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## RESOURCE ENHANCEMENT BY INDIRECT EFFECTS OF GRAZERS: ARMORED CATFISH, ALGAE, AND SEDIMENT<sup>1</sup>

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**Abstract.** Armored catfish (Loricariidae) are the major grazers of attached algae in pools of the Rio Frijoles, Panama (9°9' N, 79°44' W). In the dry season, sunny pools were inhabited by  $\approx 6$  individual loricariids per square metre of grazeable substratum. At these densities, armored catfish depleted algae and cleared sediment from bedrock substrata, leaving sparse standing crops of small, adnate diatoms (primarily *Achnanthes* spp.). To study the effects of armored catfish at  $\frac{1}{6}$  their natural density, I stocked four 6-7 cm (SL), 10-g *Ancistrus* (the most common size class of the most common species in stream pools) in each of five stream pens. Pens enclosed 4 m<sup>2</sup> of bedrock substratum, and were alternately stocked or left empty during three consecutive periods of 29, 11, and 11 d. At the end of each period, standing crops of sediment and attached algae, and rates of photosynthesis by attached algae, were measured. The attached algae that developed with sparse *Ancistrus* had higher standing crops with larger cells or colonies, and higher primary productivity, than did periphyton subjected to heavy grazing by unconfined armored catfish. Even heavy grazing, however, was less deleterious to attached algae than prolonged sedimentation on substrata in enclosures left empty for 11 or 29 d. The net effect of *Ancistrus* on their algal food changed from depletion at high grazer densities to enhancement at low grazer densities, as sedimentation became more limiting to algae than grazing.

**Key words:** algal productivity; catfish; grazing; loricariids; Panama; periphyton; sedimentation; streams.

### INTRODUCTION

Grazers affect their food directly through depletion, and indirectly through their interactions with other controls on its productivity. Direct effects of species on other members of their communities can be outweighed by their indirect effects, but how often and under what conditions this occurs is generally unknown (Vandermeer 1980, Wilson 1986, Yodzis 1988). Population density is one important determinant of a species' local impact. This impact can change qualitatively as density fluctuations alter the relative importance of a species' direct and indirect effects (Allee et al. 1949, Yodzis 1988). For example, consumers that when dense deplete a food species may prefer as prey a competitor of this species. When the consumers are sparse, they may facilitate their less preferred prey by limiting its competitor (Levine 1976, Lynch 1978). In other cases, prey may benefit when one of their predators consumes another potential predator (Kneib 1988). Indirect mutualisms can also occur when consumers modify the physical environment of their prey. Seaweeds (Menge 1975, Black 1976) and mussels (Witman and Suchanek 1984) benefit when mobile grazers remove fouling organisms, reducing drag and therefore the probability of detachment by storm waves. Armored catfish grazing periphyton from substrata in

Neotropical streams clear off sediment that can otherwise smother the attached organisms. Here I report a density-dependent shift in the net effects of these catfish on their algal food.

### BIOTA AND STUDY SITE

Four species of armored catfish (Loricariidae) graze substrata in pools of the Rio Frijoles of Central Panama (9°9' N, 79°44' W). The river remains free-flowing throughout the year, but baseline discharge varies in the 3-km reach studied, from  $\approx 0.1$  m<sup>3</sup>/s in the dry season (December through March) to 0.5 m<sup>3</sup>/s in the rainy season (April through November), corresponding to an average increase of 10-20 cm in stream depth. Densities of armored catfish were from 2-3 times higher in the dry season than in the rainy season, corresponding to a two- to three-fold contraction of their habitat with falling river level (Power 1987).

When armored catfish attain lengths >4-5 cm SL (Standard Length, Lagler 1956), they live in pools >20 cm deep. *Ancistrus spinosus* is the dominant species grazing in most pools, accounting for 74% of 4151 loricariid sightings in censuses of 16 stream pools over a 12-mo period (Power 1984a). Pre-reproductive, 6-7 cm SL, 10-g live mass *Ancistrus* comprised the most common size class, accounting for 37% of all *Ancistrus* counted in pools. *Hypostomus plecostomus* and *Rineloricaria uracantha* are also common in stream pools, while a fourth species, *Chaetostoma fischeri*, was un-

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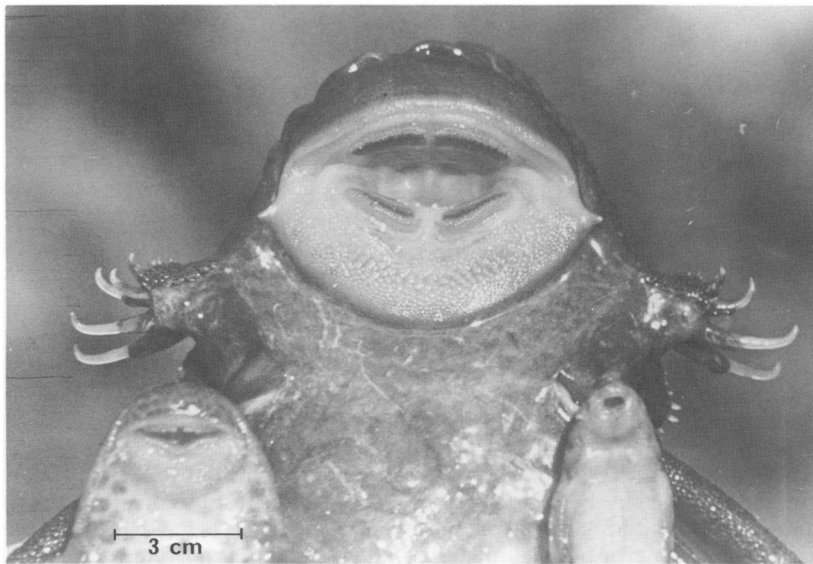


FIG. 1. Ventral view of mouths of the three most common loricariid catfish in the Rio Frijoles, Panama: *Ancistrus spinosus* (center), *Hypostomus plecostomus* (lower left), and *Rineloricaria uracantha* (lower right).

common generally and appeared restricted to faster flowing habitats (Power 1984a).

Loricariids, with entirely ventral suctional mouths and comb-like tooth plates, are morphologically specialized for scraping attached material from flat surfaces (Fig. 1). Diatoms are the most abundant identifiable items in their guts (M. E. Power and M. Luttenton, *personal observations*), and in stream pools deeper than 40 cm, loricariids are the only important consumers of periphyton (Power 1984a).

During the dry season pools become quite lentic, with no measurable flow over deeper substrata. Under these conditions substrata receive substantial sediment outfall from the water column. Little sediment or attached algae accumulates on the river bed in pools of the Rio Frijoles, however, due to heavy grazing by high densities of armored catfish (Power 1984a). Although dry season sediments are high in organic content (18–24% ash-free dry mass), this sediment is not a food for *Ancistrus*, but imposes energy costs that under experimental conditions were estimated to be 15–22% of the daily energy budget of 10-g individuals (Power 1984b). The ventral position of loricariid gills (Fig. 1) renders them subject to fouling by deposited sediment, and the energy costs measured may arise from gill-clearing activities, such as mucus secretion, or head shaking observed in loricariids on silted substrata.

Recently grazed patches on wood substrata sometimes appeared conspicuously greener than adjacent areas under light mantles of sediment (Fig. 2). This observation suggested that clearing effects of loricariids could enhance growth of attached algae that otherwise was limited by sedimentation. The net effects on periphyton of sediment clearing by loricariids could have outweighed depletion by grazing when grazers were

relatively sparse, and when sediment outfall rates were high.

#### METHODS

To compare the effects of dense and sparse populations of armored catfish on their algal foods in the dry season, I monitored sediment and attached algae in two natural pools that supported high densities of loricariids, and in five large stream enclosures where loricariid densities were manipulated. Pools had maximum depths of 113 and 92 cm; armored catfish fre-

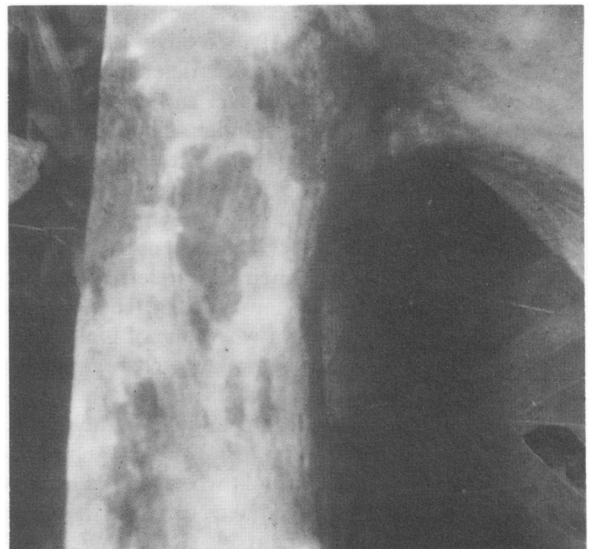


FIG. 2. Areas cleared by grazing *Ancistrus* on a submerged log. The dark patches are green with algae partially embedded in the wood; the lighter areas between have a thin mantle of sediment.

TABLE 1. Protocol for stocking of five enclosures with *Ancistrus* of the indicated standard length (SL).

Moderately sedimented enclosures						
	12 February– 13 March		13 March– 24 March		24 March– 3 April	
	No. fish	Fish SL (cm)	No. fish	Fish SL (cm)	No. fish	Fish SL (cm)
Encl. 3:	4	6–7	0		4	6–7
Encl. 4:	4	6–7	0		4	6–7
Encl. 5:		0	4	6–7		0
Heavily sedimented enclosures						
	12 February– 3 March		3 March– 13 March		13 March– 3 April	
	No. fish	Fish SL (cm)	No. fish	Fish SL (cm)	No. fish	Fish SL (cm)
Encl. 1:	8	6–7	0		1 4	16 6–7
Encl. 2:	8	6–7	8	6–7	1 4	18 6–7

quented bedrock platforms that were 35–60 cm deep. Enclosures were built in a very sunny pool ("Blue Clay Pool," Power 1984a), which had formerly supported six armored catfish/m<sup>2</sup> grazeable substratum (=bedrock, large cobbles, or submerged logs with flat surfaces relative to loriciid mouth widths). Water depth in enclosures ranged from 50 to 72 cm. Enclosures lacked roofs and floors. Walls projected ≈15 cm above the water surface. The bottom edges of walls were folded inwards to form a 30–40 cm wide skirt which was buried under gravel. Each pen enclosed 4 m<sup>2</sup> of a flat, mudstone bedrock where, prior to pen construction, loriciids in the pool had spent >95% of their grazing time. Besides this bedrock, the only substrata available to loriciids in enclosures were plastic screening (1.3-cm mesh), the iron poles supporting it, and gravel used to anchor the bottom edges of walls. Small bedrock ledges and folds in the screening provided cover.

#### *Sediment outfall rate*

Rates of sediment outfall were measured in enclosures and in natural pool habitats. I aspirated sediment from gridded areas 1–72 h after cleaning them. Monofilament gill-net cages over sampled areas prevented animal traffic from dislodging sediment, but had no measurable or observable effect on sediment movement or deposition (Power 1984b). Sediments were filtered on tared Whatman Number 2 paper immediately after collection and dried to constant mass at 70°C.

#### *Sediment effects on periphyton*

I studied the effect of sediment load on productivity of periphyton grown on 1 × 2.5 cm<sup>2</sup> unglazed ceramic tiles with textures similar to that of bedrock. Tiles were incubated in the stream until they accumulated a vis-

ible standing crop of algae. All tiles were then withdrawn and incubated in the stream at depths of 18–22 cm in 998-mL Mason jars filled with de-oxygenated stream water. Jars were incubated under full sun from 1000 to 1330 on a cloudless day for 2 h ± 15 min. Every 10–15 min jars were turned by hand to stir water over periphyton. (Algae attached to the floors of stagnant pools probably experience similarly infrequent water motion from occasional passage of fish.) Oxygen evolved was measured with a Yellow Springs Instrument Company (YSI) Model 54RC oxygen meter, calibrated to micro-Winkler oxygen measurements (modified from APHA 1985). After their initial rates of oxygen evolution had been measured, I placed the tiles under 8 cm of water in three aluminum pans. Sediment from the stream was unevenly distributed over tiles to create a range of loads, but in each pan some tiles were left sediment free to serve as controls. Groups of tiles, started on the same day, were incubated 24, 48, and 72 h in half-shaded sites (to prevent overheating) on the stream bank. After the incubation each tile was gently moved underwater into a plastic vial, and its sediment was tipped off. This sediment was filtered and weighed as described above. The oxygen evolved by each tile was measured again under light conditions similar to those during the original incubation, to determine rates of photosynthesis by attached organisms after a given sediment load of a given duration.

#### *Effects of Ancistrus on sediment and periphyton*

The five enclosures described above were stocked with *Ancistrus* or left empty according to a staggered schedule (Table 1) so that fish effects on algae and sediment could be distinguished from changes over time. Enclosures differed in their rates of sediment outfall (Fig. 3). The three moderately sedimented enclosures (3, 4, and 5) were alternately left empty or stocked with four small (6–7 cm SL) *Ancistrus* (giving one individual per square metre of grazeable substratum, which was one-sixth the natural density of the pool in the dry season). The two heavily sedimented enclosures (1 and 2) were stocked with small and large (16 or 18 cm SL) *Ancistrus* (Table 1). Coin tosses determined whether cages would initially be stocked or left empty.

After treatment periods of 11–23 d (Table 1), I sampled algae and sediment on the bedrock substratum in each enclosure on 12–14 positions adjacent to pre-marked 0.5-m square grids. The exact area sampled differed on subsequent collection dates so sampling depletion did not bias results. At each site I aspirated sediment from measured areas, and later filtered and weighed samples as described above. After aspirating sediment, I collected two chips of bedrock (8–22 cm<sup>2</sup>) from the cleared area. Net photosynthesis of periphyton on one chip was measured in light bottles as described above. The other chip was preserved in 10% formalin for microscopic examination. Samples of periphyton from the two natural stream pools were also



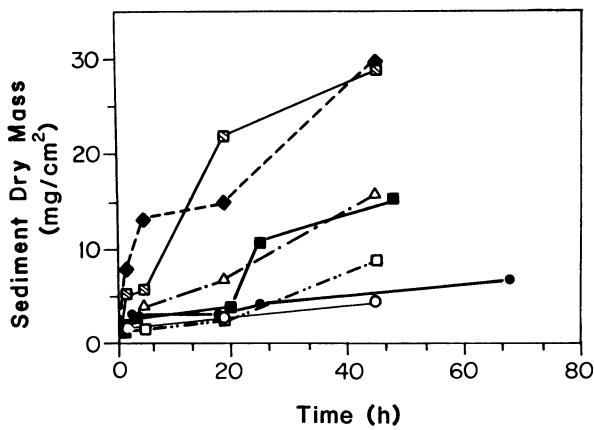


FIG. 3. Sedimentation rates in five enclosures and two natural stream pools. Points are the means of 4–6 samples in each enclosure and 12–15 samples in each pool. Standard errors, not plotted, ranged from 0.1 to 7.5 mg/cm<sup>2</sup>. Linear regressions, constrained through the origin (Krumbein and Graybill 1965), are [where  $S(t)$  is sediment load (as dry mass, mg/cm<sup>2</sup>) and  $t$  is time (h)]: Encl. 1,  $\square$ :  $S(t) = 0.75t$ ,  $r^2 = 0.80$  ( $n = 17$ ); Encl. 2,  $\blacklozenge$ :  $S(t) = 0.78t$ ,  $r^2 = 0.78$  ( $n = 16$ ); Encl. 3,  $\square$ :  $S(t) = 0.33t$ ,  $r^2 = 0.47$  ( $n = 16$ ); Encl. 4,  $\triangle$ :  $S(t) = 0.37t$ ,  $r^2 = 0.88$  ( $n = 15$ ); Encl. 5,  $\circ$ :  $S(t) = 0.11t$ ,  $r^2 = 0.63$  ( $n = 14$ ); Bat Rocks Pool,  $\blacksquare$ :  $S(t) = 0.34t$ ,  $r^2 = 0.96$  ( $n = 40$ ); Limestone Flats Pool,  $\bullet$ :  $S(t) = 0.09t$ ,  $r^2 = 0.88$  ( $n = 71$ ).

collected in this manner, from ten sites along grids nailed into grazed bedrock platforms.

These chips were later boiled in 50% nitric acid to detach diatoms (Lind 1979). Ten subsamples from each sample were counted and measured (projected area) under 400 $\times$  magnification. Diatom biomass at a site was indexed as the total projected area of diatoms per area of substratum.

#### Estimation of return times for grazing *Ancistrus*

One estimate of grazing pressure, the return time,  $T$ , of grazers to a given small site on the substratum, is:

$$T = A / \sum_{ij} (N_{ij}c_{ij})$$

where  $A$  is the area shared by  $N$  grazers of species  $i$  and size class  $j$ , and  $c$  is the per capita grazing rate (area per individual per unit of time). The average return time of any grazer to a given small site on the substratum is also the recovery time between grazing bouts for periphyton and the accrual time for sediment on the site.

From vantage points on the river bank I observed loricariids in the two natural pool habitats and *Ancistrus* in enclosures. At 15- or 30-min intervals, I counted the numbers ( $N$ ) of loricariids grazing or resting on bedrock platforms that had been marked into grids of squares 0.5 m on an edge. Between these "scan samples" (Altmann 1974) I estimated loricariid feeding rates ( $c$ ) by sketching areas covered by grazing (or resting) individuals during short (typically 5-min) observations (see Power 1984a for more details of methods).

Grazing rates of small (<7-cm) loricariids were not significantly different by day and night in natural stream pools (Power 1984a); in enclosures, only daytime observations were made. In stream pools where loricariids grazed over all of the area observed,  $A$  was the constant area demarcated by my grid. In enclosures *Ancistrus* cleared and grazed only part of the available 4 m<sup>2</sup> of bedrock. To estimate this variable  $A$ , I measured the area of cleared patches in each enclosure in the mornings before observations began.

## RESULTS

### Sediment outfall

Rates of sediment outfall in the three moderately sedimented enclosures were similar to rates in the two unmanipulated stream pool habitats. In the two heavily sedimented enclosures sedimentation rates were higher than those experienced by loricariids under natural conditions in the Rio Frijoles (Fig. 3).

### Sediment effects on periphyton productivity

Incubation under sediment reduced the rate of net photosynthesis by periphyton (Fig. 4). In this experiment, duration of incubation did not affect loss of primary productivity for a given sediment load ( $F = 0.0038$ ,  $N = 38$ ,  $P = .95$ ). Data were therefore pooled over incubation times, and the following regression was computed:

$$\ln(N_s/N_0) = -0.298 - 0.030(S) \quad (1)$$

$(F = 67.9, N = 38, P < .001)$

where  $N_0$  is the net productivity of periphyton on a tile before incubation,  $N_s$  is its productivity after incubation, and  $S$  is its sediment load (as dry mass, in milligrams per square centimetre) during incubation. The effect of incubation without sediment on control

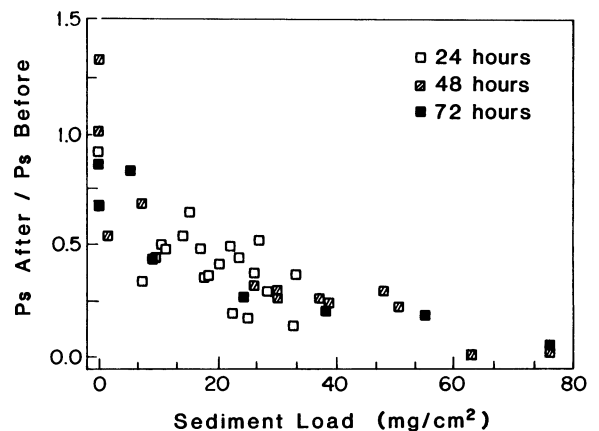


FIG. 4. Ratios of rates of net photosynthesis ( $P_s$ , measured as oxygen evolution) by periphyton on tiles before ( $P_s$  before) and after ( $P_s$  after) incubation under various sediment loads (measured as dry mass). Each data point is the ratio on an individual tile incubated 24, 48, or 72 h. For regression equation, see Results: Sediment Effects on Periphyton Productivity.

TABLE 2. Grazing by "small" (6–7 cm SL) and "large" (>14 cm SL) *Ancistrus* in enclosures and two stream pools.

	Grazing rate, $c_i$ , ( $\text{cm}^2 \cdot \text{indiv}^{-1} \cdot \text{min}^{-1}$ )			Numbers, $N_i$ , (individuals)			Area, $A$ ( $\text{m}^2$ )			Return time, $T$ (h)
	$\bar{X}$	SE	$n$	$\bar{X}$	SE	$n$	$\bar{X}$	SE	$n$	
Pools										
Limestone										
Small catfish	8.3	0.8	51	3.0	0.4	45	4.5	0	...	10.1*
Large catfish	52.7	15.7	3	0.1	0.3	45				
Bat Rocks										
Small catfish	6.0	1.3	21	2.6	0.4	34	3.5	0	...	8.8*
Large catfish	†			†			†			
Moderately sedimented enclosures										
Encl. 3										
4 small catfish	6.1	0.8	39	0.3	0.1	80	0.8	0.2	12	91.5
Encl. 4										
4 small catfish	6.7	0.8	41	0.4	0.1	82	0.8	0.1	13	56.3
Encl. 5										
4 small catfish	11.9	1.6	10	0.2	0.1	48	0.5	0.1	3	41.2
Heavily sedimented enclosures										
Encl. 1										
4 small catfish	10.8	2.0	11	0.1	0.03	90	0.1	0.02	7	12.9
4 small + 1 large catfish	†			†			0.5	0.1	9	...
Encl. 2										
8 small catfish	7.8	0.7	58	1.0	0.1	75	0.4	0.1	6	8.0
4 small	8.6	2.5	3	0.4	0.1	71	0.5	0.1	8	22.2
+ 1 large catfish	16.0	3.3	4	0.1	0.03	71				

\* Computed from additional data (Power 1984a: Table 2) on grazing by other size classes and species of loricariids in stream pools.

† Insufficient data.

tiles appeared minor, as ratios of productivity after and before incubation without sediment were close to 1.0 (averaging 0.96). Eq. 2 predicts that a sediment load of  $\approx 13 \text{ mg/cm}^2$  (which, according to regressions given in Fig. 3, would accumulate in Bat Rocks Pool after 36 h) would reduce net primary productivity by 50%.

#### *Ancistrus* grazing behavior

In stream pools, loricariids grazed virtually all bedrock substratum. I marked off easily observed portions and treated the area  $A$  as a constant in Bat Rocks (3.5  $\text{m}^2$ ) and Limestone Flats (4.5  $\text{m}^2$ ). In enclosures, however, grazers cleared only part of the available 4  $\text{m}^2$  of bedrock (Table 2), and showed a marked preference for initiating grazing bouts within previously cleared patches (Power 1983). Despite the larger area grazed by pool-dwelling loricariids, densities of grazers on platforms were higher in pools than in the moderately sedimented enclosures. In Limestone Flats Pool the average density of all loricariids on grazing platforms during scan samples was 8.4 individuals/4.5  $\text{m}^2$  (1.9 individuals/ $\text{m}^2$ ); in Bat Rocks Pool, this density was 10 individuals/3.5  $\text{m}^2$  (2.9 individuals/ $\text{m}^2$ ) (Power 1984a: Table 2). In contrast, the density (individuals per square metre of grazed area) of *Ancistrus* (the only loricariid stocked) in moderately sedimented enclosures 3, 4, and 5 averaged 0.30, 0.44, and 0.34 individuals/ $\text{m}^2$ , respectively. In the two heavily sedimented enclosures 1 and 2, density estimates were higher (1.2 individuals/ $\text{m}^2$  and 2.5 individuals/ $\text{m}^2$ , respec-

tively) because little area was kept clear when only small *Ancistrus* were stocked. When a large *Ancistrus* was introduced to enclosure 2, area cleared nearly doubled, and grazer density dropped to 0.77 individuals/ $\text{m}^2$ .

Per-capita grazing rates were similar for small (6–7 cm) *Ancistrus* in enclosures and in the two natural stream pools (Table 2,  $P = .83$  from a Mann-Whitney  $U$  test). Insufficient observations precluded comparisons of grazing rates by large (>14 cm) *Ancistrus* in pens and natural pools.

Combining estimates of loricariid densities and grazing rates gives return time estimates of 9–10 h for the two densely populated natural stream pools, 40–90 h for the three moderately sedimented enclosures, 8–13 h for the two heavily sedimented enclosures with small *Ancistrus*, and 22 h for enclosure 2 after a large *Ancistrus* was added (Table 2).

#### *Effects of loricariids on sediment and periphyton*

Mean sediment loads and photosynthetic rates in Figs. 5 and 6 are averaged over 12–14 samples collected along grids in enclosures from both cleared and uncleared sites. Therefore, these averages underestimate the grazer effects on cleared areas, but give an estimate of how overall habitat productivity was affected. In the three moderately sedimented enclosures, *Ancistrus* grazing reduced sediment accumulation and enhanced the net productivity of periphyton. Differences in both factors differed significantly between sequential fish vs.

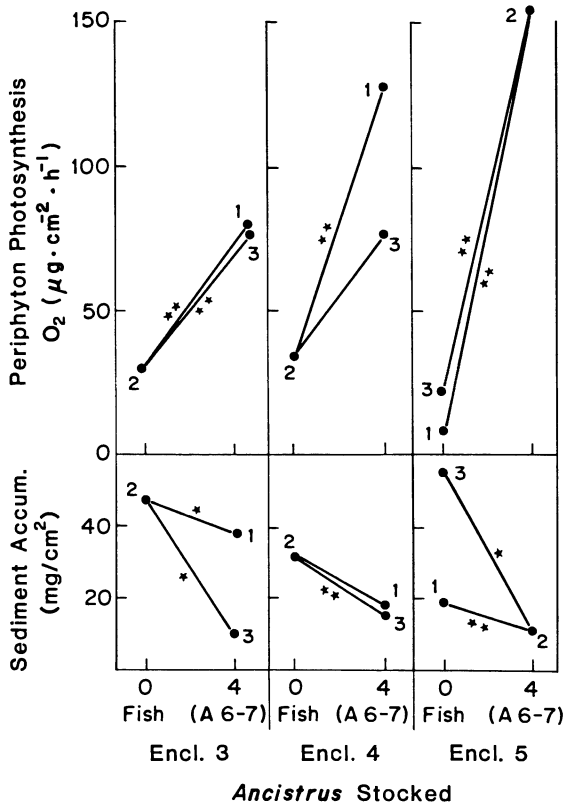


Fig. 5. Sediment accumulation and periphyton net productivity in moderately sedimented enclosures with and without small *Ancistrus*. Each point is the mean of 12–14 samples from sites along grids within enclosures. Numbers indicate the date of sample collections, each date being the end of that experimental period (1=13 March, 2 = 24 March, 3 = 4 April; see Table 1). Asterisks indicate probabilities from Wilcoxon one-tailed tests that compare sediment or oxygen evolution rates at sampling sites before and after sequential treatments (\*\*  $P < .005$ ; \*  $P < .01$ ; no symbol:  $P < .25$ ).

no-fish treatments in five out of six comparisons (Fig. 5). In contrast, in the two heavily sedimented enclosures, sediment loads increased and net photosynthesis decreased from the first to the second experimental period, whether loricariids were removed (enclosure 1), or remained (enclosure 2) (Fig. 6). High sediment outfall appeared to discourage small *Ancistrus* from grazing on the streambed, and they tended to rest or graze on vertical substrata such as the iron poles supporting the pens. After several weeks tube-building chironomids appeared under sediment deposits, and may have contributed to the consumption of oxygen by bed-rock flakes measured during the second interval (Fig. 6).

When large *Ancistrus* were stocked with four small *Ancistrus* during the third treatment period, sediment was significantly reduced and photosynthesis significantly increased in both heavily sedimented enclosures (Fig. 6).

The diatom standing crops that occurred under zero,

intermediate, and heavy grazing are shown in Fig. 7. Standing crops were highest under intermediate grazing: in the moderately sedimented enclosures stocked with 4 small *Ancistrus*. On heavily grazed substrata in natural pools, standing crops were lower than in stocked enclosures ( $P < .03$ , one-tailed Mann-Whitney  $U$  test), but were still significantly higher than were standing crops in empty enclosures ( $P < .05$ , two-tailed Mann-Whitney  $U$  test), where diatoms were subjected to prolonged burial under sediment.

Standing crops of diatoms in lightly grazed enclosures were higher than in heavily grazed pools primarily because there were more large diatoms,  $> 50 \mu\text{m}^2$  in projected area (Fig. 8). Numbers of small, adnate diatoms (predominantly *Achnanthes* spp.) did not differ between heavily grazed and lightly grazed substrata ( $P < .19$ , one-tailed Mann-Whitney  $U$  test).

### DISCUSSION

When grazers interact with other organisms or physical factors that affect their food, the net effects of grazers on their food can change from negative to positive with shifts in the relative importance of direct vs. indirect effects. Indirect facilitation by grazers of their food is particularly likely when the food organism has a morphological refuge from grazing, such as a basal meristem or a prostrate growth habit that renders it

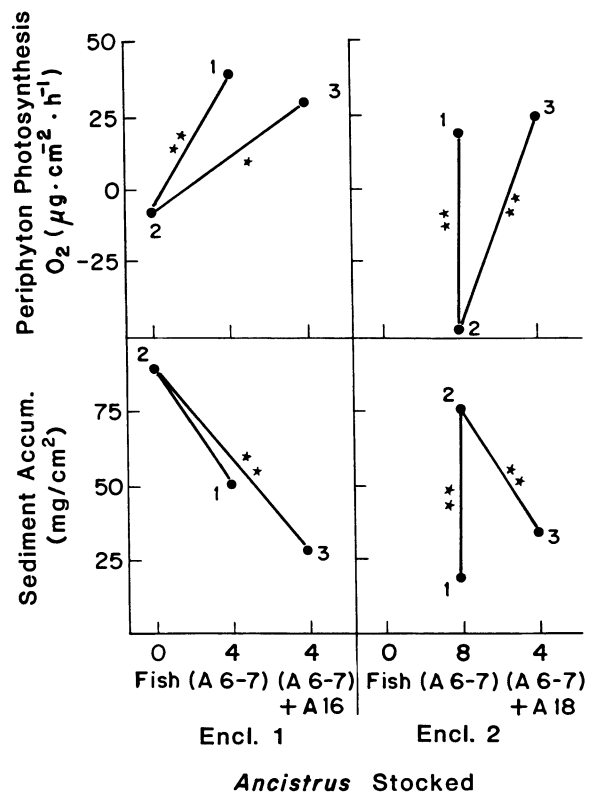


Fig. 6. Effects of small and large *Ancistrus* on sediment accumulation and periphyton net productivity in heavily sedimented enclosures; symbols as in Fig. 5.

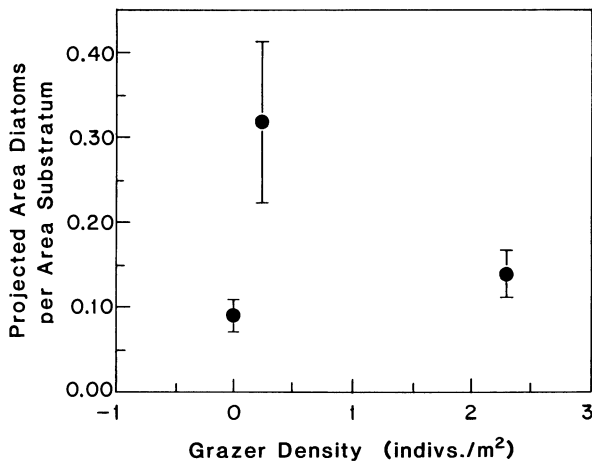


FIG. 7. Effects of no grazing, moderate grazing, and heavy grazing on diatom standing crops as estimated by total projected area of diatoms per unit area of substratum. Data for no grazing and moderate grazing are means from 10 and 11 sites, respectively, sampled along grids within three moderately sedimented enclosures with sediment outfall rates of 0.11–0.37 mg·cm<sup>-2</sup>·h<sup>-1</sup>; data for heavy grazing are means of 20 sites sampled along grids within two natural pool habitats with sediment outfall rates of 0.09–0.34 mg·cm<sup>-2</sup>·h<sup>-1</sup>. Bars are ± 1 SE.

more susceptible to overgrowth or smothering. Crustose coralline algae with basal meristems flourish when limpets clear off microphytes (Steneck 1982); epilithic diatoms benefit when chitons remove macroalgae (Dethier and Duggins 1984); and cyanobacterial felts with basal regeneration are kept free of diatom turfs by grazing minnows (Power et al. 1988). In this study sediment, rather than algal competitors, was kept in check by grazers.

Because armored catfish removed sediment that could smother attached algae, I predicted that when sediment outfall was high relative to loricariid grazing pressure, catfish would have a net beneficial effect on algae. This prediction was supported by results from three moderately sedimented enclosures stocked with *Ancistrus* at 1/6 their natural density. In these enclosures, productivity and standing crops of periphyton increased after periods with grazers, and sediment loads were reduced, in comparison to sediment and periphyton that were sampled in these enclosures after 11–23 d without grazers. In two more heavily sedimented enclosures, however, small *Ancistrus* could not “keep up” with sediment, even when stocked at twice the density of fish in the moderately sedimented enclosures. Under high sediment outfall, only groups with large *Ancistrus* cleared enough area to increase overall productivity of periphyton in the enclosure.

The ventral position of loricariid gills makes them particularly subject to fouling by deposited sediment. Larger *Ancistrus*, with larger gills elevated farther off the substratum, are probably less subject to gill fouling at a given sediment depth than are smaller individuals.

Results from heavily sedimented enclosures reported here, as well as behavior of small loricariids (Power 1984b), suggest that small individuals may benefit from being in the vicinity of larger individuals under conditions of high sediment outfall, although the size classes may compete exploitatively for food when loricariids are dense and sediment is scant (Power 1984a).

Qualitative changes in the effects of armored catfish on their food, and possibly in the effects of large *Ancistrus* on small *Ancistrus*, are more likely to arise in tropical streams during the dry season. Although heavy sediment loads are transported and sometimes deposited after rainy season floods, sediment-free grazing substratum is probably not in short supply during the rainy season due to habitat expansion and substratum scouring by fast-flowing water. During the dry season, however, tropical fish are often trapped in shrinking, stagnant pools (e.g., Lowe-McConnell 1975) where much of the habitat can become heavily sedimented. The indirect effects described here may become important during these bottlenecks, affecting loricariids' chances of survival through the dry season.

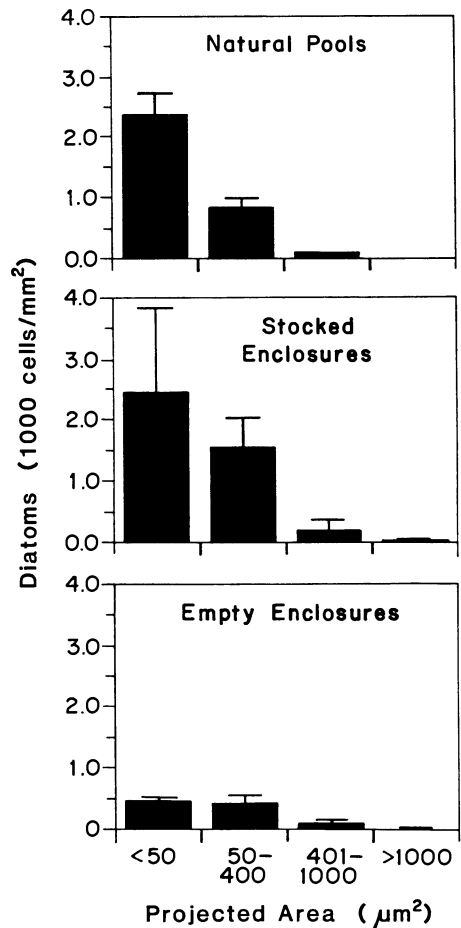


FIG. 8. Size class distributions of diatom samples in Fig. 7. Error bar shows 1 SE.



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