

Testing the Role of Sediment-Mediated Interactions between Tadpoles and Armored Catfish in a Neotropical Stream

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In Neotropical streams, benthic sediment affects community structure and may impose energetic costs for some species yet to be a resource for others. This study tested the hypothesis that removal of benthic sediment through ingestion by *Rana palmipes* (Ranidae), a detritivorous tadpole, facilitated the growth of *Ancistrus tri-radiatus* (Loricariidae), an algivorous armored catfish. We hypothesized that sediment removal by *Rana* would reduce energetic costs to respiration or digestion encountered by *Ancistrus* when grazing on periphyton and increase available periphyton biomass. Growth of *Ancistrus* was measured in a Venezuelan piedmont stream in enclosure cages in which the presence of *Rana* and ambient sediment levels were manipulated. Benthic sediment accumulation differed significantly between treatments. Growth of *Rana* was greater when sediments were present than when sediments were removed. However, there was no effect of sediment removal on *Ancistrus* growth. Total biomass of periphyton did not differ between treatments, because epipelagic diatoms were abundant in benthic sediments and presumably compensated for any negative effects of shading by sediments on total periphyton biomass. Organic-rich sediment in this system provides a net energetic benefit to *Rana*. The consequences of sediment for *Ancistrus* are less clear, but we found no evidence of a net cost. If interspecific facilitation by *Rana* occurs, it is likely limited to systems where sediment is organic-poor or to species for which costs of organic-rich sediment exceed benefits.

MANY Neotropical streams contain a diverse and abundant guild of benthic vertebrate grazers that includes both fish and tadpoles. Yet despite evidence that these grazers can have strong effects on community structure (e.g., Power, 1990; Flecker, 1992; Pringle and Hamazaki, 1997), the importance of interactions among them is poorly known. One likely mechanism for such interactions is via the modification of benthic sediments. A thick sediment layer covers the substrate in many Neotropical streams; sedimentation rates are often very high, especially during the dry season (Power, 1984; Pringle et al., 1993; Flecker, 1997). This sediment is typically organic-rich and composed of a matrix of inorganic particles, detritus, and living bacterial and algal cells and their byproducts (Bowen et al., 1984; Hall and Meyer, 1998).

For some species of fish, sediment may impose energetic costs through interference with respiration or digestion (MacLeod and Smith, 1966; Bowen, 1981). In an experiment in Panama with the algivorous armored catfish *Ancistrus spinosus* (Loricariidae), Power (1984) estimated that sediment imposed costs equivalent to 15–22% of the daily energy budget of small individuals. Conversely, sediment can be a valuable resource for species that are capable of extracting nutritional value from the organic portion. Sediment-derived detritus comprised

>98% of the organic mass in stomachs of the characin *Prochilodus platensis* (Prochilodontidae) from Rio de la Plata in Argentina and represented the fish's primary source of nutrition (Bowen et al., 1984). Flecker et al. (1999) found that tadpoles of *Rana palmipes* (Ranidae) use and compete for sediment as a nutritional resource; tadpoles had greater growth and were more likely to metamorphose when they could consume organic-rich sediments.

Because sediment may either impose large energetic costs or provide substantial energetic benefits, sediment-biota interactions might have significant effects on community structure. Power (1984, 1990) reported that areas cleared of sediment by large loricariid armored catfish were preferred by smaller conspecifics and suggested that large individuals might facilitate survival of small individuals via this mechanism. Similarly, Flecker et al. (1999) proposed that sediment clearing by *R. palmipes* might facilitate other benthic consumers. Despite these suggestions, few studies have directly examined the nature of sediment-mediated interspecific interactions in tropical streams.

In Rio Las Marias, Venezuela, epibenthic fishes and tadpoles can greatly decrease benthic sediment accrual (Flecker, 1992, 1996; Flecker et al., 1999). We hypothesized that sediment removal by tadpoles of *R. palmipes* facilitates the

growth of the armored catfish *Ancistrus triradiatus* (Loricariidae). Investigations of the feeding ecology of *R. palmipes* have indicated that it is primarily a detritivore (Flecker et al., 1999), whereas observations of gut contents and analyses of diet nutrient composition and fecal organic content suggest that *A. triradiatus* is chiefly an algivore (Hood, 2000; P. McIntyre, unpubl.). We reasoned that a thick layer of benthic sediment imposes energetic costs on *Ancistrus* that have to consume or clear sediment to access periphyton (Power, 1984) and also reduces periphyton biomass and productivity via reduced light availability (Power, 1990; Pringle et al., 1993). Therefore, removal of the sediment layer should increase allocation of energy to growth by *Ancistrus* by both reducing energetic costs and increasing the supply of periphyton food. *Rana* should facilitate the growth of *Ancistrus* if the former can sufficiently reduce benthic sediment.

MATERIALS AND METHODS

Description of study site.—This study was conducted in Rio Las Marias (9°01'N, 69°45'W), a cobble-bottom stream in the Andean piedmont of Venezuela (see detailed description in Flecker, 1996; Flecker et al., 1999, 2002). At the study site (elevation 225 m), Rio Las Marias is an open canopied, fourth-order stream with a drainage area of 210 km². The stream is transparent during the dry season (December through April), but there is considerable deposition of sediment derived mostly from decomposing periphyton and fish feces (Flecker, 1997). The experiment reported here was conducted in a single 50-m long pool of Rio Las Marias that averaged 7 m wide and 30–40 cm deep during the course of the study.

Over 85 fish species have been recorded at the study site (ASF, unpubl.), representing a great diversity of feeding habits. Benthic algivores and detritivores are especially abundant. In many years the detritivore *Prochilodus mariae* (Prochilodontidae) is the most dominant fish by biomass during the dry season (Flecker, 1992, 1997), and in some years detritivorous tadpoles of *Rana palmipes* are present in dense aggregations (Flecker et al., 1999). These epibenthic feeders clear the substrate of accumulated sediment, so that sediment-free areas are interspersed with areas in various stages of sediment accrual.

Experimental design and methods.—We used a stream enclosure experiment to examine the nature of the sediment-mediated interactions

between two benthic grazers. We stocked enclosure cages with *Ancistrus* and manipulated the presence of *Rana*. To determine whether observed interactive effects were in fact attributable to sediment modification, we also included a manual sediment removal treatment. We removed most of the sediment from the substrate in these cages by vigorously waving a 10 cm wide paintbrush through the water a few centimeters above the substrate each morning and evening. The four treatments in our 2 × 2 factorial design were (1) sediment brushed, no *Rana* present (B/NR); (2) sediment not brushed, no *Rana* present (NB/NR); (3) sediment brushed, *Rana* present (B/R); and (4) sediment not brushed, *Rana* present (NB/R). Based on the assumption that sediment imposes energetic costs on *Ancistrus* (Power, 1984) and the hypothesized facilitative effects of *Rana* on *Ancistrus*, we predicted differential *Ancistrus* growth in the four treatments, as follows: *Ancistrus* growth should be lowest in the NB/NR treatment, since sediment standing stock should be highest when there is neither *Rana* consumption nor manual removal of sediments. *Ancistrus* growth should be higher when sediments are removed from the substrate; and if manual removal and removal by *Rana* consumption reduce sediment equivalently, then *Ancistrus* growth in the B/NR and NB/R treatments should be similar. Finally, *Ancistrus* growth should be highest in the B/R treatment, where sediment accumulation is reduced by both *Rana* consumption and brushing. A secondary prediction was that *Rana* should grow more in cages with ambient sediment (NB/R) than in the manual sediment removal cages (B/R), as suggested by Flecker et al. (1999).

The experiment ran for 24 days from 17 February to 12 March 2000. We applied the four treatments in the stream in four complete randomized blocks ($n_T = 16$). Each block consisted of four 1 × 1 × 1 m enclosure cages constructed of plastic fencing (mesh size = 6.35 mm), supported by rebar and separated by 1–2 m in a square array. We placed a layer of periphyton-covered cobbles on the bottom of each cage. Blocks were spaced 6 m apart. Depth and flow, measured on day 14 of the experiment, ranged from 29–43 cm and from 0.01–0.03 m s⁻¹, respectively.

We collected all *Ancistrus* and *Rana* from a 3 km reach of Rio Las Marias and an adjoining tributary. Immediately before being placed in experimental cages all individuals were blotted dry and weighed with an Ohaus model SC2020 electronic balance. Each cage received five *Ancistrus*, one from each of five different size clas-

ses. Initial masses (mean \pm SE, $n = 16$ for each size class) of *Ancistrus* were 0.88 ± 0.04 g (Size 1); 1.69 ± 0.08 g (Size 2); 2.79 ± 0.11 g (Size 3); 4.46 ± 0.17 g (Size 4); 8.51 ± 0.63 g (Size 5). In assigning individuals to cages, we minimized the within-block variance in the weight of a size class. The use of size classes let us follow individual *Ancistrus* without a more invasive marking method that might have reduced their growth during the experiment. Cages in B/R and NB/R treatments also received 15 *Rana* (initial mass 1.97 ± 1.04 g, $n = 120$). Because all *Rana* in the stream at the initiation of the experiment were similar in size, we were unable to establish size classes that would have allowed us to follow them individually. We chose to stock *Rana* at a higher density than *Ancistrus* to maximize possible interactive effects of *Rana*. Densities of *Ancistrus* and *Rana* in cages were within the range of natural densities in the stream (Flecker et al., 1999; Hood, 2000). We deposited voucher specimens of the *Ancistrus* and *Rana* used in this study in the Cornell University Museum of Vertebrates (*Ancistrus*: CU 82603–82618; *Rana*: CU 13297–13303).

We used sediment traps (20 mL vials filled with sterilized gravel, opening = 3.8 cm^2) to determine whether differences in sediment deposition rate might confound treatment effects. On day 23, we placed two traps in each cage with their openings level with the substrate surface. Four additional traps were placed in the stream several meters upstream of selected cages. After 22 h, we removed traps and filtered sediment from each onto preashed and preweighed 47 mm Gelman A/E glass fiber filters. Filters were dried in a solar oven at 60 C, transported to the lab, frozen for 1–2 months, then dried to constant weight at 65 C. We weighed filters for total dry mass, ashed them in a muffle furnace (3 h at 500 C), and reweighed them to determine ash-free dry mass (AFDM, the organic portion of the sediment).

To compare sediment standing stock among treatments, we collected benthic sediment samples from three randomly selected rocks in each cage on days 10 and 24. We sampled sediments before brushing cages on these days; therefore, we estimated the minimum possible effectiveness of our manual sediment removal. We trapped sediments under a 6.6-cm^2 plastic cap held against a flat upper surface of each selected rock, removed the rock from the water and cleaned off the rest of the surface, used a squirt bottle to wash sediment from the capped area into a collecting pan, and then filtered and processed sediment as described above.

We collected periphyton samples on day 24

and analyzed them for chlorophyll *a* (chl*a*) as a measure of algal biomass. We selected rocks from three random locations in each cage and used a toothbrush to remove all periphyton from a 6.6-cm^2 area on the top surface of each rock. The resulting slurry was rinsed into a pan, filtered onto 25-mm Gelman A/E glass fiber filters, and immediately placed into 90% ethanol kept on ice (Nusch, 1980). Chlorophyll *a* was extracted in the dark for 24 h and then quantified using a Turner model 10-AU fluorometer. On day 24, we took one periphyton sample from each cage and preserved it with 2% formalin for determination of community composition. In the laboratory, subsamples of known volume were examined at $400\times$ magnification using a light microscope and a Palmer counting cell. Periphyton was identified to genus and enumerated until reaching 300 cells or 50 fields of view (never less than 137 cells). These data were expressed as biovolumes per area of substrate based on regressions from measurements of 30 cells for each algal taxon.

The primary responses of interest in this study were growth (change in mass) of *Ancistrus* and of *Rana*. We terminated the experiment on day 24, when *Rana* began to metamorphose. All organisms were removed from cages, blotted dry, and weighed with an electronic balance. Absolute and percent growth were determined for each individual *Ancistrus* and for the total *Rana* biomass of each cage.

Statistical analyses.—Differences in the growth of *Ancistrus* between treatments were analyzed using ANOVA for a split-plot randomized complete block design. Blocks represented different locations within the pool but were dropped from analyses when not significant at $P < 0.05$. Presence of *Rana* and brushing were considered main plot factors, and *Ancistrus* size class was considered a subplot factor. *Rana* growth data were paired by block and analyzed with *t*-tests. Chl*a* data were evaluated as two-factor randomized complete block ANOVAs, with presence of *Rana* and brushing as main effects. Periphyton community composition data were analyzed in the same manner after square-root transformation to equalize variances. Variance in sediment standing stock (dry mass, AFDM, and %AFDM) differed by one to three orders of magnitude between NB/NR (the treatment with the largest mean) and the rest of the treatments. Because we could not correct this heteroscedasticity with simple transformations, we used ANOVA on the rank-transformed data to compare treatment means in these datasets. Before running univariate ANOVAs on sediment standing stock and

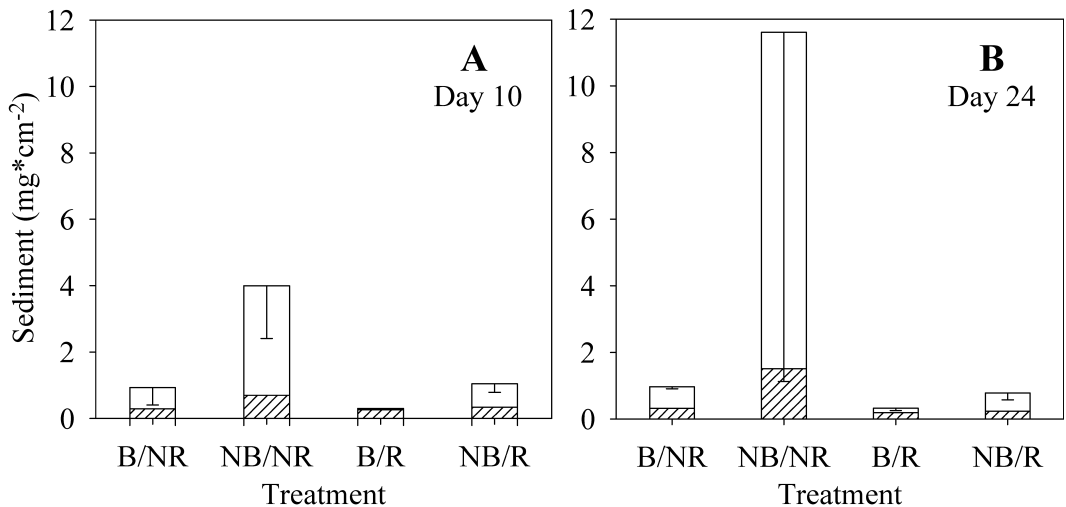


Fig. 1. Dry mass (unshaded, mean \pm 1 SE), and ash-free dry mass (AFDM, shaded) of benthic sediment samples taken on day 10 (A) and day 24 (B). Sediment standing stock was significantly decreased by both presence of *Rana* and manual removal of sediments with a paintbrush, as shown by dry mass and AFDM of benthic sediment samples taken on day 10 and day 24. Treatments: B/NR, sediment brushed; NB/NR, sediment not brushed; B/R, sediment brushed and *Rana* present; NB/R, sediment not brushed and *Rana* present. In the NB/NR treatment, a thick sediment layer accumulated over most of the substrate but *Ancistrus* grazing maintained scattered clear patches; consequently mean and variance were both high.

chl a data, we examined results of MANOVAs on dry mass and AFDM (Day 10) or on those variables plus chl a (day 24). Sediment deposition rate data were evaluated as a one-factor ANOVA with four levels, since the factorial treatment structure did not affect the deposition rate of new sediment from the stream. We used the Tukey procedure to control overall error rates at $\alpha = 0.05$ for all multiple comparisons. All analyses were performed using SAS Systems Software (vers. 8.1, SAS Institute Inc., Cary, NC, 2000).

RESULTS

Sediment deposition and standing stock.—Gross sediment deposition rates in cages measured on days 23–24 of the experiment ranged from 0.019–0.035 mg \cdot cm $^{-2}$ \cdot h $^{-1}$ and did not differ between treatments ($F_{3,12} = 0.83$, $P = 0.5$). Sedimentation rates in four traps outside of cages ranged from 0.036–0.073 mg \cdot cm $^{-2}$ \cdot h $^{-1}$; thus, cage effects on sediment accrual probably reduced differences between treatments. Nonetheless, large differences in benthic sediment standing stock between treatments were apparent almost immediately and persisted for the duration of the experiment (Fig. 1). Both presence of *Rana* and manual brushing contributed to observed differences in benthic sediment (Table 1), reducing total dry mass and AFDM while increasing the proportion of organic mat-

ter in the sediment (% AFDM). Percent AFDM on day 10 ranged from 25% \pm 2% (mean SE) in the NB/NR treatment to 49% \pm 2% in the B/R treatment. Percent AFDM on day 24 ranged from 32% \pm 9% in the NB/NR treatment to 70% \pm 10% in the B/R treatment.

Periphyton community composition and biomass.—The periphyton community on day 24 was dominated by filamentous cyanobacteria, filamentous green algae, and diatoms (Table 2). There was a significant positive effect of brushing on biovolume of filamentous green algae ($F_{1,11} = 7.71$, $P = 0.02$), whereas *Rana* had a significant negative effect on biovolume of diatoms ($F_{1,11} = 11.25$, $P = 0.006$). Despite these differences in biovolume for some taxa, overall periphyton biomass (chl a) did not differ between treatments on day 24 (Tables 1–2).

Rana growth.—The number of surviving *Rana* at the end of the experiment varied independently of treatment from 12 to 15 individuals in all but one block. Only nine of the original 15 tadpoles were recovered from the B/R cage in Block D. On Day 6–7 this cage was nearly submerged during a flood; hence, some *Rana* may have escaped. Thus, we excluded Block D from the analysis since *Rana* growth is density-dependent (Flecker et al., 1999). *Rana* growth (change in total *Rana* biomass in each cage) over the 24-

TABLE 1. SUMMARY OF STATISTICAL ANALYSES FOR SEDIMENT STANDING STOCK AND PERIPHYTON BIOMASS (CHL a) DATA ON DAYS 10 AND 24 OF THE EXPERIMENT. Within each cell, results are given for Type III tests of main effects of presence of *Rana* and manual brushing of sediments and for the interaction of these effects. The last row in each column gives the results of MANOVA on the variables in that column.

Response	Day 10	Day 24
Sediment dry mass	<i>Rana</i> : $F_{1,12} = 7.25$ $P = 0.02$	<i>Rana</i> : $F_{1,12} = 10.62$ $P = 0.007$
	brush: $F_{1,12} = 19.13$ $P = 0.001$	brush: $F_{1,12} = 3.39$ $P = 0.09$
	<i>R</i> × <i>b</i> : $F_{1,12} = 0.11$ $P = 0.7$	<i>R</i> × <i>b</i> : $F_{1,12} = 1.28$ $P = 0.3$
Sediment AFDM	<i>Rana</i> : $F_{1,12} = 6.39$ $P = 0.03$	<i>Rana</i> : $F_{1,12} = 12.38$ $P = 0.004$
	brush: $F_{1,12} = 26.50$ $P = 0.0002$	brush: $F_{1,12} = 0.48$ $P = 0.5$
	<i>R</i> × <i>b</i> : $F_{1,12} = 1.72$ $P = 0.2$	<i>R</i> × <i>b</i> : $F_{1,12} = 0.80$ $P = 0.4$
Periphyton chl a	<i>Rana</i> : $F_{1,12} = 0.66$ $P = 0.4$	<i>Rana</i> : $F_{1,12} = 0.66$ $P = 0.4$
	brush: $F_{1,12} = 0.79$ $P = 0.4$	brush: $F_{1,12} = 0.79$ $P = 0.4$
	<i>R</i> × <i>b</i> : $F_{1,12} = 1.05$ $P = 0.3$	<i>R</i> × <i>b</i> : $F_{1,12} = 1.05$ $P = 0.3$
MANOVA	<i>Rana</i> : Wilks' $\lambda = 0.507$ $F_{2,8} = 3.89$ $P = 0.06$	<i>Rana</i> : Wilks' $\lambda = 0.329$ $F_{3,7} = 4.75$ $P = 0.04$
	brush: Wilks' $\lambda = 0.196$ $F_{2,8} = 16.40$ $P = 0.002$	brush: Wilks' $\lambda = 0.412$ $F_{3,7} = 3.34$ $P = 0.08$
	<i>R</i> × <i>b</i> : Wilks' $\lambda = 0.666$ $F_{2,8} = 2.00$ $P = 0.2$	<i>R</i> × <i>b</i> : Wilks' $\lambda = 0.775$ $F_{3,7} = 0.68$ $P = 0.6$

day experiment was significantly greater in ambient sediment cages (NB/R) (6.77 g ± 0.52 SE) than in brushed cages (B/R; 5.17 g ± 0.50 SE; $t_2 = 700$, $P = 0.01$).

Ancistrus growth.—Individual *Ancistrus* gained an average of 20% (4% SE) of their initial mass during the course of the experiment; of 80 individuals, all but two showed positive growth. However, *Ancistrus* growth was not affected by presence of *Rana* ($F_{1,9} = 0.37$, $P = 0.6$), removal of sediment ($F_{1,9} = 0.01$, $P = 0.9$), or the interaction of those two treatments ($F_{1,9} = 0.11$, $P = 0.7$; Fig. 2). There was a significant effect of size class on growth, whereby growth increased with size ($F_{4,4} = 8.95$, $P = 0.03$), but there was no interaction between size and presence of *Rana* ($F_{4,4} = 0.65$, $P = 0.7$) nor between size and brushing ($F_{4,4} = 0.13$, $P = 0.9$).

DISCUSSION

This experiment demonstrates that detritivorous *Rana palmipes* tadpoles can greatly reduce sediment accrual (Fig. 1, Table 1) despite heavy sediment deposition and that *Rana* grow better with sediment present than when it is absent. Because neither biomass nor community composition of periphyton differed between the two *Rana* treatments (Table 2), the resource that appeared to determine *Rana* growth was organic detritus, rather than living epipellic periphyton. These results support previous findings that benthic sediment represents an important nutritional source for *R. palmipes* tadpoles (Flecker et al., 1999), although sediments are not an adequate food resource for tadpole species in some temperate systems (Ahlgren and Bowen, 1991; Kupferberg et al. 1994). We observed sed-

TABLE 2. CHARACTERIZATION OF PERIPHYTON COMMUNITY AT THE END OF THE EXPERIMENT (DAY 24). The first column of data gives biomass (mg chlorophyll $a \times m^{-2}$ substrate) of the entire community. Remaining columns give biovolumes (mm³ cell volume $\times cm^{-2}$ substrate) of aggregate taxa. Data are mean (SE); $n = 4$ in all cases except $n = 3$ for NB biovolumes. Superscripts indicate significant differences between treatments (Tukey's multiple comparison, $P < 0.05$). Treatments: B or NB indicates sediment brushed or not brushed away from the substrate; R or NR indicates *Rana* present or not present.

Treatment	Algal biomass	Cyanobacteria	Filamentous green algae	Unicellular green algae	Diatoms
B/NR	13.07 (2.82)	55.6 (27.7)	104 (8.73) ^a	1.42 (1.41)	10.8 (3.36) ^{ab}
NB/NR	7.95 (2.80)	26.0 (23.0)	33.2 (26.4) ^{ab}	0.772 (0.465)	27.4 (13.2) ^a
B/R	8.15 (1.89)	54.1 (22.5)	54.7 (25.6) ^{ab}	1.06 (0.360)	3.81 (1.23) ^b
NB/R	8.53 (3.07)	108 (45.1)	15.9 (11.5) ^b	0.566 (0.566)	3.15 (0.832) ^b

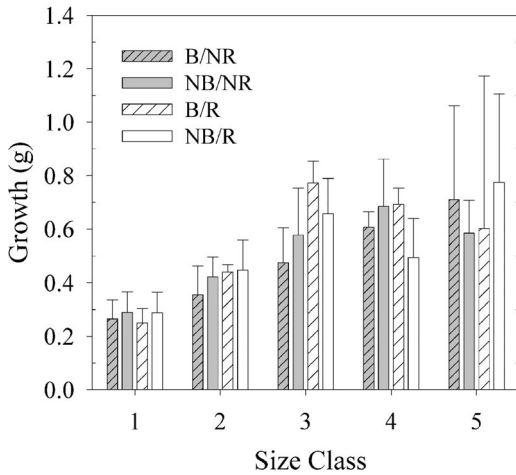


Fig. 2. There were no significant treatment effects on growth of *Ancistrus* from day 0 to day 24. Each bar represents the mean (± 1 SE) gain in mass of *Ancistrus* in that size class and treatment. Initial masses (mean ± 1 SE) of *Ancistrus* in each size class were 0.88 ± 0.17 g (Size 1); 1.69 ± 0.31 g (Size 2); 2.79 ± 0.43 g (Size 3); 4.46 ± 0.69 g (Size 4); 8.51 ± 2.50 g (Size 5). Treatments: B/NR, sediment brushed; NB/NR, sediment not brushed; B/R, sediment brushed and *Rana* present; NB/R, sediment not brushed and *Rana* present.

iment organic contents as high as 32%–70% by the end of the experiment, and Power (1984) observed sediment organic contents as high as 18–24% in a Panamanian stream. In contrast, published values for sediment organic content in temperate systems are generally between 1% and 14% in low-order streams (e.g., Osgood and Boylen, 1990; Gelwick and Matthews, 1992). The high organic content typical of sediments in Neotropical streams may make detritivory more profitable than in temperate streams and could explain why detritivory is widespread among Neotropical fishes (Bowen, 1983).

There was no evidence to support the hypothesis that sediment removal by *Rana* facilitates the growth of *Ancistrus* (Fig. 2), even though average sediment accumulation was four to 10 times greater in NB/NR than in other treatments (Fig. 1). We had based this hypothesis on two premises. First, we assumed that periphyton biomass increases in the absence of sediment caused by increased light availability (Pringle et al., 1993). In our study this premise did not hold, because there were no differences in total periphyton biomass (Table 2) despite significant sediment differences between treatments (Fig. 1). Epipellic diatoms in the sediment layer can be a major component of total periphyton biomass (Table 2; C. Solomon, un-

publ.); thus, sediment may inhibit epilithic periphyton but have no net effect on periphyton biomass, which may help explain why *Ancistrus* grew well even in high-sediment treatments. The importance of understanding sediment-algae-grazer interactions of this distinction between epilithic and epipellic periphyton has not been widely recognized.

Our second premise was that sediment imposes substantial energetic costs on *Ancistrus*. *Ancistrus spinosus* starved in shaded plastic pools with presumably little periphyton lost more fat reserves when the bottom of the pool was covered with sediment than when it was bare (Power, 1984). Power speculated that interference of sediment with respiration or digestion led to energetic costs, which she estimated at 15–22% of the daily energy budget of 10 g fish. We found no evidence of sediment-induced net costs to *A. triradiatus* despite large differences in sediment accumulation. Although it seems likely that there are at least some sediment-induced costs to respiration and digestion, they may be balanced by nutritional benefits when the sediment contains abundant high-quality organic matter. Organic content of sediment in our study was very high (mean AFDM 36% on day 10, 46% on day 24), and the epipellic algae, detritus, and associated bacterial and fungal communities likely provided a higher-quality food resource than was available to *Ancistrus* in the shaded artificial pools of Power's (1984) study.

When considered together with Power's (1984) study, our results suggest that the nature of the *Rana-Ancistrus* interaction varies spatially or temporally depending on sediment organic content. In systems with high sediment organic content and deposition rate (such as dry season Rio Las Marias), there may be no net positive or negative interaction, as the two species share sediment resources when they are abundant and *Ancistrus* switches to epilithic periphyton as necessary when sediment becomes scarce. Nevertheless, it is possible that in systems with low sediment organic content (such as disturbed watersheds where inorganic siltation is high, or perhaps even Rio Las Marias during the wet season) the costs of sediment to *Ancistrus* (Power, 1984) may greatly outweigh the benefits, and *Rana* may facilitate *Ancistrus*.

Species that are unable to capitalize on the high organic content of accumulated sediments also may benefit from sediment clearing by detritivores. For example, benthic insectivores, such as South American darters (*Characidium*), must sift through sediment to acquire prey but are probably not morphologically equipped to derive nutrition from detritus or epipellic pe-

riphyton. Such species may be facilitated by the tadpoles (this study and Flecker et al., 1999), fishes (e.g., Power, 1990; Flecker, 1996; Pringle and Hamazaki, 1998), and shrimps (Pringle et al., 1993; Pringle and Hamazaki, 1998) that reduce sediment accumulation in Neotropical streams. It is particularly important to understand interactions involving species that remove sediment in light of increasing human-induced changes (e.g., deforestation) to stream ecosystems. This study points to the need for additional work to determine the environmental contexts under which interspecific interactions are important in structuring tropical stream communities.

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