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Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river

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Abstract. The Cinaruco River, a lowland floodplain river in the Venezuelan llanos, has a strongly seasonal hydrology, low nutrient concentrations, and high fish diversity and abundance. Fish exclosure/enclosure experiments were conducted in the littoral zone of the river channel and connected lagoons to examine seasonal variation in the magnitude of fish effects on benthic organic matter and algal biomass. During the dry season, large-fish exclosures in the channel accrued significantly more sediment, organic material, and chlorophyll than control cages after 20 d. Grazing scars suggested the bocachico, *Semaprochilodus kneri*, was a major consumer of organic-rich sediments. Further experiments were conducted to test the hypothesis that the relative strength of top–down (grazer) control of organic matter in sediments varies according to species, hydrologic period, and habitat. At flooding onset (May), *S. kneri* migrate to the Orinoco River to reproduce and feed. Thus, their densities are extremely low in the Cinaruco during the interval when nutrient inputs from newly flooded plains should be greatest, whereas densities are highest during the low-water season. Experiments conducted during the low-water period in the river channel and floodplain lagoons revealed significant treatment (large-fish exclosure, total fish exclosure, *S. kneri* enclosure, control) effects for accumulation of sediment mass, organic material mass, and chlorophyll *a* on tiles after 8 d. Chlorophyll *a* concentrations were significantly greater in lagoons than river-channel sites. Mean mass of sediments and organic material matched our prediction of grazer control during the low-water season. Experiments during the early rising-water period, when *S. kneri* emigrate from the Cinaruco, yielded no significant habitat or treatment effects after 3 d. Overall, our results support a model predicting continuous, gradual change in the magnitude of top–down effects of benthivorous grazing fishes on organic material on sediments as a function of seasonal changes in water level.

Key words: algivore, periphyton, seasonal hydrology, *Semaprochilodus kneri*, top–down control, Venezuela.

Intense interest in the relative effects of bottom–up control (productivity or donor control) vs top–down control (consumer control) on community structure was stimulated by a provocative paper by Hairston et al. (1960). Abundant evidence indicates that top–down control occurs in many ecosystems, despite the many factors that can preclude its development, including

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defended plants and omnivory (Strong 1992, Polis and Strong 1996). A growing number of studies in freshwater lotic systems have demonstrated strong top–-down control of benthic algae (e.g., Power et al. 1985, 1989, Power 1990, 1992, Flecker 1992, 1996, Gelwick and Matthews 1992, Pringle et al. 1993, Pringle and Hamazaki 1997, Nakano et al. 1999) even though aquatic communities, including those with low species diversity, generally have well-defended primary producers (e.g., aquatic cyanobacteria) and highly reticulate food webs with high incidences of omnivory (Winemiller 1990). Top–down control in many systems depends on spatial or temporal heterogeneity that creates a foodweb subsidy allowing consumer biomass to be maintained at levels capable of suppressing their in situ resources (Persson et al. 1996, Polis et al. 1996, 1997, Persson 1999). Without such subsidies (yielding unbalanced reciprocity), donor control should drive the system to equilibrium with production attenuating at successively higher trophic levels (Lindeman 1942) and with resource competition occurring within trophic levels (Tilman 1982).

A major challenge is to determine those factors that control, under varying conditions, the strength of interactions among trophic levels (Matson and Hunter 1992). In a recent review of bottom–up and top–down control of autotrophic biomass in streams, Hillebrand (2002) concluded "there is little consensus about the relative importance of the two factors under varying environmental conditions". Few studies have demonstrated how spatial and temporal heterogeneity naturally create the kinds of subsidies that lead to top–down control (Polis and Strong 1996, Polis et al. 1997, Huxel et al. 2004). Spatial subsidies (allochthonous inputs) have tended to be easier to identify than subsidies derived from temporal dynamics (e.g., asynchronous responses by consumers and resource populations to environmental variation; see Sommer et al. 1986, Roelke et al. 1997). Here, we examine the relative strength of top–down control in a lowland river ecosystem in a tropical savanna region with strong wet–dry seasonality.

Annual floods of the Cinaruco River cause dilution of dissolved nutrients and increases in water velocity, both of which reduce water-column productivity (Cotner et al. 2006, Montoya et al. 2006, Roelke et al. 2006). The magnitude of top–down (grazing) and bottom–up (nutrient supply for primary production) control should vary in a predictable manner in response to the cyclic annual hydrologic regime of this river. The per-unit-area density of benthivorous fishes is greatest during the low-water period when aquatic habitat is reduced, and densities are lowest during the peak of the flood pulse when fishes are dispersed in expanded aquatic habitats. At the onset of flooding, the principal large grazing fish in the system, the bocachico (*Semaprochilodus kneri*, Prochilodontidae), migrates from the Cinaruco to the Orinoco River where they spawn and feed. Thus, we predicted negligible effects from large grazing fishes, and very weak effects from small benthivorous fishes (e.g., omnivorous characids, anostomids and loricariids; detritivorous curimatids and hemiodids) during the flood period.

We proposed that benthic grazers, especially the migratory bocachico, regulate levels of benthic algae and fine particulate organic matter within sediments in a manner similar to that demonstrated in an Andean piedmont stream in Venezuela (Flecker 1992, 1996). We further proposed that the magnitude of this top–down effect of large benthic grazers would be greater during the low-water phase than the flooding phase of the annual flood cycle (see above), and might vary according to habitat (lotic channel vs lentic lagoon sites). These hypotheses were tested using field experiments designed to reveal impacts of large grazing fishes and a diverse assemblage of small detritivorous and herbivorous fishes on accumulation of algae and organic matter.

Study area

The Cinaruco River, a clearwater river within Venezuela's Santos Luzardo National Park, Estado Apure, has a drainage basin of ~10,000 km^2 and is a major tributary of the Orinoco River, the world's 3rd largest river according to annual discharge. The Cinaruco has few suspended solids, low conductivity (2–9 μS/cm), low pH (5.0–6.5), and low concentrations of dissolved inorganic nutrients (detailed descriptions appear in Cotner et al. 2006, Montoya et al. 2006, Roelke et al. 2006). Tropical blackwater and clearwater rivers often support little aquatic macrophyte growth and planktonic primary productivity is low (Lewis 1988). Tropical river ecosystems with little apparent in situ primary production can nevertheless support impressive fish biomass and diversity. Over the past 10 y, >280 fish species have been documented in the Cinaruco River (data archived in the Museo de Ciencias Naturales, Guanare, Venezuela).

Secondary production is supported, to some degree, by direct and indirect consumption of terrestrial primary and secondary production (Layman et al. 2005). Nonetheless, most of the fish biomass in Neotropical rivers seems to be derived from aquatic sources of primary production (Araujo-Lima et al. 1986, Hamilton et al. 1992, Forsberg et al. 1993, Lewis et al. 2001), and stable isotope data from the Cinaruco support this view (Jepsen and Winemiller 2002, Layman et al. 2005). In temperate blackwater rivers, the microbial loop is especially significant and constitutes an important energy link for consumers (Meyer 1990), a situation also documented in wetlands and peat lakes (Jones et al. 1999, Morales and Ward 2000).

Semaprochilodus kneri and other detritivorous fishes that feed heavily on fine pariculate organic matter are abundant in the Cinaruco (Winemiller and Jepsen 1998, 2004, Hoeinghaus et al. 2003, Layman and Winemiller 2005). Prochilodontids possess fleshy lips and tiny teeth that probably aid in dislodging flocculent material from solid substrates. Fine inorganic sediments, particulate organic matter, and associated algae and other microorganisms are ingested via suction. A larger congeneric species (sapuara, *S. laticeps*) is the only other prochilodontid known to occur in the Cinaruco, but is uncommon in gillnet and castnet samples (Layman and Winemiller 2005).

The Cinaruco has a strongly seasonal hydrograph (Montoya et al. 2006), with rapid ascension from late May to August, and gradual retreat of floodwaters from September to May. Soluble reactive P, dissolved inorganic N, and dissolved organic C enter the river channel and lagoons from terrestrial sources via hyporheic flow, sheet flooding (wet season), and an extensive mosaic of lagoons and creeks draining the floodplain. Initial findings indicate that water-column production tends to be ~3× higher and more seasonally variable than benthic primary production, and water-column production also is higher in lagoons than in the river channel (Cotner et al. 2006, Roelke et al. 2006).

Methods

February 2002 (low-water) experiment

An initial cage experiment was conducted in the main channel during February 2002 to determine if large benthivorous fish are responsible for low standing mass of organic sediments in the Cinaruco during the low-water period. Twelve blocks consisting of one large-fish exclosure (LFE) (1.8 × 1.8 m cages with 2.5-cm-mesh poultry wire) and one control (CTRL) (1.8 × 1.8 m area with only 2 sides having poultry wire) were placed on 12 beaches. This mesh size (same mesh size as in Layman and Winemiller 2004) allowed small fishes to pass but effectively restricted passage by large fishes, including all size classes of the abundant bocachico (small juveniles of this migratory species are only found in the Orinoco and its floodplains) and adult size classes of other benthivorous characiforms (e.g., Hemiodidae, Curimatidae). This mesh size is large enough to allow water to mix freely inside and outside cages. Littoral habitats had low flow velocities (0–0.20 m/s). Debris accumulation on cages was minimal and was removed every 2nd d. A ceramic brick (14 × 18.5 × 29 cm) was placed inside each cage to provide a uniform substrate on which to collect organic sediments and algae. Experiments ran for 20 d, after which each brick was removed, and sediment samples were collected from 2 areas (each 29.5 cm^2) on the horizontal surface of the brick. One sample was used for analysis of sediment mass and the other for analysis of sediment chlorophyll *a* (CHLA). Sediment samples were immediately frozen and stored in a freezer before being transported, still frozen, to the US for processing. Half the sediment samples were dried and weighed to obtain total sediment dry mass (SDM), and then were combusted (500°C) and weighed to give sediment ash-free dry mass (SAFDM). Chlorophyll was extracted from the remaining sediment samples using 90% acetone, and CHLA concentrations were estimated using spectrofluorometric and spectrophotometric methods (APHA 1998).

March (low-water) and May (rising-water) 2002 experiments

Additional experiments were conducted during March 2002 (low water) and May 2002 (rising water) to test our prediction that large grazing characiform fishes, especially *S. kneri*, have a greater influence on the benthic ecosystem than the species-rich guild of small detritivorous and omnivorous fishes, and that the magnitude of this effect varies according to the stage of the annual hydrological cycle. During each experiment, fish effects on SDM, SAFDM, and sediment CHLA on ceramic tiles placed in the plots were estimated using fish enclosures/exclosures in a factorial design (4 treatments × 2 habitats) with 3 randomized blocks within each habitat category (channel vs lagoons). The CRTL treatment was a plot surrounded on 3 sides by 25-cm-mesh poultry wire that allowed all fishes to pass freely in and out. The open side of the plot always was oriented toward deeper water. The LFE treatment was a 4-sided cage with 2.5-cm-mesh poultry wire that excluded large fishes, including large benthic grazers, but allowed small benthic feeding fishes and invertebrates to pass. The total fish exclosure (TFE) treatment was a 4-sided cage with 0.7-cm-mesh wire screen that excluded all fishes. The *S. kneri* enclosure (SKE) treatment was a 4-sided cage with 2.5-cm mesh that confined 2 adult *S. kneri* within the experimental area (0.6 ind./m^2) and allowed small fishes to pass. The precise per-unit-area density of *S. kneri* in the river is impossible to know, but our cage density was <½ standard deviation above the mean catch per unit effort (CPUE, expressed as ind./m^2) estimated for *S. kneri* in the littoral zone of lagoons during March (based on 95 throws of a castnet, castnet area = 4.67 m^2, total area netted targeting *S. kneri* = 443.6 m^2). Feeding by captive *S. kneri* was verified by the presence of grazing scars on tiles and examination of stomach contents of euthanized specimens at the completion of trials.

During the low-water experiment, tiles with sediment samples were collected after 8 and 16 d. The water level rose rapidly (1.5 m/d) during late May when the high-water experiment was conducted. Thus, to ensure that water did not completely submerge cages, tiles were collected after 3 d. The SKE treatment could not be created during the high-water experiment because *S. kneri* had already initiated their downstream migration to the Orinoco River (mean CPUE of *S. kneri* based on 116 castnet throws = 0.0009 ind./m^2 during May).

Analyses

Each experiment tested the hypothesis that large benthivorous fishes reduce sediments, organic matter, and chlorophyll (sediment accumulation in CTRL < LFE). In addition, the March 2002 and May 2002 experiments tested the hypothesis that small benthivorous fishes remove additional sediment mass (sediment accumulation in LFE < TFE). The March 2002 experiment also examined the prediction that an abundant large benthivorous species, *S. kneri*, is the specific agent responsible for most of the sediment removal in CTRL plots (SKE = CTRL). The null hypothesis was that no significant differences were observed among experimental treatments or habitats for the response variables (SDM, SAFDM, CHLA on tiles). Data were $\log_{10}(x + 1)$-transformed to achieve distributions suitable for parametric tests. The February 2002 experiment in the river channel compared mean differences between the 2 treatment populations using a Student's *t*-test. For subsequent experiments (March and May 2002), a factorial analysis of variance (ANOVA) was used to examine treatment, habitat, and interaction effects. Statistical significance of pairwise mean differences among treatments and habitats were tested using the Tukey–Kramer Honestly Significant Difference (HSD) test. Results yielding $p < 0.05$ were considered statistically significant.

November 2002 (falling-water) experiment

We were interested in comparing the magnitudes of fish effects on sediment accrual, and findings based on 2-sided (February 2002) and 3-sided (March 2002) CTRL plots differed for the low-water period. Therefore, an additional experiment was conducted in November 2002 (falling-water period) to examine the influence of alternative CTRL plot designs on the behavior of large benthivorous fish. We compared 1.8 × 1.8 m plots with 1 side (1-sided CTRL), 3 sides (3-sided CTRL), and 4 sides (LFE). If 3-sided CTRL plots were avoided by *S. kneri*, then organic matter accrual should have been as follows: 4-sided LFE ≥ 3-sided CTRL > 1-sided CTRL. Large numbers of *S. kneri* had already migrated into the system from the Orinoco when this experiment was initiated. Seven experimental blocks were constructed in channel and lagoon sites (yielding 14 blocks of 3 treatments each). This experiment was terminated after 6 d because of rapidly falling water levels.

Results

February 2002 (low-water) experiment

Results from the initial exclosure experiment were consistent with the prediction that large benthivorous fishes remove sediments, organic matter, and algae (CHLA) from littoral habitats of the river channel during the low-water period (Fig. 1). Each of the 3 response variables was significantly higher in LFE plots than CTRL plots ($t_{SDM} = 3.26$, df = 10, $p = 0.008$; $t_{SAFDM} = 3.66$, df = 10, $p = 0.004$; $t_{CHLA} = 2.64$, df = 11, $p = 0.023$). The mean concentration of CHLA recorded from sediments on ceramic bricks in CTRL plots was almost identical to the mean concentration recorded from natural sandy substrate at 5 channel sites during the same period (Fig. 1). The surfaces of most ceramic bricks from the CTRL plots had grazing scars that were distinctive for feeding by prochilodontid fishes (Fig. 2, see also fig. 1 in Flecker 1992).

March 2002 (low-water) experiment

Tiles sampled after 8 d in the March 2002 experiment revealed a significant treatment effect on SAFDM ($F_{3,16} = 3.40$, $p = 0.043$; Fig. 3B), but not on SDM ($F_{3,16} = 1.57$, $p = 0.235$; Fig. 3A) or CHLA ($F_{3,12} = 2.42$, $p = 0.116$; Fig. 3C). The only significant habitat effect was on CHLA (CHLA $F_{1,12} = 5.80$, $p = 0.033$; SDM and SAFDM $p > 0.38$; Fig. 4A, B, C), and there were no significant interactions between treatment and habitat (all $p > 0.15$).

Treatments significantly affected all 3 response variables for tiles collected after 16 d: SDM ($F_{3,15} = 4.00$, $p = 0.028$; Fig. 3A), SAFDM ($F_{3,15} = 5.41$, $p = 0.010$; Fig. 3B), and CHLA ($F_{3,15} = 5.88$, $p = 0.007$; Fig. 3C). The only significant habitat effect was on CHLA (CHLA: $F_{1,15} = 6.00$, $p = 0.027$, SDM and SAFDM: p

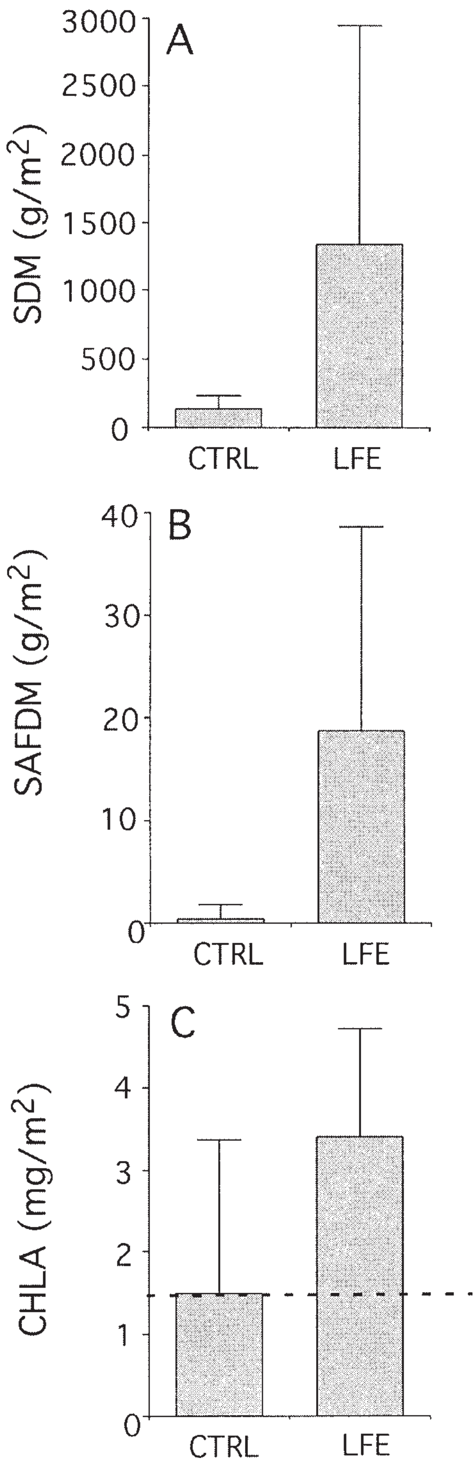

FIG. 1. Comparison of mean (+1 SE) concentrations of sediment dry mass (SDM) (A), sediment ash-free dry mass (SAFDM) (B), and chlorophyll *a* (CHLA) (C) accumulated on the surface of ceramic bricks in control (CTRL) and large-fish exclosure (LFE) plots in the Cinaruco River channel after 20 d during February 2002. Horizontal dashed line represents mean concentration of CHLA in natural channel sediment samples on 24 February 2002.

> 0.10; Fig. 4A, B, C), and there were no significant interactions between treatment and habitat (all $p > 0.50$). Mean values of all 3 response variables for tiles collected after 16 d were significantly higher in TFE and CTRL plots than in SKE plots (Tukey–Kramer HSD, $p < 0.05$; Fig. 3A, B, C).

Thus, treatment effects were stronger after 16 d, and results matched predictions of top–down control of sediments, organic matter, and algae by benthivorous fishes (predicted accumulated mass: TFE > LFE > CTRL = SKE), except that values in CTRL plots matched values in the LFE plots and contained more sediments and organic matter than the SKE plots (observed accumulated mass: TFE > LFE = CTRL > SKE). The mean concentration of CHLA on natural substrates at 5 channel sites surveyed on March 28 was 1.2 to 2.0 mg/m^2 below the means obtained for CTRL plots but intermediate between mean values obtained on days 8 and 16 for SKE plots (Fig. 3C). The mean CHLA concentration from natural substrates at 5 lagoon sites on the same date was only slightly greater than values from CTRL plots (difference <0.5 mg/m^2 for day 8, <0.1 mg/m^2 for day 16; Fig. 3C).

The significant habitat effect observed for CHLA concentration resulted from higher mean values for tiles in lagoon plots relative to channel plots on both days 8 and 16 (Fig. 4C). The mean CHLA concentration on natural substrates at 5 channel sites on March 28 was slightly lower than the means from all experimental plots combined from the channel on day 8 (<0.4 mg/m^2) and day 16 (<0.1 mg/m^2) (Fig. 4C). The mean concentration of CHLA recorded from natural substrates at 5 lagoon sites on March 28 was lower than the mean obtained from all experimental plots in lagoons on day 8 (0.9 mg/m^2) and virtually the same as the mean obtained from experimental plots in lagoons on day 16 (Fig. 4C).

May 2002 (rising-water) experiment

This experiment was conducted during late May and early June, a period that coincided with the first heavy rains. Because the water level increased an average of 0.3 m/d, tiles were sampled after 3 d. There were no significant treatment effects ($F_{2,13} < 1.65$, $p > 0.229$), habitat effects ($F_{1,13} < 1.19$, $p > 0.29$), or interactions between treatment and habitat (all $p > 0.70$) for any of the 3 response variables. *Semaprochilodus kneri* undergo their annual spawning migration at onset of flooding, so we had predicted no effect from LFE and only a weak grazing effect from small grazers that were dispersing within expanding aquatic habitats (predicted accumulated mass: TFE > LFE = CTRL). The results were statistically nonsignificant,

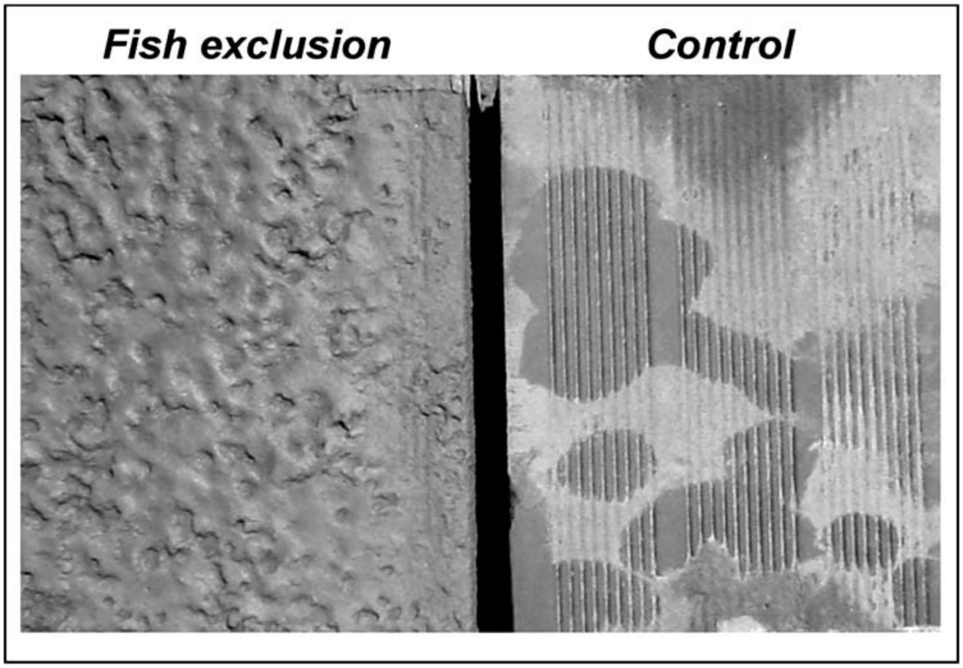

FIG. 2. Photograph of bricks removed from large-fish exclosure (left) and control (right) plots placed in the main channel of the Cinaruco River during the low-water period (February 2002). Clean oval patches on the control brick probably were created by suctorial feeding of the benthic detritivore *Semaprochilodus kneri*.

but mean values for SDM, SAFDM, and CHLA were higher in TFE plots than in other treatments, and means for CTRL plots and LFE plots were very similar (Fig. 5A, B, C). The mean concentration of CHLA on natural sediments at 10 channel and lagoon sites over the same period of time was only slightly greater (<0.1 mg/m^2) than the means obtained for the CTRL and LFE plots (Fig. 5C).

November 2002 (falling-water) test of CTRL plots

If CTRL plots with 3 walls actually had been avoided by some *S. kneri* during the low- and rising-water experiments, then organic matter accrual should have been as follows in our November experiment: 4-sided LFE $\geq$ 3-sided CTRL $>$ 1-sided CTRL. Treatments significantly affected SDM ($p < 0.05$), but habitat did not, and no significant interaction effects were found. Treatment ($p < 0.01$) and habitat ($p = 0.01$) significantly affected SAFDM and CHLA, but no significant interactions were observed ($p > 0.25$). Mean accrual of SDM after 6 d was significantly greater (Tukey–Kramer HSD, $p < 0.05$) in 4-sided LFE plots (1197.0 $\pm$ 1422.7 mg/m^2) than 1-sided CTRL plots (172.1 $\pm$ 231.6 mg/m^2), with 3-sided CRTL plots being intermediate (321.0 $\pm$ 519.1 mg/m^2). SAFDM was significantly greater in 4-sided LFE plots (18.67 g/m^2) than 3-sided CTRL plots (6.49 mg/m^2 $\pm$7.65) and 1-sided CTRL plots (3.98 $\pm$ 4.16 mg/m^2). Mean CHLA concentration in 1-sided CTRL plots (1.20 $\pm$ 1.68 mg/m^2) was significantly lower than concentrations from 3-sided CTRL (2.24 $\pm$ 1.90 mg/m^2) and 4-sided LFE plots (3.06 $\pm$ 2.32 mg/m^2), a result that supports the hypothesis that 3-sided CTRL plots were avoided to some degree by large grazers. Mean CHLA concentrations on tiles in 1-sided CTRL plots were only slightly greater (difference <0.6 mg/m^2) than mean concentrations recorded on sandy substrates at 10 channel and lagoon sites during the same period.

Discussion

Importance of S. kneri *grazing*

Our experiments demonstrated effects of benthivorous fishes on the quantity and nutritional quality (organic matter and CHLA) of sediments in a floodplain river draining a nutrient-poor tropical landscape. During the annual low-water period, top–down effects of large fishes (i.e., those incapable of passing through 2.5-cm mesh) on sediments were stronger than those of small fishes. Grazing scars on bricks and tiles strongly suggest that *S. kneri* is the most important large grazer of organic sediments in this system. CHLA of sediments from CTRL plots with 2 wire-mesh sides (February 2002 experiment) closely matched the concentrations recorded from natural sandy substrates in channel and lagoon littoral

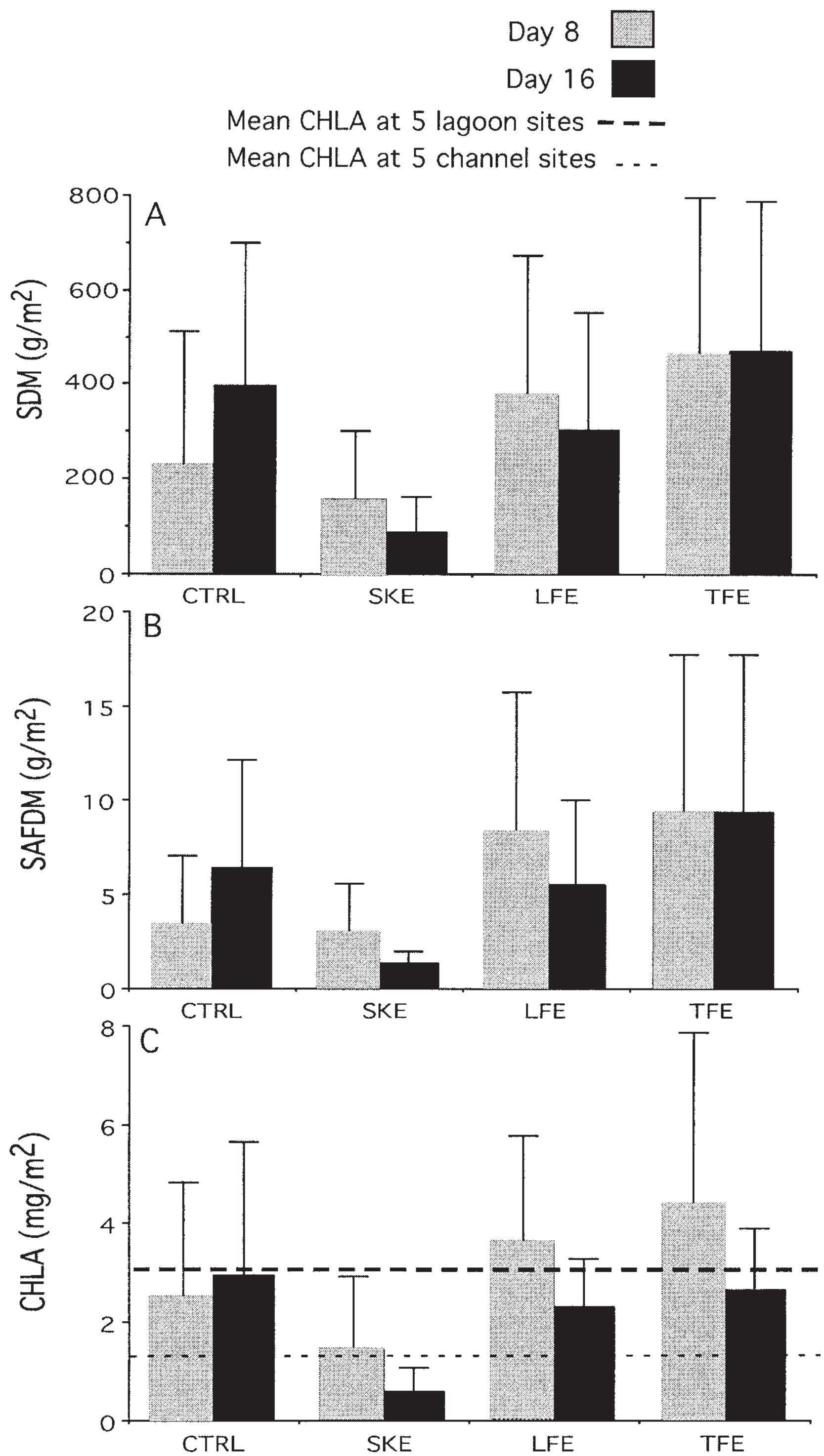

FIG. 3. Comparison of mean (+1 SE) concentrations of sediment dry mass (SDM) (A), sediment ash-free dry mass (SAFDM) (B), and chlorophyll *a* (CHLA) (C) accumulated on ceramic tiles in control (CTRL), *Semaprochilodus kneri* enclosure (SKE), large-fish exclosure (LFE), and total fish exclosure (TFE) plots in the Cinaruco River (channel and lagoon sites combined) after 8 d and 16 d during the low-water period (March 2002). CHLA samples in natural channel and lagoon sediment samples were taken on 28 March 2002.

habitats at the same depths. In the March low-water experiment, 3-sided CTRL plots accumulated more sediments, organic matter, and CHLA compared to natural sediments and SKE plots containing 2 *S. kneri*. Two explanations could account for this pattern. First, *S. kneri* may have avoided 3-sided CTRL plots so that these plots functioned more like our 4-sided LFE plots (yielding CTRL = LFE). Second, the density of *S. kneri* within enclosures could have been higher than natural densities (yielding CTRL > SKE).

We experimentally tested the 1st hypothesis during November 2002, and results supported the hypothesis that 3-sided CTRL plots probably are avoided by at least some *S. kneri* and perhaps by other large grazers. Further evidence in support of using 1-sided and 2-sided CTRL plots was provided by the similarity in CHLA concentrations on tiles inside these CTRL plots and on unmanipulated substrates in both river and lagoon habitats during the same periods. With regard to the 2nd hypothesis, SKE plots containing 2 *S. kneri* yielded benthic CHLA concentrations similar to values obtained from natural sediments in channel sites during March 2002, but lower than values from natural sediments from lagoon sites during that period (Fig. 3C). Thus, *S. kneri* density in SKE plots may have been higher than natural mean densities in lagoons.

Top–down vs bottom–up effects

The top–down effect of benthivorous fishes observed during the low-water period is consistent with findings from similar experiments conducted in an Andean piedmont stream by Flecker and colleagues (Flecker 1992, 1996, 1997, Flecker et al. 2002). Río Las Marias is a whitewater river (high conductivity and suspended sediment loads, neutral pH) draining nutrient-rich landscapes of the Andean Cordillera in western Venezuela. During the dry season, the migratory coporo (*Prochilodus mariae*, Prochilodontidae), a benthic detritivore/algivore with body size and feeding habitats similar to *S. kneri*, migrates into Las Marias from locations downstream. Exclosure/enclosure experiments revealed strong effects of coporos on benthic sediment mass, organic mass, algal assemblage composition, aquatic insect abundance and diversity, and nutrient dynamics. The mean sediment accrual in large fish exclosures after 14 d in the Andean piedmont river was nearly 2× as great as the mean accumulation in our LFE plots after 16 d in March and similar to the mean accumulation in LFE plots after 20 d in February (~800 g/m^2). The accumulation of organic matter was ~3 to 6× greater in the Andean river (Flecker 1996).

Like the Cinaruco (Cotner et al. 2006), Las Marias

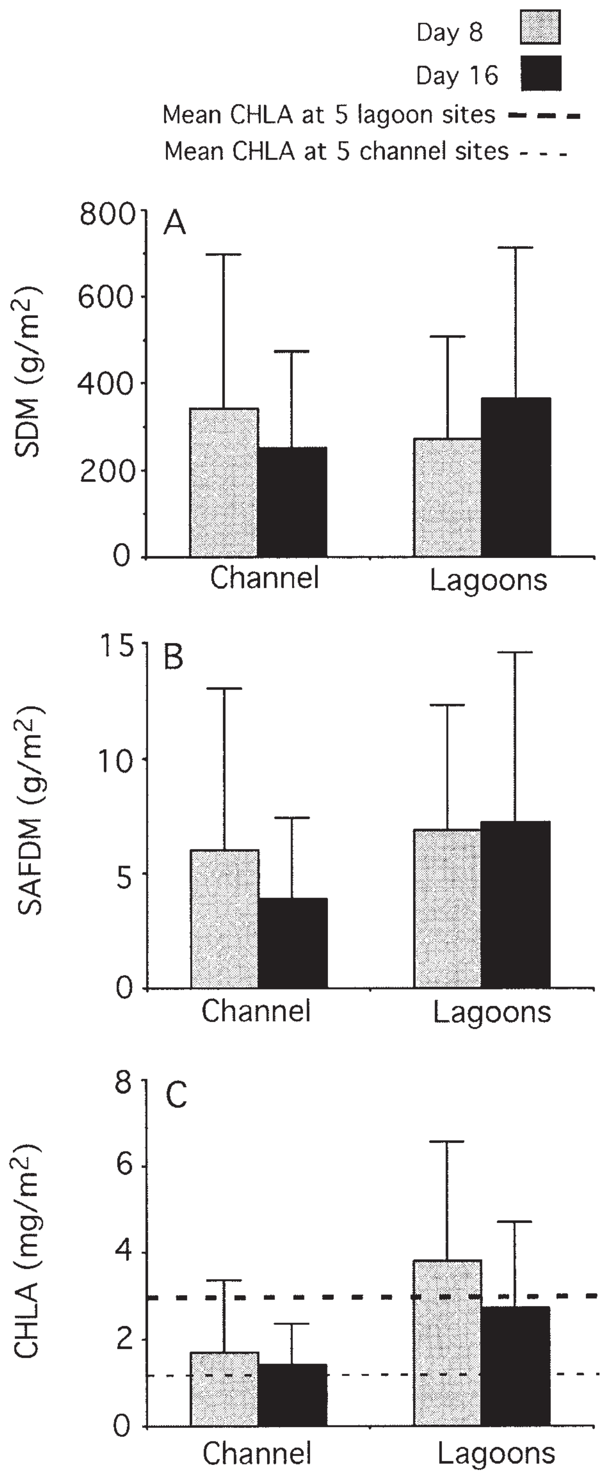

FIG. 4. Comparison of mean (+1 SE) concentrations of sediment dry mass (SDM) (A), sediment ash-free dry mass (SAFDM) (B), and chlorophyll *a* (CHLA) (C) accumulated on ceramic tiles in sites in the littoral zone of the river channel vs sites in lagoons (all experimental treatments combined) after 8 d and 16 d during the low-water period (March 2002). CHLA samples in natural channel and lagoon sediment samples were taken on 28 March 2002.

appears to be a strongly N-limited system. Flecker et al. (2002) found that both N addition and algivores significantly affected algal standing biomass and assemblage composition, but consumer limitation was much stronger than nutrient limitation. This piedmont river experiences frequent abrupt and catastrophic floods during the wet season, so experimental research is nearly impossible and benthic ecosystem dynamics for this part of the year remain undocumented.

Unlike Río Las Marias and tropical wet-forest streams where similar studies have demonstrated top–down effects of benthic grazers (e.g., Power 1990, Pringle and Hamazaki 1997), the Cinaruco, a lowland floodplain river, undergoes fairly gradual and predictable hydrologic dynamics. The Cinaruco also tends to have lower water velocities than these other tropical streams, especially during the dry season and within lagoons. This lower velocity allows significant phytoplankton production to occur. Primary production seems to be greater in the water column than on sediments during the low-water period (Cotner et al. 2006, Roelke et al. 2006). We hypothesize that the chlorophyll that accumulates on tiles may be partially, perhaps largely, derived from deposition of algal cells from the water column. The fact that deposition on tiles was always greater in lagoons compared with channel sites supports this view. Lewis (1988) observed that phytoplankton production in 3 Orinoco tributary rivers was higher during the low-water period, and that <1% of estimated annual phytoplankton production in floodplains was transported to river channels. This result indicates that phytoplankton are consumed in situ, either within the water column or on sediments.

Production (P)/biomass (B) ratios (based on CHLA) suggest that benthic algae turn over more rapidly than phytoplankton (mean benthic P/B = 2.37, mean water column P/B = 0.55). One explanation for higher benthic turnover is direct losses to grazing or hydrologic disturbance (i.e., scouring flows). P/B ratios indicate that algal biomass turned over more rapidly during November (high water) than March (low water), both in the sediments and water (Cotner et al. 2006). This result suggests that scouring and dilution losses that are important during high water may have a greater effect than fish grazing during low water on standing crops of periphyton. The relative

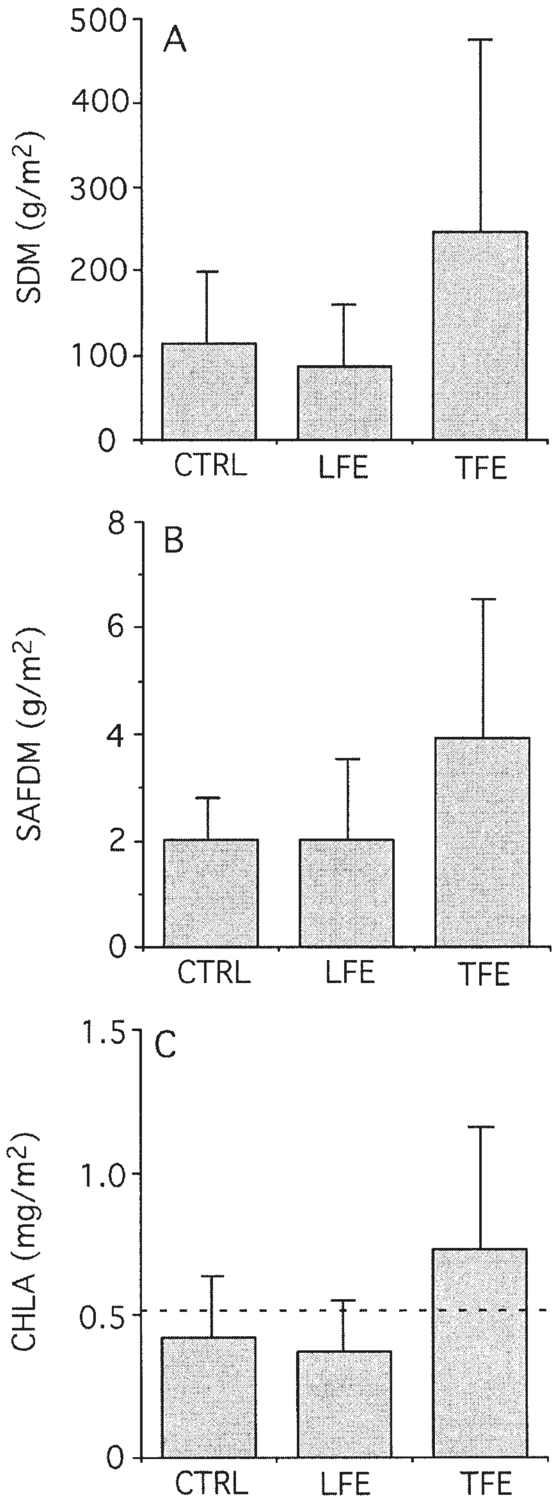

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FIG. 5. Comparison of mean (+1 SE) concentrations of sediment dry mass (SDM) (A), sediment ash-free dry mass (SAFDM) (B), and chlorophyll *a* (CHLA) (C) accumulated on ceramic tiles in control (CTRL), large-fish exclosure (LFE), and total fish exclosure (TFE) plots in channel and lagoon sites of the Cinaruco River after 3 d during the rising-water period (May 2002). Horizontal dashed line represents mean concentration of CHLA for 10 natural sediment samples from channel and lagoon sites on 31 May 2002.

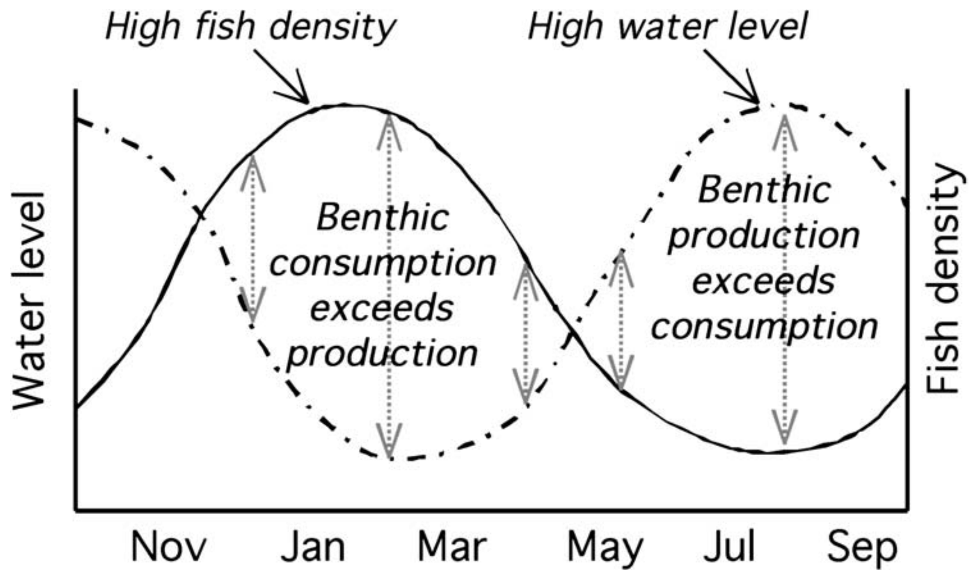

FIG. 6. Conceptual model of continuous shifts in relative magnitudes of bottom–up (production) and top–down (consumption) influences on sediment fine particulate organic matter and algal density during phases of the annual flood-pulse regime of a tropical river. Strongest top–down effects from benthivorous fishes occur during the low-water phase when per-unit-area density of fishes is at its peak.

contribution of periphyton growth is unknown, but future research will examine algae taxonomic composition in these samples. Also, the roles played by *S. kneri* and other large benthivorous fishes in the resuspension of fine particulates and in excretion of dissolved nutrients (Vanni et al. 2002) are currently unknown. Highest dissolved nutrient concentrations were recorded during the low-water phase (Cotner et al. 2006, Montoya et al. 2006) when fish densities are highest.

Seasonal variation in grazing pressure

Our experimental results are consistent with a model of seasonal variation in grazing pressure on organic sediments that is a function of changing fish densities that, in turn, are a function of: 1) volume of available aquatic habitat, 2) *S. kneri* migration, and 3) resident fish population dynamics (Fig. 6). However, the absence of statistically significant fish effects during the rising-water period (May 2002 experiment) probably was affected by large within-treatment variation in response variables and especially by the shorter duration (3 d) of these experiments that was mandated by the rapid rise in water level. During the low-water period when fixed plots could be monitored for longer time periods, concentrations of sediments and CHLA on tiles in TFE plots increased on a daily basis as a sigmoidal function that reached an asymptote at about day 10 (KOW, unpublished data). We assume that organic matter would have continued to accumulate during the rising-water period at a comparatively greater rate within the TFE plots than in other treatments had the experiment extended over a longer time interval. Given the problems discovered with the 3-sided CTRL plots and the fact that mean values from CTRL plots and LFEs were very similar on day 3 (Fig. 5), it is unclear if a significant effect of large grazers could have been detected over a longer time interval. Again, grazing pressure should have been low during May because *S. kneri* were emigrating and large resident grazers, such as hemiodids, were dispersing within the expanding aquatic habitat.

Future research to improve estimates of seasonal shifts in controlling factors

Investigation of community trophic dynamics has matured to the point that field experiments are showing how spatial and temporal environmental variation influences the relative magnitudes of bottom–up and top–down effects on communities and ecosystem attributes (e.g., Power 1990, Gelwick and Matthews 1992, Carpenter and Kitchell 1993, Wootton et al. 1996, McPeek 1998, Mulder and Ruess 1998, Menge et al. 1999). The annual flood pulses of tropical rivers provide outstanding opportunities for research that identifies specific agents of control and temporal shifts in their relative influence on ecosystem components. Many key ecosystem features have fairly predictable dynamics in response to seasonal hydrology. The low-water period in the Cinaruco River is accompanied by reduction of aquatic habitat, high water-column nutrient concentrations and primary productivity, high rates of particulate organic matter sedimentation, and strong effects of grazing by benthivorous fishes. Seasonal variation of N limitation on phytoplankton and periphyton standing crops should be tested experimentally to integrate bottom–up control with our model of shifting strengths of top–down effects in response to seasonal hydrology.

Unlike small tropical streams (Pringle et al. 1993, Crowl et al. 2006), the Cinaruco River contains a relatively low abundance of grazing macroinvertebrates, especially in the sandy littoral habitats that dominate the river landscape. In the Cinaruco, shrimp and aquatic insects are most common where there are accumulations of leaf litter or coarse woody debris (JVM and KOW, unpublished data), a situation that parallels temperate blackwater rivers (Benke et al. 1984, 1985). Thus, we predict that fishes will have the strongest effects on benthic ecology, and that invertebrate assemblages will respond largely to environmental variation induced by fishes and abiotic factors. This hypothesis could be tested with appropriately designed experimental enclosures.

To increase precision and accuracy of our estimates of the magnitude of grazer control in the Cinaruco River, we recently repeated our experiments during rising-, falling-, and low-water periods with greater replication of experimental blocks in both habitats (findings will appear in a future report). We are interested in estimating temporal variation in the magnitude of top–down control, so the new experiments use 1-sided CTRL plots that more accurately reflect natural conditions. We also are examining more response variables associated with sediments, including benthic production and respiration, algal assemblage composition, and meiofauna. This research is particularly urgent given the severe and growing negative impacts of fisheries and dams on stocks of migratory prochilodontid fishes in Venezuela (Winemiller et al. 1996, Barbarino Duque et al. 1998). These abundant fishes are ecosystem engineers (Flecker 1996, 1997), and they are important prey for piscivores (Winemiller and Jepsen 2004). Some species or guilds can have disproportionate effects on community ecosystem dynamics (e.g., keystone species) even within reticulate, species-rich food webs (Menge et al. 1994, Power et al. 1996, Polis et al. 2000). Prochilodontid fishes, which make up only a handful of taxa within the species-rich Neotropical ichthyofauna, appear to have major effects on ecosystem dynamics via direct grazing and in the form of a spatial subsidy for top predators.

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