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Alexander S. Flecker

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ECOSYSTEM ENGINEERING BY A DOMINANT DETRITIVORE IN A DIVERSE TROPICAL STREAM¹

ALEXANDER S. FLECKER

Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, New York 14853 USA

Abstract. *Prochilodus mariae* (Characiformes: Prochilodontidae) is a detritivorous fish distributed throughout the Orinoco river basin of South America. Spectacular migrations of these fishes occur at the end of the rainy season into the Andean foothills. *Prochilodus* ingest large quantities of sediments and may thereby modify habitats in neotropical streams. The major objectives of this study were (1) to explore experimentally the importance of *Prochilodus* in structuring a tropical stream in the Venezuelan Andean piedmont, and (2) to determine whether there was sufficient ecological redundancy in a diverse and abundant assemblage of epibenthic fishes to compensate for the removal of *Prochilodus*. Community structure was compared among three experimental treatments: (1) *Prochilodus* exclusion, (2) *Prochilodus* enclosure, and (3) the natural fish assemblage. Selective exclusion of *Prochilodus* resulted in striking changes in community structure as measured by patterns of sediment accrual and the composition of algal and invertebrate assemblages. Highly significant increases in total dry mass and in ash-free dry mass of sediments accruing on stream-bottom substrates were observed almost immediately following the exclusion of *Prochilodus*. Moreover, the composition of algal and invertebrate assemblages was significantly modified by *Prochilodus*. Taxa such as diatoms were reduced in number when *Prochilodus* was present; in contrast, *Prochilodus* appeared to facilitate nitrogen-fixing cyanobacteria. Total invertebrate densities were greatest in the *Prochilodus* removal treatment; however, a variety of responses to the experimental treatments was observed among different taxa analyzed individually, including density reductions, increases, and no measurable effects. This study suggests that the detritivore *Prochilodus* is a functionally dominant species in Andean foothill streams via sediment-processing activities. Moreover, it provides little evidence to support the notion that strongly interacting species are limited to simple systems with few food web components.

Key words: Andean streams; community structure; detritivory; disturbance; ecological redundancy; fish; habitat modification; neotropics; sediments; spatial heterogeneity; species interactions.

INTRODUCTION

In spite of the cosmopolitan occurrence of detrital-feeding organisms, manipulative experiments by community ecologists seldom focus on this group of consumers. In sharp contrast, ecologists interested in ecosystem dynamics historically have devoted considerable effort to understanding detritivory as a crucial pathway of energy and nutrient flux in ecosystems (e.g., Lindeman 1942, Odum 1971, Wetzel 1983, DeAngelis 1992). Although a number of authors have recently suggested that detritivory needs to be better incorporated into food web theory (e.g., Polis 1991, Bengtsson et al. 1995), there are relatively few empirical demonstrations that detritivores can indeed exert strong community-level interactions on a par with those of predators and herbivores.

In this paper, I focus on the importance of detritivorous fishes in influencing patterns of species abundance and distribution in neotropical streams by acting as key sources of biological disturbance. I suggest that

biological disturbance of sediments is a form of ecosystem engineering (sensu Jones et al. 1994) that may be especially important in neotropical streams for a number of reasons. First, neotropical freshwater systems often contain a remarkable diversity of detritivorous fishes (Bowen 1983). For example, Goulding et al. (1988) reported that at least 132 species from 13 fish families feed on fine detritus in the Rio Negro of Brazil. Of particular significance in South America are two families of characoids, Prochilodontidae and Curimatidae, which are highly specialized for deriving nutrition from a diet of fine detritus (Bowen 1983). Prochilodontids and curimatids feed largely on flocculent organic material (Bowen et al. 1984, Vari 1989, Flecker 1992a), leaving characteristic feeding scars that can be readily quantified. Second, detritivores often comprise the bulk of the fish biomass in South American streams. Bonetto (1986) reported that the detritivore *Prochilodus platensis* alone comprised as much as 50–60% of the fish biomass in the Rio Paraná, with standing crops >1000 kg/ha. Elsewhere in South America, *Prochilodus* has been reported to be the most dominant component of fish assemblages in terms of biomass (Taphorn 1992). Third, since fine detritus is generally a

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nutritionally poor food source, a necessary solution for making a living on sediments is to process large volumes of material (Lopez and Levinton 1987). Thus, due to their striking diversity, abundance, and nutritional habits, detritivorous fishes are likely to be dominant players in the ecology of neotropical streams.

However, sediment disturbance by detritivores in stony-bottom streams may differ substantially from bioturbation described in other aquatic systems. Bioturbation generally has been associated with soft-bottom marine and lentic systems (e.g., Rhoades 1974, Nalepa et al. 1980, Brenchley 1981, Levinton 1995), where deposit-feeding organisms such as burrowing worms and bivalves change the physical characteristics of the fine-sediment habitat. Instead, detritivorous fishes in streams can reduce sediments accruing on hard stony substrates, and are likely to be important in generating habitat heterogeneity. A main effect of disturbance by fishes may be to modify microhabitat quality (Flecker 1992a). Such habitat modification may simultaneously limit some species that thrive in sediment-rich environments, yet facilitate other taxa that depend on the presence of hard stony substrates largely free of fine sediments.

The major objective of this study was to explore the importance of biological disturbance in Venezuelan Andean streams by the migratory detritivore *Prochilodus mariae*. *Prochilodus* migrates into Andean piedmont streams during the dry-season months, when it can comprise a significant portion of the fish biomass. Previous research had established that the assemblage of epibenthic-feeding fishes played a major role in structuring piedmont stream communities (Flecker 1992a), however, the relative importance of *Prochilodus* was not determined. Here, I ask three related questions: (1) Does *Prochilodus* significantly influence patterns of sediment accrual on stony-bottom substrates?, (2) Is the structure of invertebrate and algal assemblages strongly altered if sediment distributions are indeed modified?, and (3) Is there sufficient ecological redundancy such that other fish species compensate for the removal of *Prochilodus* in species-rich tropical stream systems? In contrast to the strong bias in the literature towards studies examining interaction webs among predators and herbivores (see Strong 1992, Bond 1993, Menge et al. 1994), my goal is to suggest that interactions involving detritivores may be a feature central to the organization of diverse neotropical stream communities.

Description of the study site

The study was conducted in Rio Las Marias, located in the Andean piedmont of Venezuela. Rio Las Marias is found in the Rio Apure drainage of the Rio Orinoco. Rio Las Marias is a fourth-order stream in Estado Portuguesa and the main study site is found at an elevation of ≈ 180 m ($9^{\circ}10'$ N, $69^{\circ}44'$ W). Rio Las Marias has a stony bottom and warm water, with diel temperatures

ranging from ≈ 25 – 32°C (Flecker and Feifarek 1994). Rivers in the Andean piedmont are distinctly seasonal. The region experiences two seasons each year, a wet season that generally lasts between May and November, and a dry season from about December to April. Average annual rainfall recorded near Rio Las Marias over an 11-yr period was 1886 mm (Flecker and Feifarek 1994). In general, very little rainfall occurs during the dry season; stream discharge falls steadily throughout the period and in some years (e.g., 1988, 1995) the stream dries up completely (Flecker and Feifarek 1994; A. Flecker, *unpublished data*). Andean piedmont streams are transparent during the dry months, whereas water clarity is low during the rainy season when streams carry heavy sediment loads. Seasonal variation in invertebrate densities reflects extremes in flow regimes. Life cycles of at least some common taxa are relatively brief (i.e., 10–15 d), and insect densities can quickly return to pre-flood densities (Flecker and Feifarek 1994 and *unpublished data*). Field work reported in this paper was conducted during January and February 1991 and no rainfall was recorded at the study site during this period. The experiment was performed in a series of slow-moving runs, where the depth range was ≈ 15 – 35 cm and stream width was ≈ 6 – 12 m.

Fish assemblages of piedmont streams are diverse, composed largely of characiforms (tetras and allies) and siluriforms (catfishes). I have recorded more than 75 fish species at the study site and continue to add fish species. Many fish in the region cannot be readily classified into distinct feeding guilds; however, bottom feeding is clearly a widespread phenomenon throughout piedmont fish assemblages (see Winemiller 1990 for a detailed food web from a nearby stream). The most diverse components of the fish fauna are: (a) small tetras (Characidae), many of which are trophic generalists, (b) long-whiskered catfish (Pimelodidae), most of which are insect and/or fish predators, and (c) armored catfish (Loricariidae), most of which are epibenthic grazers on algae and detritus. Grazing fish are extremely abundant in the Andean piedmont. In addition to a diversity of armored catfish, the characid *Parodon apolinari* (Parodontidae) is one of the most common grazers in the piedmont region (Taphorn 1992). Finally, the detritivore *Prochilodus mariae* (Prochilodontidae) is generally the dominant fish by biomass during the dry-season months (Taphorn 1992; A. Flecker, *personal observation*). Thus, this tremendous influx of detritivore biomass into the Andean piedmont has potentially interesting consequences for stream community organization.

METHODS

Experimental design.—This experiment was designed to tease apart the relative strength of interactions involving the detritivore *Prochilodus mariae*. Prior experimentation suggested that removal of the entire assemblage of benthic feeding fishes significantly altered

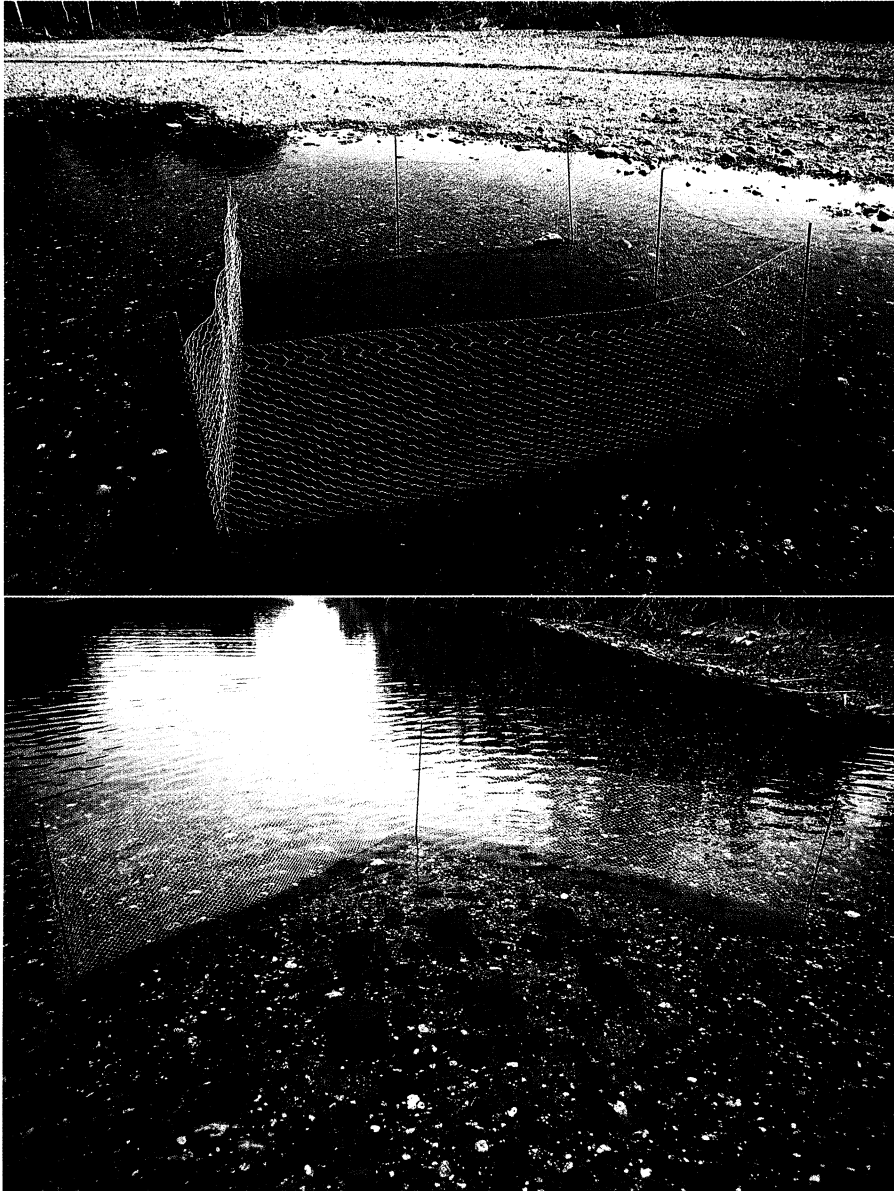


FIG. 1. Photographs showing striking differences in sediment accretion between a *Prochilodus* exclusion (top photo) and control (bottom photo).

community structure (Flecker 1992a); however, it remained unclear whether this was due to the diffuse effects of a diverse group of benthic fishes, or strong impacts of relatively few species. I took advantage of the fact that *Prochilodus* can be selectively removed because it is generally the largest benthic-feeding fish present at the study site during the dry-season months (standard length up to 350 mm, Taphorn 1992). In order to separate the effects of *Prochilodus* alone and together with other benthic fishes, an enclosure/exclosure experiment was set up with three treatments: (1) *Prochilodus* exclusion, (2) *Prochilodus* enclosure, and

(3) open cage. Cages were 2×2 m in dimension, constructed of poultry wire walls supported by steel concrete-reinforcing rod at each corner (Fig. 1). Cages were built without floors so that the bottom of each cage was natural stream. By using a relatively large mesh size (25 mm) I selectively excluded *Prochilodus*. I was able to exclude virtually all *Prochilodus* because individuals do not migrate into the Andean piedmont until after they have attained a body diameter greater than the mesh. This mesh size also could exclude large individuals of some armored catfish (Loricariidae: *Anacistrus*, *Chaetostoma*, *Hypostomus*) present at the study

site; however, this was unlikely to be a major concern because large size classes of these species were relatively rare. Thus, the *Prochilodus* exclusion treatment effectively allowed access to the full complement of the natural benthic fish assemblage except *Prochilodus*. The *Prochilodus* enclosure contained eight individual fish. This density (i.e., two fish per square metre) was within the natural range of variation in *Prochilodus* density encountered in Andean piedmont streams. Finally, cage controls were open on the downstream side and allowed visitation by the natural fish assemblage (Fig. 1). The three treatments were replicated in four randomized complete blocks placed in slow-moving runs, and blocks were separated by a minimum distance of 25 m.

Eight baskets of cobble substrates (dimensions 25 × 19 × 5 cm) were placed directly on the bottom of each cage (Fig. 1). Cobbles were gathered from the stream to ensure that substrates had a live periphyton layer. After 7 and 14 d, baskets were collected for invertebrates, algae, and sediments. I chose to run this experiment for a relatively short period because: (1) sediment feeding by fishes is a dynamic process, resulting in a patchy distribution of sediments on a time scale of hours to days, (2) insect colonization is extremely rapid (Flecker 1992a, b), and (3) previous studies indicate that life cycles of common insects are short in piedmont streams (Flecker and Feifarek 1994 and unpublished data). Four baskets of substrate were removed on each sampling date by placing a 200- μ m mesh net behind (downcurrent of) each basket to catch stray invertebrates. Invertebrates were collected from two baskets and immediately preserved in 95% ethanol mixed with rose bengal as a colorant. Sediments were sampled from the remaining two baskets in each cage by gently lifting the basket out of the water and removing the sediment from a 18.9-cm² circle on each of two stones. The sampling area was delineated using a plastic jar lid as a circular 18.9-cm² template. Sediment was brushed away from all but the area immediately beneath the template, leaving a distinct circle of sediment. This remaining sediment was subsequently filtered onto glass fiber filters (Whatman GF/C) and sun dried in the field. Periphyton was sampled from the two flattest stones from each of the four baskets. Similar to the sediment sampling, a 18.9-cm² circle of periphyton was removed from each stone using a hard-bristle toothbrush and immediately preserved in \approx 5% formalin.

In the laboratory, all invertebrates retained in a 200- μ m screen were counted to the lowest taxon readily identified (genus for most groups). Dry mass and ash-free dry mass (AFDM) of sediments were determined by drying sediment samples in an oven at 60°C for 24 h, after which they were weighed, ashed in a muffle furnace for 2 h at 550°C, and reweighed. Algae were subsampled in the laboratory and counted at 400 \times using a compound microscope and a Palmer counting cell.

A total of 50 fields of view was counted per subsample; the number of algal filaments was recorded for filamentous algae, whereas the number of cells was quantified for unicellular algae. Diatoms were identified to genus, with the exception of a category called "naviculoid" diatoms composed of *Navicula*, *Achnanthes*, and *Nitzschia*.

Statistical analyses.—The experiment was analyzed as a repeated-measures ANOVA using a randomized complete block design, with blocks representing different locations in the stream. I considered baskets as subsamples and cages as replicates; therefore, the means of multiple values (baskets) for each date were used as a single datum per cage for statistical analyses. Data were $\log(x + 1)$ transformed, which corrected problems of non-homogeneity of variance before transformation. Differences between treatments were analyzed for the number of invertebrates, algal density, sediment dry mass, and sediment AFDM. Subsequently, Bonferroni post-hoc comparisons were used to evaluate differences among treatments. The criterion for analyzing an invertebrate taxon separately was a mean density >10 individuals/m² in at least one treatment. Analyses were conducted using the statistical package STATISTIX, version 4.0 (Analytical Software 1992).

RESULTS

Fish effects on sediment accrual.—There were strong effects of fish treatment on patterns of sediment accrual ($P < 0.0018$, Figs. 1 and 2, Table 1). Dramatic increases in the accrual of sediments were quickly observed when *Prochilodus* was excluded. Within days, a readily visible sediment layer covered the bottom of *Prochilodus* exclusion cages; in contrast, little sediment was present in open cages accessible to the entire fish assemblage (Figs. 1 and 2). Relatively little sediment was also observed in the *Prochilodus* enclosures compared to the exclusion treatment, yet reductions in sediment accrual were not as extensive as those in open cages (Fig. 2). AFDM generally comprised 8–10% of sediment dry mass. Similar patterns among treatments were observed regardless of whether sediments were analyzed as dry mass or AFDM. However, AFDM in *Prochilodus* enclosures could not be distinguished statistically from either the exclusion or the open treatment. There was no significant date \times treatment interaction on sediment accrual ($P < 0.89$). Therefore, it appears that differences among treatments in sediment mass were quickly established, but sediments did not progressively accumulate throughout the experiment. This would be expected if sediment began to partially erode from *Prochilodus* exclusions once a thick (2–5 mm) layer had accrued.

Fish effects on algal assemblages.—Highly significant effects of the fish treatments were observed on the composition of algal assemblages (Fig. 3, Table 1). Algal assemblages were dominated by the filamentous cyanobacteria *Calothrix* and several genera of diatoms

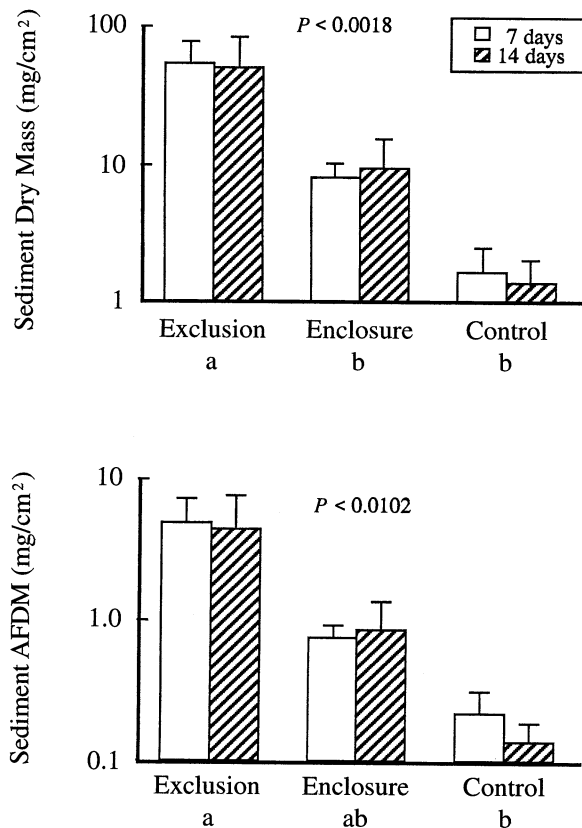


FIG. 2. Sediment dry mass (top panel) and sediment ash-free dry mass (AFDM, bottom panel) from the three experimental treatments (*Prochilodus* enclosure and enclosure, and control). Data are means and 1 SE. Probabilities and *F* statistics for treatment effects are listed in Table 1. Significant differences among treatments were determined using Bonferroni multiple comparisons; treatments with different letters beneath histogram bars differ significantly from each other.

(i.e., "naviculoids," *Cocconeis*, and *Synedra*). Responses of *Calothrix* and diatoms to the fish treatments were strikingly different (Fig. 3). Densities of the cyanobacteria *Calothrix* were significantly greater in treatments with *Prochilodus* present (i.e., open cages and *Prochilodus* enclosures) compared to *Prochilodus* exclusions ($P < 0.0005$), suggesting that fish facilitate this common alga. No differences were observed between the *Prochilodus* enclosures and open cages. In contrast to cyanobacteria, numbers of diatoms were highest in the *Prochilodus* exclusion treatment ($P < 0.0245$, Fig. 3). Significant differences could be distinguished, however, only between the *Prochilodus* exclusions and open cages.

Fish effects on insect density.—There were highly significant differences among treatments in the number of total invertebrates colonizing stony substrates ($P < 0.0006$, Fig. 4, Table 1). On both dates, insect densities were 70–400% greater in the *Prochilodus* exclusions compared to treatments with *Prochilodus* (i.e., *Prochilodus* enclosures and open cages). Insect densities

TABLE 1. Effects of the experimental treatments (*Prochilodus* enclosure and enclosure, and control) on an Andean stream (repeated-measures ANOVA on $\log(x + 1)$ -transformed data, followed by Bonferroni multiple comparisons).†

Source of variation	<i>F</i> _{2,6}	<i>P</i>	Treatment comparisons		
			Excl.	Encl.	Cont.
Sediment dry mass	21.49	.0018	a	> b	= b
Sediment AFDM	10.84	.0102	a	≅ ab	≅ b
<i>Calothrix</i>	34.84	.0005	b	< a	= a
Diatoms	7.33	.0245	a	≅ ab	≅ b
Total invertebrates	32.06	.0006	a	> b	> c
Ephemeroptera:					
<i>Tricorythodes</i>	11.46	.0089	a	≅ ab	≅ b
Ephemeroptera:					
<i>Baetis</i>	3.15	.1162
Ephemeroptera:					
<i>Camelobaetidius</i>	30.00	.0008	b	< a	= a
Trichoptera:					
<i>Neotrichia</i>	4.81	.0567
Trichoptera: total					
Hydroptilidae	33.10	.0006	a	> b	> c
Trichoptera:					
<i>Polycentropus</i>	0.47	.6453
Diptera:					
Chironomidae	33.36	.0006	a	> b	> c
Diptera: <i>Bezzia</i>	40.62	.0003	a	> b	= b
Coleoptera:					
Elmidae	23.83	.0014	a	> b	= b
Lepidoptera:					
Pyralidae	3.01	.1245
Hydracarina	3.11	.1183

† Bonferroni comparisons are included only for taxa in which there were significant overall effects of fish treatment based on repeated-measures ANOVA. Treatments that are significantly different are indicated by different letters. Excl. = *Prochilodus* exclusion, Encl. = *Prochilodus* enclosure, Cont. = control.

in *Prochilodus* enclosures were significantly lower than when *Prochilodus* was excluded. Moreover, when the rest of the natural assemblage of fishes was present in open cages, further reductions in invertebrate numbers were observed. Patterns of insect densities closely resembled those of sediment accrual (Figs. 2 and 4), and a highly positive Pearson product-moment correlation was observed between sediment dry mass and insect abundance ($r = 0.715$, $P < 0.001$).

Fish-treatment effects were widespread within the invertebrate assemblage, although the strength of the response varied among taxa. More than half of the taxa analyzed separately displayed significant treatment effects, and several common patterns were observed (Table 1, Fig. 5). For example, there were significant differences among each of the treatments for the most abundant taxon, chironomid larvae ($P < 0.0006$), as well as for hydroptilid caddis larvae ($P < 0.0006$). These taxa were significantly less abundant in treatments with *Prochilodus* (i.e., *Prochilodus* enclosures and open cages) compared to exclusions, and further reductions in insect numbers were observed in open vs. *Prochilodus* enclosure treatments. Another pattern was displayed by elmid beetles ($P < 0.0014$) and the

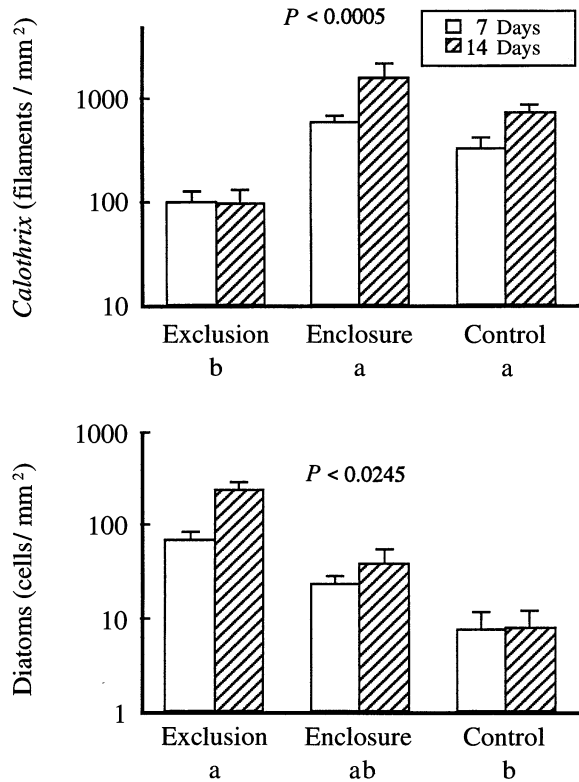


FIG. 3. Densities of the cyanobacteria *Calothrix* (top panel) and total diatoms (bottom panel) from the three experimental treatments. Data presentation and comparisons are as in Fig. 2.

ceratopogonid fly larvae *Bezzia* ($P < 0.0003$); highly significant reductions in densities were found in the treatments with *Prochilodus*, but in these cases no significant differences were observed between *Prochilodus* enclosure and open treatments. The abundant mayfly *Tricorythodes* ($P < 0.0089$) showed more ambiguous treatment effects, with significant differences observed only between *Prochilodus* exclusions and open cages. Finally, densities of the mayfly *Camelobaetidium* ($P < 0.0008$) were significantly greater in *Prochilodus* enclosures and open cages compared to the exclusion treatment.

There were few instances where significant treatment \times date interactions were found (total invertebrates, $P < 0.024$; hydroptilid larvae, $P < 0.036$; *Bezzia*, $P < 0.020$). In each of these cases, differences between *Prochilodus* enclosures and open cages varied according to date, although strong effects of the *Prochilodus* exclusion were consistently observed (Fig. 5).

DISCUSSION

Strong interactions in a diverse tropical community.—The selective removal of *Prochilodus* resulted in dramatic changes in community and ecosystem attributes. Most striking was the rapid accrual of sediments in the absence of this single fish species (Figs. 1 and

2). Relatively minor differences in sediment buildup were found between the *Prochilodus* enclosures and the natural fish assemblage (i.e., open treatment), and these differences were not significant. Highly significant effects were observed in the composition of algal and invertebrate assemblages (Figs. 3–5). Although in some instances significant treatment effects also were observed between *Prochilodus* enclosures and the natural fish assemblage (i.e., open cages), differences were generally much smaller in magnitude than those between open cages and *Prochilodus* enclosures. These results support the notion that *Prochilodus* plays a central role in the structure of this Andean stream community, and sediment processing appears to be at least one major mechanism.

The finding that *Prochilodus* depressed diatom densities yet facilitated the cyanobacteria *Calothrix* was consistent with studies of the impact of grazing fishes on the composition of algal assemblages in temperate streams (Power et al. 1988, Gelwick and Matthews 1992). The mechanism to explain these results is not entirely clear. It is likely that grazing fishes selectively remove some diatom species, although the elimination of suitable microhabitat by sediment-feeding fishes may better explain reductions of those diatom taxa generally associated with a loose sediment layer (e.g., *Nitzschia*, *Surirella*). Similarly, Hill and Knight (1987) argued that the mayfly *Ameletus* depressed densities of a number of diatom taxa by modifying the availability of sediments (see *Ecosystem engineering* section below). In contrast, the cyanobacteria *Calothrix* may persist under conditions of intense grazing pressure due to characters that confer grazer resistance including the formation of tufts with basal regeneration and the secretion of copious mucilage (Power et al. 1988). It remains to be seen whether detritivory works to mediate competition for nutrients between diatoms and cyanobacteria, or whether detritivores alter light levels that differentially affect the growth of different algal taxa.

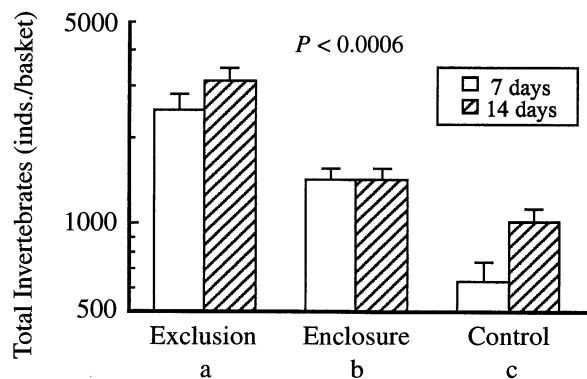


FIG. 4. Comparisons of total insect abundance from the three experimental treatments. Data presentation and comparisons are as in Fig. 2.

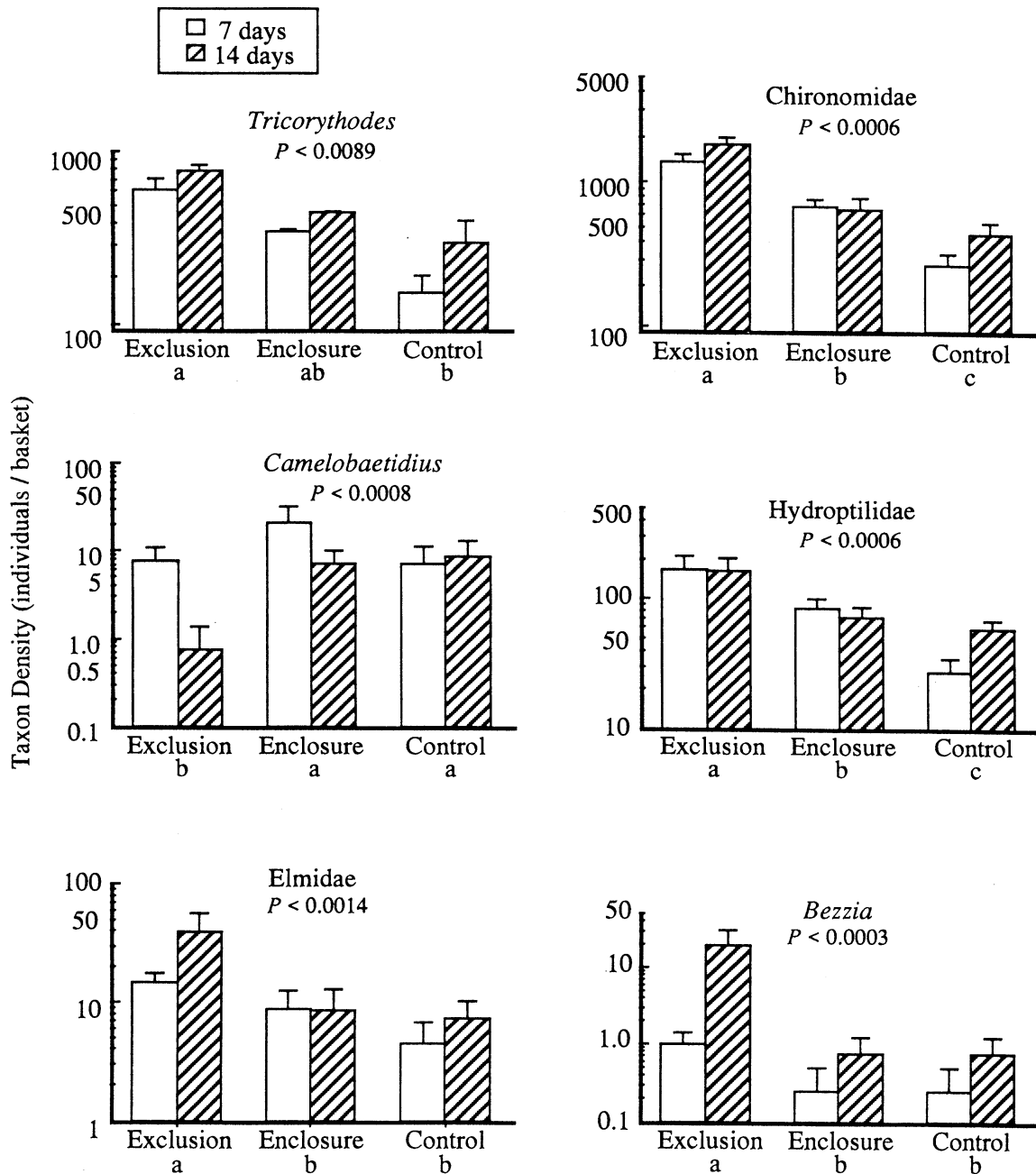


FIG. 5. Patterns of abundance of various insect taxa from the three experimental treatments of insect taxa that displayed significant treatment effects. Data presentation and comparisons are as in Fig. 2.

Results from this study present the interesting question of why other members of Rio Las Marias' diverse fish assemblage (with >75 species) did not compensate for the selective removal of *Prochilodus*. In other words, why is *Prochilodus* such a functionally dominant species, given the prevalence of other epibenthic feeders? Ecologists are divided on whether strongly interacting species should even occur in diverse communities. Strong (1992) asserted that high diversity

systems are rarely controlled by just a few species, and when this does occur it may be largely an anomaly of human interference. His argument was that trophic architecture in speciose ecosystems is characterized by a high degree of omnivory, extensive food web looping and connectivity, and minimal food web compartmentalization; such features should buffer systems from the rampant consumption typical of at least some strongly interacting species. Although his hypothesis is intu-

itively appealing, my own observations of *Prochilodus* as a strong interactor in Rio Las Marias provide little support for this view. Menge et al.'s (1994) recent analysis of keystone predation similarly failed to corroborate Strong's contention that low diversity distinguishes systems driven by a few strongly interacting consumers. Instead, other characteristics appear to be more important than community diversity per se in determining whether a species is a strong interactor. In the case of *Prochilodus*, the essential features may be the efficacy of this abundant detritivore in modifying microhabitat structure and resource distributions.

One potential explanation for the apparent lack of functional redundancy may be linked to the fact that the relative nutritional value of epibenthic resources to consumers varies greatly among fish species. Although a mix of periphyton and fine detritus is found in the diet of many species, there may be few fishes that actually derive nutrition from harvesting a sediment layer. Prochilodontids are exceptional in that they are highly specialized for exploiting a sediment-rich diet (Bowen 1983). A suite of morphological features in the alimentary canal allows for efficient ingestion, sorting, sifting, and grinding of fine detrital particles; furthermore, research on a closely related prochilodontid species (*Prochilodus platensis*) indicates that they are dependent on fine detritus, rather than algae or micro- or macro-organisms, for deriving the bulk of their nutrition (Bowen et al. 1984). In contrast, other epibenthic-feeding fishes such as the extremely diverse armored catfishes (Loricariidae) may gain little or no nutritional value from ingesting sediments (Bowen 1983). For example, Power (1984) reported a net energy expenditure of up to 22% when the armored catfish *Ancistrus* was fed a sediment-rich diet. Thus, fishes other than *Prochilodus* may avoid patches of heavy sediment when sediment processing requires considerable energy expenditure, especially when patches are available where little sediment has accrued. Indeed such options exist within the context of the present study.

Ecosystem engineering of sediments as a key organizing feature of stream communities.—A major finding of this research is that sediment-processing activities of fishes are key to structuring biotic communities of Rio Las Marias. One reason why sediment-processing fishes are strong interactors is their ability to modify habitat structure and resource availability (Flecker 1992a). This is consistent with a growing body of evidence from other systems that habitat modification may be a process central to the organization of many natural communities. In a recent stimulating paper, Jones et al. (1994) outlined different ways in which organisms create, modify, and maintain habitats, and they referred to such organisms as ecosystem engineers. Striking examples of ecosystem engineers that strongly alter a suite of community and ecosystem attributes are scattered in the ecological literature (see Jones et al. 1994, Lawton and Jones 1995); some of the

best known cases include beavers (Naiman et al. 1986, 1988), earthworms (Darwin 1881, Parmelee 1995), burrowing mammals (e.g., Huntly and Inouye 1988, Whicker and Detling 1988), and marine deposit feeders (e.g., Rhoades 1974, Meadows and Meadows 1991, Levinton 1995). Although Lawton and Jones (1995) argue that ecosystem engineers are likely to be ubiquitous, they explicitly point out that they "know of very few field manipulation experiments designed to quantify the impact of ecosystem engineers by removing or adding species." Due to their impact on habitat structure and the availability of resources, organisms that modify habitat have great potential to be strong interactors in natural communities.

Until recently, habitat modification by consumers has not been recognized as one of the major structuring mechanisms in running-water communities (see Lake 1990). Although beavers represent an extreme example of engineering through their abilities to change stream channel morphology (e.g., Naiman et al. 1986, 1988), in fact, organisms that more subtly modify habitat structure may be commonplace in riverine systems. In particular, biological disturbance of sediments may be widespread, with different sets of ecological players being the dominant sediment processors in geographically distinct localities. Experimental studies explicitly testing how organisms alter sediment distributions in streams have been few; yet those instances where investigators have paid close attention to animal influences on sediments have been quite revealing and often dramatic. Thus, the common thread emerging from studies of stream community organization in the tropics is a consistently strong role of biological disturbance of sediments (Power 1984, 1990, Flecker 1992a, Pringle et al. 1993, Pringle and Blake 1994). For example, Power's (1984, 1990) seminal work on grazing fishes in Panama demonstrated that sediment processing is a major mechanism whereby, depending on grazer density, grazers can either facilitate or inhibit algal standing crops. In Puerto Rican streams with few fish, freshwater shrimp instead act as major sources of biological disturbance of sediments; sediment accrual is highly modified via sediment ingestion and bioerosion, which in turn strongly alters the composition of benthic assemblages (Pringle et al. 1993, Pringle and Blake 1994).

The influence of stream biota on sediment distributions, however, is not limited to the neotropics. In the central United States, stoneroller minnows (*Campostoma*) are undeniably strong interactors, and their potent effects as sediment processors on community structure and ecosystem function have been well described in prairie streams (e.g., Power et al. 1985, Matthews et al. 1987, Gelwick and Matthews 1992). Elsewhere in North America, fishes such as hog suckers (Catostomidae: *Hypentilium nigricans*) can efficiently clear sediments from stony substrates (A. S. Flecker, *personal observation*), but to my knowledge there have

been no experimental studies of these epibenthic fishes on their role in organizing stream communities. In addition to fishes, invertebrates can significantly alter patterns of sediment accrual and resuspension. Harvey and Hill (1991) reported that field manipulations of a common snail (*Elimia*) in a Tennessee headwater stream resulted in clear reductions in sediment accumulations where snails were present. They argued that habitat alteration of silt by snails was one mechanism to explain an observed negative interaction with other invertebrates. In a study in California, Hill and Knight (1987) posited that the mayfly *Ameletus* reduced silt availability, accounting for declines in the abundance of diatom taxa commonly associated with inorganic sediment. Likewise, crayfish may be important ecosystem engineers at other localities. In a Michigan stream, crayfish indirectly decreased sedimentation by eliminating the filamentous alga *Cladophora*, which otherwise acted as an effective sediment collection trap; diatoms intolerant of siltation increased in abundance and were thereby facilitated by crayfish grazing activities (Hart 1992, Creed 1994). Recent work with stoneflies suggests that these insects may enhance rates of sediment resuspension through their foraging activity (B. A. Zanetell and B. L. Peckarsky, unpublished data).

In summary, field experimentation with the detritivore *Prochilodus* provides strong evidence that ecosystem engineering in the form of biological influences on sediments can be critical to the organization of at least some stream communities. In Rio Las Marias, detritivorous fishes such as *Prochilodus* are dominant sediment processors, in spite of high species diversity. In running-water systems elsewhere, a different set of ecological players may similarly control community and ecosystem dynamics through sediment-biota interactions. Finally, the strong influence of *Prochilodus* on community structure and function has important implications for the conservation of neotropical streams. *Prochilodus* fisheries are heavily exploited in South America (e.g., Goulding 1981, Quirós and Cuch 1989, Valderrama-Barco and Zárate-Villareal 1989, Novoa and Ramos 1990), and the ongoing construction of impoundments as barriers to movement into spawning areas are major concerns for the conservation of many migratory fishes. The apparent lack of functional redundancy in this diverse tropical stream community suggests that the loss of *Prochilodus* would have broad consequences manifested throughout Andean stream ecosystems.

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