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16. Grazing Fishes as Components of North American Stream Ecosystems: Effects of *Campostoma anomalum*

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Abstract

Algivorous fishes in North American streams have been largely overlooked by ecologists. Our work indicates that a widespread and abundant grazing minnow *(Campostoma anomalum)* can strongly influence distribution or standing crop of attached algae in streams; they thus have the potential to significantly impact biological processes fundamental to stream ecosystems. Studies of this species in a southcentral Oklahoma prairie-margin stream (Brier Creek) showed that: (1) *Campostoma* can control the pool-to-pool distribution of algae, and (2) the presence of predators *(Micropterus)* influences the distribution of *Campostoma.* Other streams in the Ozark and Ouachita uplifts in Oklahoma and Arkansas showed very different patterns of *bass-Campostoma-algae* distributions. In Ozark and Ouachita streams, *Campostoma* were larger, more abundant, and foraged more freely than in Brier Creek. Grazing by *Campostoma* in Ozark and Ouachita streams appears to have a strong influence on the kinds and standing crops of attached algae. We review the distribution of other potentially important algivorous North American stream fishes and outline certain interactions between grazing fishes and other ecosystem components that a priori are likely to be important.

Recent reviews and conceptual syntheses of stream ecology (Vannote et al., 1980; Barnes and Minshall, 1983; Fontaine and Bartell, 1983) have illuminated the historical dichotomy between those stream ecologists who study fishes and those who do not. These important publications include only two chapters specifically addressing stream fishes, plus a few basic statements about longitudinal distribution patterns of fish in streams. Much contemporary literature in stream ecology ignores the fact that large, active, and abundant fishes may play important roles in system-level processes in streams. Most authors have failed to consider the role that herbivorous fishes can potentially play in influencing the distribution or standing crops of periphyton, the sites or rates of primary production, or the processing of organic matter, as observed for grazing or scraping invertebrates by Cummins (1978), Gregory (1983), and McAuliffe (1984).

Important interactions occur between grazing fishes and their plant "prey" in marine habitats such as reefs (Lobel, 1980; Montgomery, 1980; Montgomery et al., 1980; Sammarco, 1983; Meyer and Schultz, 1985), sea-grass beds (Weinstein et al., 1982), intertidal zones (Lubchenco, 1982; Miller, 1982), and tropical freshwaters (Lowe-McConnell, 1975; Goulding, 1980; Power, 1983, 1984b). Hynes (1970) described much of the basic ecology of stream fishes but included little information on the ecology of grazing fishes. Several studies have suggested the importance of carnivorous or detritivorous fishes at the ecosystem level in North Temperate waters (Juday et al., 1932; Hall, 1972; Rickey et al., 1975; Durbin et al., 1979). Nevertheless, native grazing fishes have remained largely ignored as components of temperate stream ecosystems; most studies of organic-matter processing continue to focus on activities of invertbrates, fungi, or bacteria.

At least 42 species of stream fish in North America are largely herbivorous; 24 of these species feed predominantly by grazing attached algae (Lee et al., 1980). Several species (e.g., *Cyprinodon* spp. and *Gila* spp.) occur only in spring or sinkhole systems in the western United States. However, these restricted species are often abundant where they occur and can rival invertebrates as consumers of attached algae or higher plants. Some large, abundant catostomids that are primarily herbivorous (e.g., *Catostomus santannae,* which occurs in four river systems of southern California) can comprise a large part of the biomass of certain western streams.

Many species of algivorous minnows occur in the eastern half of the United States. Some, such *as Notropis pilsbryi and Notropis cerasinus,* occasionally have large quantities of filamentous algae in their guts (Matthews et al., 1979; Surat et al., 1982), although in such cases algae likely are consumed incidentally with aquatic insects. Others, such as *Notropis nubilus, Phoxinus erythrogaster*, and *Phoxinus cumberlandensis*, feed almost exclusively on algae, which they scrape from the surfaces of rocks. Several of these minnows are among the most abundant fish species in their respective habitats.

The most abundant and widespread algivorous minnows in eastern and central North America are in the genus *Campostoma. Campostoma anomalum* ranges across more than half of North America (Burr, 1980a). *Campostoma oligokpis* occurs in the uplands of the Midwest and in the Tennessee River and Mobile Bay drainages, and *Campostoma pauciradii* is found in eastern Gulf Coast drainages (Burr and Cashner, 1983). *Campostoma anomalum* is a large minnow (to 230 mm [SL]) that can be extremely abundant in small or medium-size streams, sometimes dominating the fish community numerically and on the basis of biomass (cf. Lennon and Parker, 1960; Beets, 1979). In one pool (about 100 m long) in an Ozark stream, for example, our snorkeling surveys have provided estimates of more than 5,000 *C. anomalum*, many more than 120 mm total length.

In this chapter we summarize our studies of the ecology of *C. anomalum* and attached algae in streams of the Midwest. We recapitulate studies involving interactions between the grazer and its food and describe a three-trophic-level interaction in which predators (bass) control distributions of *Campostoma* and, indirectly, attached algae. We also present new data providing a broader view of predator-*Campostoma*-algae relationships in several midwestem streams and offer explanations for differences in the patterns observed in different stream systems. Finally, we speculate from preliminary data about the ecological significance of *Campostoma* (and other grazing fishes) in North Temperate stream ecosystems.

Campostoma Anomalum In Brier Creek, Oklahoma

Brier Creek, in south-central Oklahoma, is a small prairie-margin stream of the Red River drainage. A 1-km mid-reach section consisting of a series of 14 pools and their attendant riffles contains a substantial number of *Campostoma anomalum*; this section of stream serves as the site for studies by our research group.

Power and Matthews (1983) noted that *Campostoma* influenced standing crops of attached algae in this stream reach. Four of the 14 sequential pools in the study site contained large schools (50-400 individuals) of *Campostoma* and lacked large predatory fishes. These "*Campostoma* pools" were essentially devoid of algae except along shallow pool margins. Nine other pools lacked *Campostoma* and contained 3-8 large (>70 mm SL) largemouth *(Micropterus salmoides)* or spotted *(Micropterus punctulatus)* bass. All these "bass pools" had prominent growths of filamentous green algae (primarily *Spirogyra* sp. and *Rhizoclonium* sp.). Bass and *Campostoma* co-occurred in only one relatively large pool. Bass occupied deeper areas of the pool, and *Campostoma* occupied shallower areas. Within this pool attached algae occurred in deep areas where bass patrolled but not in shallow areas occupied by *Campostoma.* As far as we know, this was the first indication in a freshwater stream that piscivorous fish could influence distribution of a smaller herbivorous fish, which in turn influenced the distribution of attached algae.

We (Power and Matthews, 1983) transferred various algae-covered substrates from bass pools to a *Campostoma* pool to assess short-term grazing impacts of *Campostoma. Campostoma* immediately swarmed to and actively fed on all these new algae-covered substrates but virtually ignored bare control cobbles relocated within the same pool. Algal biomass on the transferred substrates was dramatically and rapidly reduced; in 24 h ash-free dry weight of algae on the cobbles was <25% of its initial value.

In the initial study we also showed that bass could alter the use of habitat by *Campostoma.* Algae-covered substrates were again transferred into a *Campostoma* pool, and these substrates were actively grazed by these minnows. A largemouth bass (300 mm SL) was then tethered near the algae-covered rock with a line attached to its lower jaw. Over the next four days the tethered bass effectively "guarded" the transferred algae-covered cobbles; similar cobbles placed 1.3 m away were grazed frequently by *Campostoma.*

Five other snorkeling surveys of fish in the Brier Creek study reach were made in 1983. The occurrence (presence-absence) of bass and *Campostoma in* the 14 pools was inversely related in all but one of these censuses (Power et al., 1985). Bass and *Campostoma* co-occurred in more than 2 of the 14 pools on only two occasions—after major floods. In late summer and in both autumns of the study algae and *Campstoma* were inversely distributed in the pools. However, during spring some algae (predominantly *Spirogyra)* accumulated despite grazing by *Campostoma and became* conspicious in most pools.

Algae were also intermittently scoured from most stream substrates by large floods. During and immediately after periods of high discharge, then, algal standing crop may have little relation to distribution of grazers (cf. Fisher et al., 1982; Power and Stewart, in press). However, during extended periods without floods (i.e., "normal" low-flow regimes), grazing by *Campostoma* in Brier Creek establishes a clear and recurrent pattern: there is a markedly lower standing crop of algae in Brier Creek *"Campostoma"* pools than in pools that lack *Campostoma.*

Grazing by *Campostoma* can apparently regulate standing crops of attached algae, even when *Campostoma* densities are somewhat less than normal. In autumn 1983 a pool containing bass and large quantities of attached algae was split longitudinally by a plastic fence, and we removed the bass and all large sunfish by electroshocking (Power et al., 1985). We stocked *Campostoma* on one side of the pool (at a density slightly less than that found in most *Campostoma* pools) and left the other side of the pool (and another, nonmanipulated *Campostoma* pool) as a control. Over the next five weeks attached algae on the *Campostoma* side of the pool declined rapidly and remained low for the duration of the experiment. On the side of the pool lacking *Campostoma*, a bloom of algae (largely *Spirogyra)* occurred. During the experiment filamentous green algae were conspicuous in other pools of the reach that lacked *Campostoma*, but not in pools containing *Campostoma.*

Two other experiments in 1983 and in 1984 evaluated the impacts of predators (largemouth bass) on the distribution and use of habitat by *Campostoma*. In these experiments (Power et al., 1985) we added largemouth bass to a pool containing a school of *Campostoma*. In both experiments addition of bass resulted in immediate changes in habitat used by *Campostoma:* some emigrated from the pool, and others moved to shallow-water areas near the margin of the pool. *Campostoma* remaining in the pool after bass were added spent significantly less time feeding and more time hiding among cobbles than they did in the pool before bass were added. Substantial regrowth of attached algae occurred one to two weeks after addition of bass in both experiments.

Collectively, our observations and experiments in Brier Creek indicate that during periods of normal flow (1) *Campostoma* can regulate standing crops and distribution of attached algae and (2) bass can influence distribution of *Campostoma*, both within and among pools. The results from the Brier Creek study suggested two broader questions: First, are the patterns evident in Brier Creek typical of those in other stream systems in the Midwest? Second, does grazing by *Campostoma have* predictable effects on stream algae and stream ecosystem processes? We address these questions below.

Stream Surveys of Bass-Campstoma-Algae

In September 1983 and in June—July 1984 we quantified distribution of bass, *Campostoma,* and algae in two Ozark uplift streams and in a stream in the Ouachita Mountains of LeFlore County, Oklahoma (table 16.1). In April 1984 we conducted a similar survey in Brushy Creek (Johnston County, Oklahoma), and in July 1984, we surveyed Tyner Creek (Adair County, Oklahoma). In all of the surveys Matthews snorkeled slowly upstream through each pool, recording numbers of *Campostoma* and numbers and species of *Micropterus;* sizes of all bass were estimated to the nearest inch total length (TL). Algal height and composition were determined by Stewart and Power (September 1983—April 1984), who used methods described in Power and Matthews (1983). In July 1984 algae were asssessed more rapidly by scan surveys. In each pool numbers of invertebrates were estimated by having one person spend 10 minutes picking organisms from all available kinds of substrates with forceps.

In Brushy and Tyner Creeks (table 16.2) so few bass were present that these streams appear to represent *Campostoma* distribution in essentially predator-free environments. In these two streams *Campostoma* were present in relatively low numbers but were widely distributed in almost all pools. One exception was that no *Campstoma* occurred in the four most densely shaded pools of Tyner Creek where substrates on the stream bed were virtually devoid of algae. In all other surveyed pools at least thin, slick coatings of epilithic diatoms occurred on submersed rocks. In the four canopied pooh of Tyner Creek rocks were not even slippery to the touch, suggesting that *Campostoma* may avoid areas of extremely low primary productivity.

One Ozark stream (War Eagle Creek) and the Ouachita Mountain stream (Big Eagle Creek; table 16.2). had intermediate densities of bass *(Micropterus* > 150 mm TL in 17-50% of all pools; some pools had as many as 8 bass). In these two streams, however, *Campostoma* were present in virtually all pools, including those with bass (table 16.2). The second Ozark uplift stream (Baron Fork, in northeast Oklahoma) had the largest number of bass per pool that we observed in these stream surveys (table 16.1). Despite the presence of 20 or more bass in some Baron Fork pools, however, *Campostoma* remained abundant. Even a brief inspection of table 16.1 shows that the strong "Brier Creek type" of pool-to-pool complementarity of bass and *Campostoma* does not occur in streams we surveyed in the Ozark and Ouachita mountains; there bass and *Campostoma* distributions among pools were independent ($x^2 = 0.942$; $P = 0.33$; 2 x 2 contingency analysis). Of 86 pools surveyed outside Brier Creek, *Campostoma* occurred without bass in 51 pools but co-occurred with bass (> 150 mm TL) in 29 pools.

At least three factors could account for the lack of a *bass-Campostoma* complementarity pattern in streams of the Ozark and Ouachita uplands: (1) pool size, (2) ease of movement across riffles between pools, and (3) aspects involving prey size and/or predator capabilities. Some Ozark-Ouachita stream pools may simply be too large to be effectively patrolled *even* by several bass. In larger Ozark pools bass often occupied deeper portions of the pool, while schools of *Campostoma* remained near the substrate on gravel slopes at distances > 1m from larger bass.

Riffles connecting Ozark pools are deep (often 10-15 cm) compared to those in Brier Creek (2-4 cm). Hence most riffles in Brier Creek can preclude movement of large fish like bass at normal flow; but *Campostoma* and bass can readily traverse most riffles in the Ozark-Ouachita streams. Formation and maintenance of *bass-Campostoma* complementarity in Brier Creek may therefore depend in part on restricted movement of fish between pools (which allows time for attrition of *Campostoma)* or on more frequent pool-to-pool movement of prey *(Campostoma)* than of predators (bass).

The specific type of predator and size of prey may also influence *bass-Campostoma* interactions in Ozark streams. Most bass in Ozark and Ouachita streams are smallmouth bass *(Micropterus dolomieui)* (table 16.1), which have relatively smaller mouths than largemouth bass. Additionally, smallmouth bass typically eat crayfish more often than fish (Lewis and Helms, 1964; Carlander, 1977), although they do *feed* on a variety of minnows (Scott and Crossman, 1973). In this context it may also be important *that Campostoma* in virtually all the Ozark and Ouachita streams are larger than those in Brier Creek. To date we have used nondestructive census methods and thus lack precise length-frequency data for *Campostoma in* these streams. However, the same individual (Matthews) has made all snorkeling observations, standardizing the estimates to a large degree. *Campostoma* larger than 150 mm TL are very rare in Brier Creek; the largest individuals we have collected there are about 125 mm TL. In Ozark streams schools of *Campostoma* (often 100-500 individuals) frequently consist of individuals 125-150

Table 16.1. Numbers of Campostoma (Minnows), Bass (by Size, Class, **TL**), and Invertebrates in Pools of Streams in Oklahoma and Arkansas

Stream (Date)	Pool													
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Brushy Creek (April 1984)														
Campostoma	0	9	19	18	17	10	19	30	32	82	5	1	9	
SMB* 150-250 mm														
SMB 0250 mm														
L IB†≥150 mm				1										
Invertebrates	18	32	31	39	20		24	22	20	39	21	53		
Tyner **Creek** (July 1984)														
Campostoma	540	110	13	104	23	17	0	0	0	0	23			
SMB 150-250 mm		1									1			
SMB •**250** mm														
LMB□50 mm														
Invertebrates	25	16	21	11	25	13	32	33	‡	‡	‡			
War Eagle Creek (September 1983)														
Campostoma	630	0	800	503	3,000	500								
SMB 150-250 mm						6								
SMB •**250** mm														
LMB□50 mm														
Invertebrates														
War Eagle Creek (June 1984)														
Campostoma	210	33	22	202	210	1,820	120	765	310	25	109	655	254	
SMB* 150-250 mm				3		2						2		
SMB ’250 **mm**				4								1		
LMBt□50 mm														
Invertebrates	9	10	8	14	11	6	13	17	9	11	12	6	19	
Big Eagle Creek (September 1984)														
Campostoma	112	70	50	10	60	550								
SMB 150-250 mm	3				6	1								
SMB 250 mm	2				2									
LMB **≥150** mm														
Invertebrates	51	48	30	45	41	51								
Big Eagle Creek (July 1984)														
Campostoma	186	60	36	10	277	370	105	88	44	250	58	19	37	23
SMB 150-250 mm	3				7	2					2			1
SMB **250** mm														
LMB 0150 mm														
Invertebrates	9	13	‡	12	37	27	21	31	29	35	25		30	

Note: Numbers of **invertebrates** = **numbers** of **individuals** collected in 10 minutes of picking with **forceps** by one **investigator**.
•SMB smallmouth **bass.**
= **largemouth** bass.
‡**No invertebrate** sample taken.

Table 16.1. Continued

Stream (Date)	Pool													
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Baron Fork (September 1983)														
Campostoma	800	1,000	500	232	2,450	800	50	5,350	3,000					
SMB* ≥150–250 mm		7	3	1	38		6	20	17					
SMB **≥250** mm					6			7						
LMB ≥150 mm					2									
Invertebrates	76	95	107	111	136	134	70	99	91					
Baron Fork (July 1984)														
Campostoma	1,003	1,000	350	1	1,920	1,020	550	16	1,195	120	76	1,490	385	1,220
SMB 150-250 mm +					13	6	5	2	14			5		
SMB ot250 **mm**					8	1								
LMB **≥ 150** mm														
Invertebrates	7	19	18	44	19	46	30	32	42	20	33	25	30	35

mm TL, and specimens as large as 160-175 mm are not uncommon. Smallmouth bass, therefore, may be less effective predators on the large *Campostoma* in Ozark streams than are largemouth bass that prey on *Campostoma* in Brier Creek. In feeding experiments (April 1985) medium-sized smallmouth bass (ca. 250 mm TL readily ate *Campostoma* as large as those typical for Brier Creek.

Campostoma Behavior

Regardless of the ultimate causes, *Campostoma in* Ozark streams occur in most pools, where large individuals move and feed with little apparent restriction by predators. Understanding the feeding ecology of *Campostoma* permits greater insight into the potential consequences of such unrestricted grazing.

***Campostoma* typically feed in large schools, even at temperatures as low as 7° C (table 16.2). In Brier Creek pools with slow flow of water, *Campostoma* school when undisturbed. They browse substrates, but schools move little. In larger pools and in shallow areas of Baron Fork pools *where* flow is greater, schools of *Campostoma* exhibit a distinct pattern of grazing and movement. A school of about 200-500 individuals, for example, often grazes on algae attached to cobble or gravel. Individuals are typically about 10 cm apart, and most orient upstream. The school as a discrete unit often grazes in a given area for 1-2.5 min; members of the school then cease feeding in unison, drift 3-5 m downstream, and resume grazing. A series of such grazing-drifting sequences continues until the school is displaced a considerable distance downstream. Eventually fish in the school move upstream, and the entire grazing-drifting sequence is initiated again.**

The pattern is not always as consistent as described; sometimes *Campostoma* schools browse upstream into the current or show little net movement. However, repeated observations suggest that (1) the schools have discrete grazing patterns, (2) schools *graze* relatively large areas each day, and (3) within-pool grazing movements may depend on pool size, depth, and water velocity. The extent to which *Campostoma* grazing and movement depend on availability of algae or on predators, or what cues influence their behavior, remains unknown.

***Campostoma* have distinct feeding modes that appear to be influenced by availability of particular types of food. The most common feeding mode in Brier Creek, where** Campostoma **often forage in deposits of detritus or on epiphytes growing on *Chara,* is "nipping"; this mode is similar to that described for *Poecilia* (Dussault and Kramer, 1978). In nipping, *Campostoma* incline their bodies at about 45 to the substrate and take small, rapid bites. At times several individuals may take turns nipping at one small location on the substrate, suggesting that they are selective and that they receive foraging cues from each other. Detritus in Brier Creek *"Campostoma* pools" contains few high-quality food items (intact algal cells), and these pools also have a low algal standing crop. In such conditions selectivity would be beneficial.**

"Swiping" is the most common feeding mode displayed by *Campostoma* in Ozark streams. This mode is used to detach blue-green and diatomaceous algae growing as dense, 1-to 2-mm-thick felts on rock surfaces. In swiping, *Campostoma* position themselves above the substrate, hold their bodies rigid, manuever with rapid pectoral fin beats, and then strike the algae suddenly with sharp sideways thrusts of the head so that the cartilaginous lower jaw scrapes algae from

Table 16.2. Feeding Rates of ***Campostoma****

Date	Temp. (°C)	Location	SL (mm)	I	SE	*N*†
Nov. 1982	17	Brier Creek	50-60	16.7	1.5	28
Nov. 1982	17	Brier Creek	50-60	8.9	1.9	21
Dec. 1982	7	Brier Creek	50-60	11.2	2.1	10
Nov. 1982	10	Baron Fork	50-130	15.2	3.1	17
June 1984	25	Brier Creek	40-80	10.8	2.3	35

***Bites per** minute.

†**Number of individual fish** observed **and** dined.

the rocks. This feeding mode is physically more vigorous than nipping. Swiping leaves distinct grazing scars on rock, wood, or leaf substrates (Matthews et al., 1986). Often a fish makes two "swipes" in rapid succession, leaving a pair of grazing scars. Grazing scars are common where schools of *Campostoma* have fed.

A third grazing mode, "shoveling," is used by *Campostoma* when they feed on algae attached to large, smooth rock surfaces. In shoveling, *Campostoma* push their lower jaws against the substrate and swim forward, removing algae en route. *Campostoma* feeding in this manner make grazing trails several cm long; these trails are readily distinguished from the more meandering trails left by snails. Kraatz (1923) observed similar behavior of *Campostoma* feeding on diatomaceous mats on aquarium walls.

When grazing on blue-green algal felts, *Campostoma* do not remove algae down to the bare rock surface. Microscopic examination of typical scars indicates that the fish remove only the upper layers of algae and on epialgal layer of mucilaginous material heavily invested with bacteria. A thin film of algae (about 10% of the pregrazed crop) typically remains within the scars.

The grazing scars left by *Campostoma* often cover much of the available rock substrates where schools have recently worked. We (Matthews et al., 1986) quantified the number and sizes of grazing scars left by *Campostoma* in a pool with bedrock substrate and predominantly blue-green algal felts (Tyner Creek, Oklahoma). At depths of 10 to 59 cm the number of grazing scars attributable to *Campostoma* averaged 1,800 per m^2; these data included numerous sites in water < 20 cm deep, where there were few or no scars. At depths > 40 cm we found > 5,000 grazing scars per m^2. The size of individual scars was highly variable but averaged 0.57 cm^2 ($N = 90$). Thus across all depths in this part of Tyner Creek about 10% of the submersed substrate area exhibited evidence of grazing by *Campostoma*. In deeper areas with > 5,000 scars per m^2, as much as 28.5% of surface areas of substrate was, on average, recently grazed.

Consequences of Herbivory by *Campostoma*

Huge schools of *Campostoma*, some containing thousands of individuals, are common in some Ozark streams. Such streams show evidence of intense grazing by *Campostoma; the* grazing scars produced by these minnows often coalesce, covering most of the surface area of heavily grazed substrates. In Baron Fork of the Illinois River, *Campostoma* are extremely abundant, and the standing crop of algae is consistently low. Epilithic communities of algae in this stream are primarily slick, dark-colored blue-green felts 1-2 mm thick. Although thin, these felts are highly productive (0.6 g 02/m^2/h; Stewart, unpub. data), suggesting that the relatively low standing crop of algae (108-325 g dry weight/m^2) is more likely the result of biomass removal by grazing than of low rates of algal growth (cf. Gregory, 1983). On the basis of our censuses and observations to date, *Campostoma appear* to be the major herbivores in this and many other Ozark Mountain streams. What are the ecological consequences of intense herbivory by stream fishes?

Consequences of Herbivory by *Campostoma* to algae

In October 1984 we incubated glazed ceramic tiles in Fiberglas troughs in Baron Fork. The troughs permitted substantial through-flow of water but excluded *Campostoma*, snails, and crayfish. Chironomids gained access to the tiles, but their characteristic grazing pattern (a circular area cleared around their point of attachment) permitted areas they affected to be readily identified. In the stream outside the troughs, where *Campostoma* grazed heavily, the typical algal flora consisted of a 1- to 2-mm-thick felt of epilithic blue-green algae (largely *Calothrix*, *Phormidium* and *Oscillatoria* spp.). Tiles incubated within the troughs rapidly developed a diatomaceous flora dominated by *Melosira, Cymbella* and *Synedra* spp. (Power et al., unpub. data). When these tiles were moved to the stream bed, they were actively grazed by *Campostoma;* the diatoms turfs were within weeks replaced by blue-green felts. Conversely, natural felt-covered slate substrates transferred from the stream bed into the troughs were overgrown by diatoms within 4-10 days. *Campostoma* finally gained access to the ends of the troughs (because of sagging of the ends) and grazed on algae growing on the tiles. These grazed tiles also developed blue-green felts, thereby ruling out "trough effects" as a cause of differences noted for substrates exposed to and protected from grazing by *Campostoma.* These results show that (1) grazing by *Campostoma can maintain* low standing crops of algae on rocks of Ozark streams, and (2) grazing by *Campostoma* alters taxonomic composition of the algal community that develops.

That herbivory by *Campostoma* has the potential to regulate standing crops or kinds of stream algae during much of the year is suggested by all of our studies in Brier Creek and in streams of the Ozark region. Because grazing by *Campostoma* typically removes mainly the algal overstory, light and nutrients are more available to algae remaining within the grazing scars. Moderate intensities of grazing by *Campostoma* therefore stimulate primary productivity per unit algal biomass. Additionally, microscopic examination of *Campostoma* feces shows that some fraction of the ingested algae pass succcessfully through the gut and remain viable. Although we have some data suggesting that epiphytic diatoms suffer greater mortality than their filamentous green algal hosts in passage through the alimentary canal of *Campostoma*, additional data are needed before we can determine the consequence to algae of passing through the gut of *Campostoma. Campostoma* could conceivably benefit some filamentous algae (e.g., *Rhizoclonium*) by "stripping" them of encrusting epiphytes (cf. Lubchenco, 1983).

Campostoma feces contain both "regenerated" nutrients and viable algae; the feces accumulate in large quantities in deeper areas of all Brier Creek "*Campostoma* pools," and are reworked frequently by *Campostoma* when algae are scarce. Nutrient translocation as a result of fish activity is important in reef systems (c.f. Meyer and Helfman, 1983; Meyer and Schultz, 1985) and has been shown to be important in freshwater streams (Hall, 1972; Durbin et al., 1979). The significance of the accumulation of *Campostoma* feces to the ecology of algae that are not consumed or to those that are consumed but survive gut passage remains unknown.

To date we know little about relationships between *Campostoma* and the spatial distribution of algal biomass and productivity. In a tropical stream Power (1983, 1984) showed that densities of grazing catfish tracked algal productivity; catfish were seven times more dense in sunlit pools, where primary productivity was 6-7 times higher than in dark pools. Our data from Tyner Creek suggest that *Campostoma* are absent where extensive canopy cover limits algal growth. Although removal of algae by grazing and subsequent recovery of algae in previously grazed areas undoubtedly affects the way stream habitat is used by *Campostoma* and other stream algivores, data addressing these aspects are still unavailable; much remains to be learned about dynamics of grazing fishes and the distributions of algae in North American streams.

Consequences to Other Stream Biota

Periphyton communities provide refugia for a variety of invertebrates (Cuker, 1983), and removal of erect or foliose algae has important consequences to stream invertebrates. We found relatively similar numbers of invertebrates in pools with few or many *Campostoma in* the Ozark and Ouachita streams we surveyed (table 16.1), but the scale of our observations or our collecting techniques may have been inadequate to detect differences. Herbivory by *Campostoma* might influence stream invertebrates in two ways: first, grazing by *Campostoma* alters the standing crop and growth forms of algae and so alters the types or amounts of food or shelter available to grazing invertebrates; second, *Campostoma* could promote downstream drift of stream invertebrates if their disturbance of algae and rock substrates causes invertebrates to enter the water column. If *Campostoma* remove algae that harbors invertebrates or increases their emigration, a given stream reach may support fewer invertebrates and, therefore, be a less profitable place for insectivorous minnows to forage. Our snorkeling observations suggest that stream reaches containing many *Campostoma* have a lower diversity of other small fishes (compared to typical stream segments not dominated by *Campostoma),* but additional data in a range of stream types are needed to evaluate quantitatively the impact of high densities of *Campostoma* on fish-community structure.

Positive interactions between *Campostoma* and other fishes could also exist. For example, our snorkeling observations in numerous Ozark streams reveal that *Campostoma* and *Notropis pilsbryi* often occur in the same pools, in very close proximity or actually intermixed. Feeding opportunities for *N. pilsbryi* may be improved by the grazing activities of *Campostoma,* the former consuming invertebrates made available in the water column by grazing activities of the latter.

Consequences to the Stream Ecosystem

Grazing by *Campostoma* initiates a cascade of effects apparent at both large and small spatial scales. At the whole-stream level these effects can be expected to include large-scale changes in patterns of nutrient uptake, regeneration, and downstream transport; changes in overall rates of primary production and in the sites and rates of decomposition; and increases (or *decreases,* depending on flow regimes) in the degree of spatial heterogeneity of various biotic processes. We offer here speculations about the possible range and types of processes and conditions that herbivory by *Campostoma may* initiate and mantain in stream ecosystems.

Our observations and experiments imply that in Ozark streams such as Baron Fork schools of *Campostoma* generate and maintain "grazing lawns" (sensu McNaughton, 1984), much as herds of ungulates do on the Serengeti grasslands. The algal lawns maintained by *Campostoma* in Ozark streams consist largely of tightly attached blue-green algae (notably *Calothrix*) that have prostrate growth forms; like grasses, *Calothrix* has a "basal meristem" (most cell divisions occur just above the basal heterocyst; B. Whitton, University of Durham, England; pers. comm. with Stewart). This spatial "growth refuge" allows *Calothrix to* persist despite intense grazing by *Campostoma.* The *Calothrix* lawn that forms in response to grazing by *Campostoma* can be expected to alter large-scale nitrogen cycling characteristics of the stream, for *Calothrix* fixes N2, while diatoms (which flourish when *Campostoma* are excluded) do not. Because many blue-green algae can fix N2 and *because* nitrogen content of food is sometimes an important determinant of food quality for herbivorous invertebrates (Ward and Cummins, 1979) and fish (Hornet al., 1982; Horn and Neighbors, 1984), *Campostoma* may indirectly influence growth rates or use of space by other stream algivores such as crayfish, snails, and aquatic insects (see also Hart, 1985; McAuliffe, 1984).

Changes in algal community composition owing to grazing by *Campostoma* may also have consequences to the cycling of nitrogen and carbon at very small spatial scales. Microscopic examination of the blue-green algal communities dominating when *Campostoma* were present showed that many bacteria were attached to the mucilaginous sheaths of *Calothrix;* diatoms dominating when *Campostoma* were excluded supported visibly fewer bacteria. Jones and Stewart (1969) found that *Calothrix scopulorum* released combined nitgrogen compounds that were readily assimilated by various fungi and bacteria; other filamentous blue-greens do so also (Paerl, 1978). We do not yet know the extent to which bacteria influence nutrient and energy fluxes in Baron Fork, but Cole (1982), Newbold et al., (1983), and Currie and Kalff (1984) show that this possibility should not be overlooked.

The effects of *Campostoma* on nutrient cycling may change seasonally. In early spring, for example, *Campostoma* often grazed on bedrock substrates in shallow, fast-flowing areas of Brier Creek; these substrates supported visually uniform thin layers of attached diatoms dominated by species of *Synedra, Gomphonema,* and *Cymbella. Campostoma* feces were displaced from three areas by water currents and accumulated downstream in crevices and *deeper* pockets in microdepositional zones. Water level and velocity in Brier Creek decline in summer, and most riffles become so shallow that *Campostoma* no longer feed there. *Campostoma* then graze almost exclusively in deeper areas of pools; and owing to lack of downstream transport, their feces accumulate where feeding occurs. Over larger spatial scales herbivory by these minnows in summer lowers spatial heterogeneity of algae within pools ("*Campostoma* pools" are uniformly low in algae) but increases heterogeneity of algal biomass (and possibly growth) between pools ("*Campostoma pools*" versus "bass pools"). By late summer most "*Campostoma* pools" are so nearly devoid of algae that bare substrates predominate in sites that are frequently grazed; bare sites will alter sediment-water exchange characteristics for most nutrients (cf. Mulholland et al., 1983).

When primary productivity is nutrient-limited and the rate of regeneration of nutrients from *Campostoma* feces is low, sustained grazing may gradually lower productivity and distort normal patterns of nutrient spiraling in streams by converting nutrients into inaccessible forms. Conversely, if algae are nutrient-limited and regeneration of nutrients from *Campostoma feces proceeds* rapidly, moderate grazing may increase productivity by favoring algae with higher rates of turnover (see also Mulholland et al., 1983; and Hom, 1982). In streams where algae are not nutrient-limited, grazing by *Campostoma* could increase primary productivity by removing algal "overstories" that reduce light to understory communities or by altering feeding behavior of other algivores. Conversely, they may decrease total productivity on an areal basis if they remove excessive quantities of algal biomass or if they promote the development of algal lawns comprised of species with lower productivity but which persist by virtue of having polar cell division (such as *Gloeotrichia* or *Calothrix)*. In general, intense grazing by *Campostoma* will alter spatial distributions and relative intensities of biotic (algae and bacteria) and abiotic (exposed sediment) processes controlling nutrient uptake and release. The consequences of such changes to nutrient-spiraling characteristics at very large spatial scales (km reaches) remain unknown.

In the arguments above, a very fundamental question remains unanswered: How much of the ecological theory generated from studies of grazers in low-vectored terrestrial or lake systems (cf. Noy-Meir, 1975; McNaughton, 1979, 1984; McNaughton et al., 1982; Caughley and Lawton, 1981) can *be* applied directly to grazing processes in streams that include some factors that are strongly *vectored* by the flow of water? In aquatic ecosystems many of the obvious ecological consequences of grazing are immediately nutrient-related, because nutrient availability limits productivity in aquatic ecosystems more often than in terrestrial ecosystems (cf. Ricklefs, 1979). Nutrients released by stream herbivores can be effectively carried away from sites of nutrient uptake by the flow of water.

In summary, our studies to date suggest that *Campostoma,* as abundant, active algivores, may strongly influence a variety of very basic processes in North American streams. As yet we have investigated only a few aspects of the ecology of *Campostoma in* detail; other features about its ecology for which we have only preliminary data further suggest its potential influence in biotic communities and in stream ecosystems. Our work has focused on a single species of large herbivorous minnow, but many other abundant or widespread fish taxa may play similarly important roles in streams throughout the United States. We hope that ichthyologists and stream ecologists in general will be stimulated to consider in more detail the potential significance of grazing fishes in various stream ecosystems.'

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