pool 9 (<30 cm deep) was not significantly different from that found before bass were added. In deeper water, however, standing crops had become significantly higher ($P < .01$, Wilcoxon Test), due to the development of a 2–10 mm high "fuzz" of diatoms, *Rhizoclonium* and *Spirogyra*, on bedrock and cobbles that were formerly bare.

DISCUSSION

Processes that govern the distribution of algae, bass, and *Campostoma* among pools in Brier Creek operate on three different spatial scales. First, biotic processes (local algal growth, *Campostoma* grazing and predator avoidance, predation by bass) affect standing crops and distributions of fish and algae within pools. Second, movements of bass, minnows, and drift algae from pool to pool may alter within-pool patterns. Third, seasonal and successional changes and fluctuations in stream discharge have large-scale effects on biota of long reaches of stream.

Stream processes acting over different spatial scales clearly interact. For example, movements and drift that redistribute fish and algae among pools are more likely to occur during periods of high stream discharge. Depletion of food within pools may provoke emigration of bass or *Campostoma*, as Fox (1977) has suggested for stream insects.

Our results (this study, Power and Matthews 1983) suggest that local biotic processes: grazing, predation, and predator avoidance, exert strong, rapid effects on the distribution of *Campostoma* and algae within pools. These within-pool processes contribute strongly to a recurrent pattern that develops in Brier Creek between major flood events. Pool-to-pool complementarity of bass and *Campostoma* throughout the year, and of *Campostoma* and algae in late summer and autumn, recurred despite changes in the composition of specific

pools. State changes, observed 21 times in 7 censuses of 14 pools, occurred within weeks or months, suggesting that when complementarity of bass and *Campostoma,* or *Campostoma* and algae were disrupted, the within-pool dynamics that restored the pattern were rapid. While we cannot directly extrapolate from experimental results obtained in single pools to account for patterns and dynamics observed in our study reach, our manipulations do show that when bass or *Campostoma* are transferred into new pools, changes in algal standing crop (recovery or depletion) proceed rapidly. *Campostoma* were able to reduce algae to low levels within 9 d of their introduction to Pool 5. Bass displaced *Campostoma* from deep to shallow areas in Pool 9 2 h and 40 min after their introduction in September 1983, and changes in the distribution and activity of *Campostoma* caused by bass led to increases in algae within 1 wk. Similar rapid dynamics were demonstrated in June 1984, when large *Campostoma* shifted to shallower water, reduced their feeding activity, and emigrated within 24 h after bass were added. The within-pool processes demonstrated by our experiments proceed at rates sufficient to account for similar abrupt state changes observed in the natural stream.

The strong influence of predation, predator avoidance, and grazing on biotic pattern in Brier Creek appears related to long periods of relatively constant low discharge in this stream. At low discharge (0.01–0.02 m³/s), pools in Brier Creek typically are separated by long, shallow riffles. The riffles effectively reduce pool-to-pool movements of fish and drift algae that would disrupt complementarity patterns. Furthermore, during periods of low discharge, stream pools are smaller and have less structural complexity. Consequently, if patterns are disrupted, biotic processes can potentially restore them rapidly.

Biotic interactions become less important in streams when scouring floods or episodes when the stream dries completely are frequent (e.g., Fisher 1983, Schlosser 1983). During large floods, algae in Brier Creek are scoured from most stream substrates, and recover conspicuous standing crops only after 4–5 wk (M. E. Power and A. J. Stewart, *personal observation*; see also Fisher et al. 1982). Conversely, during periods of extreme low water, algae on previously submersed substrates become stranded and die. More moderate increases in discharge following small spates appear to stimulate algal growth, perhaps by increasing available nutrients. When nutrients are abundant, algal growth rates in Brier Creek may exceed the ability of *Campostoma* to deplete them. This condition may have held in early June 1983, when pools containing *Campostoma* also supported large standing crops of algae. Seasonal changes in phenology, daylight, or water temperature may also influence algae over large reaches of Brier Creek.

Pool-to-pool complementarity of bass and *Campostoma,* and of *Campostoma* and algae, emerge and per-

sist in Brier Creek both because responses to predation, predator avoidance, and grazing are rapid, and because major and minor disruptive processes (floods and pool-to-pool movements, respectively) are infrequent. If dynamics of within-pool processes that lead to complementarity are rapid, and if between-pool movements that disrupt the pattern are infrequent, the probability of observing this pattern in a stream inhabited by bass, *Campostoma,* and algae is high. Conversely, if predation, grazing, or predator avoidance within pools is less intense, or if disruptions are frequent, the probability of observing complementarity in streams with bass and *Campostoma* is correspondingly lower. Our preliminary data from a number of Oklahoma and Arkansas streams indicate that *Campostoma*-bass complementarity does not occur among pools in larger streams. For example, in the Baron Fork of the Illinois River, *Campostoma* and bass frequently co-occur in pools. The Baron Fork is a fourth-order channel with deep riffles, a much greater discharge than Brier Creek, and large, spatially complex pools. These pools may have sufficient volume or physical (or biotic) complexity to delay local extermination of *Campostoma* by bass, a phenomenon well known in other predator-prey interactions (e.g., Huffaker 1958). In addition, the dominant bass in Baron Fork is the smallmouth (*Micropterus dolomieui*), which may prey on crayfish (abundant in the Baron Fork) in preference to fish (Lewis and Helms 1964, Carlander 1977, *personal communication* from local fishermen). Prolonged within-pool dynamics in large, complex pools, and movements of fish among pools through deep riffles may preclude the development and maintenance of distinctive "*Campostoma*" and "bass" pools in streams like the Baron Fork.

Theoretical models predict that coexistence of predators and prey is favored when dispersal rates of prey exceed those of predators (Murdoch and Oaten 1975, Hastings 1977, 1978, but see Crowley 1981), or when prey are highly mobile and predators migrate only during restricted periods (Maynard Smith 1974). Dispersal of predators and prey in streams may be strongly, but differentially, influenced by discharge. Because stream discharge varies markedly over space and time, studies of predator-prey interactions in streams may provide useful tests of these models in natural systems.

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