INTERACTIONS BETWEEN HERBIVOROUS FISHES AND LIMITING NUTRIENTS IN A TROPICAL STREAM ECOSYSTEM

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Abstract. Ecologists have long been interested in understanding the strengths of consumer and resource limitation in influencing communities. Here we ask three questions concerning the relative importance of nutrients and grazing fishes to primary producers of a tropical Andean stream: (1) Are stream algae nutrient limited? (2) Are top-down and bottom-up forces of dual importance in limiting primary producers? (3) Do grazing fishes modulate the degree of resource limitation?

We obtained several lines of evidence suggesting that Andean stream algae are nitrogen limited. Addition of nitrogen in flow-through channels resulted in major increases in algal standing crop, whereas there were no measurable effects of phosphorus enrichment. Interestingly, the N_2-fixing cyanobacteria *Anabaena* was one of the taxa that responded most dramatically to the addition of nitrogen. Moreover, nutrient uptake rates were significantly higher for inorganic nitrogen (NO_3-N and NH_4-N) compared to phosphorus (PO_4-P).

Nutrients and the presence of grazing fishes were manipulated simultaneously in a series of experiments by using nutrient-diffusing substrates in fish exclusions vs. open cages accessible to the natural fish assemblage. We observed strong effects of both nitrogen addition and consumers on algal standing crop, although consumer limitation was found to be of considerably greater magnitude than resource limitation in influencing algal biomass and composition. Finally, the degree of resource limitation varied as a consequence of grazing fishes. Experiments examining nutrient limitation in the presence and absence of fishes showed that the response to nitrogen enrichment was significantly greater on substrates accessible to natural fish assemblages compared to substrates where grazing fishes were excluded. These experiments demonstrate simultaneous and interactive effects of top-down and bottom-up factors in limiting primary producers of tropical Andean streams. Whereas other studies have shown that consumers affect nutrient supply in ecosystems, our findings suggest that consumers can play an important role in influencing nutrient demand.

Key words: algae; Andes; community structure; cyanobacteria; food webs; grazing fishes; herbivory; nitrogen limitation; nutrient uptake; stream; top-down and bottom-up effects; tropics.

INTRODUCTION

Questions about the importance of consumers and resources in limiting community dynamics have sparked lively debate for decades (e.g., Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1987, Fretwell 1987, Menge and Sutherland 1987, Power 1992,

Hairston and Hairston 1993, Persson et al. 1996, Polis and Strong 1996). The ecological literature is replete with food chain models of community limitation, which run the gamut from top-down to bottom-up to colimitation by consumers and resources (Power 1992). Understanding the conditions in which top-down and bottom-up forces operate represents a major challenge for ecologists, and there have been increasing efforts to tease apart the interactive nature of consumers and resources (Hunter and Price 1992, Power 1992, Wootton and Power 1993, Persson et al. 1996, Pace et al. 1999, Forkner and Hunter 2000). One of the most promising approaches is to experimentally manipulate consumers and resources in tandem (Lamberti 1996), and research from freshwater pelagic food webs provides an excellent example (Brett and Goldman 1997, Carpenter et al. 1998). However, there exists a need to expand our empirical database of experimental studies, as the di-

versity of ecosystems in which top-down and bottom-up factors have been explicitly manipulated simultaneously remains surprisingly sparse (Stiling and Rossi 1997, Forrester et al. 1999, Miller et al. 1999).

Nutrients are often limiting resources in ecosystems and an environmental template of geological, climatic, and ecological features ultimately delimits their availability. At a local scale, nutrients interact with consumers in a variety of ways. Models suggest that food chain length and strength of trophic interactions can be driven by productivity (Fretwell 1977, Oksanen et al. 1981, Oksanen 1988; but see Hairston and Hairston [1993], Post et al. [2000]), which in many systems is constrained by nutrient supply. Furthermore, consumers can be important pools of nutrients and strongly influence nutrient fluxes in ecosystems via a host of direct and indirect mechanisms. The notion that nutrients and consumers are intimately linked is implicit in the recent elaboration of nutrient stoichiometry theory and the development of the trophochemical food web concept (Sterner et al. 1996). The tacit assumption of research examining roles of consumers in nutrient recycling (Sterner 1990, Vanni and Findlay 1990, Elser 1992, Kraft 1992, Sterner and Hesson 1994, Schindler et al. 1996, Vanni 1996, Sterner and George 2000) is that nutrients are sufficiently limiting such that changes in their availability via consumer activity measurably influence primary productivity.

This study examines nutrient limitation and the interactive effects of algal consumers and nutrient availability on primary producers of an Andean piedmont stream. We began by asking a simple question about tropical Andean streams: Are primary producers nutrient limited? To our surprise, remarkably few data were available for neotropical streams to address this question (Downing et al. 1999a). To date, little experimental work on nutrient limitation of stream periphyton has been conducted outside temperate climes (Borchardt 1996, Downing et al. 1999a; but see Pringle et al. [1986], Paaby-Hansen [1988], Pringle and Triska [1991]), which has resulted in a large gap in our fundamental understanding of tropical stream ecosystems (Jackson and Sweeney 1995).

Moreover, neotropical streams are known to contain abundant and diverse assemblages of consumers (Lowe-McConnell 1987, Winemiller 1990). Grazing fishes in tropical streams strongly influence benthic algal standing crops, species composition, and productivity (Power 1984, 1990, Flecker 1992, 1996, Wootton and Oemke 1992, Pringle and Hamazaki 1997, 1998). However, it is less clear how changes in productivity modify links between grazers and primary producers. Grazing catfishes in Panama have been found to respond numerically to gradients of primary productivity, as grazer numbers are higher in open stream pools with greater light availability compared to pools with heavy canopy cover (Power 1983). These observations suggest a potentially strong role of grazers, and raise the

question: Are the impacts of grazers in tropical streams modified by different nutrient regimes?

The objectives of this study were threefold. First, we aimed to determine whether primary producers in an Andean piedmont stream were limited by nutrient availability, namely nitrogen and phosphorus. Second, we wanted to compare the relative importance of top-down limitation of stream algae by a diverse and abundant guild of herbivorous fishes to the bottom-up influences of nutrient availability. Finally, we asked whether herbivores interact with primary producers by modifying the relative degree of nutrient limitation. Our findings bolster evidence from other systems suggesting that both nutrients and herbivores can play strong concurrent roles in determining algal standing crop, and that the importance of these limiting factors should not be decoupled as independent and noninteractive influences on primary producers.

STUDY SITE

The study was conducted in Rio Las Marias, a mid-sized stream of the Apure drainage of the Orinoco River system in Venezuela. The study site is located in the Andean piedmont region at ~225 m (9°10′ N, 69°44′ W) (see description in Flecker [1996]). Rio Las Marias substrates are dominated by cobble and gravel. Stream temperatures are warm and exhibit diel fluctuations within ~25–32°C. The site is distinctly seasonal with a single dry season generally occurring during December–April and a rainy season during the remainder of the year. Rio Las Marias is relatively transparent during the dry season months, whereas water clarity is low during the rainy season when streams carry heavy sediment loads. Fieldwork reported in this paper was conducted during the dry season during January–March of 1998 and 1999. Experiments were performed in a series of shallow (<30 cm) runs that ranged in width ~3–10 m, and flows ranged within 1–25 cm/s. At the study site, the stream has an open canopy with minimal shading, so light is unlikely to be a major limiting factor for primary producers.

Rio Las Marias has moderate amounts of dissolved nitrogen and phosphorus. Dissolved nitrogen measurements during the dry seasons of 1998 and 1999 were quite similar between years, with mean values of 34.9 and 35.4 μg/L for NO_3-N, 23.0 and 21.9 μg/L for NH_4-N, and 8.3 and 14.9 μg/L for soluble reactive phosphorus, respectively (Table 1).

Rio Las Marias has a diverse assemblage of fishes. We have collected more than 80 fish species at the site, and we continue to find additional fish species. Herbivorous fishes and amphibians are extremely abundant in the Andean piedmont and include a diversity of armored catfish (Loricariidae), characoids such as the abundant grazer *Parodon apolinari* (Parodontidae), and tadpoles of the families Bufonidae and Ranidae. Some years, the flannelmouth characin, *Prochilodus mariae* (Prochilodontidae), a migratory detritivore, is the dom-

TABLE 1. Concentrations of dissolved nutrients (soluble reactive phosphorus-P [SRP-P], ammonium-N [NH_4-N], and nitrate-N [NO_3-N]) sampled from Rio Las Marias, Venezuela, during the 1998 and 1999 dry seasons.

Date	SRP-P (μg P/L)	NH_4-N (μg N/L)	NO_3-N (μg N/L)
1998			
7 Jan	9.3	10.2	NA
25 Jan	6.6	20.2	19.8
29 Jan	6.9	16.8	36.9
5 Feb	10.2	11.0	31.2
7 Feb	6.7	13.9	39.8
12 Feb	NA	NA	33.6
13 Feb	5.5	12.6	32.6
14 Feb	8.9	39.4	37.9
17 Feb	7.9	38.4	41.5
1 Mar	12.8	44.5	40.7
Mean ± 1 SE	8.3 ± 0.8	23.0 ± 4.6	34.9 ± 2.2
1999			
23 Jan	22.3	17.0	NA
17 Feb	11.5	25.0	17.8
20 Feb	14.7	42.6	NA
22 Feb	14.7	22.9	59.2
27 Feb	13.1	23.9	27.5
28 Feb	12.7	28.0	39.0
5 Mar	16.9	8.9	33.7
10 Mar	17.9	22.3	NA
16 Mar	14.7	10.4	21.6
20 Mar	12.4	9.6	45.5
22 Mar	13.0	30.2	38.9
Mean ± 1 SE	14.9 ± 0.9	21.9 ± 3.1	35.4 ± 4.7

Notes: Water samples were collected in the thalweg, filtered in the field through rinsed glass fiber filters (Gelman type A/E; pore size = 1 μm; Gelman Sciences, Ann Arbor, Michigan, USA), stored in new polyethylene bottles rinsed with deionized water, and immediately frozen (1998) or preserved with 0.4% chloroform (1999). Nutrients were analyzed as described in *Methods: Nutrient releases*. Dates with no available data are denoted as NA.

inant fish by biomass during the dry season months (Flecker 1996). This abundant assemblage of epi-benthic feeding fishes may be important in keeping algal standing crop low in riffles (1999 dry season chlorophyll means, 11.4–22.7 mg/m^{-2}) and runs (1999 dry season chlorophyll means, 8.4–16.7 mg/m^{-2})(Table 2).

METHODS

We used three approaches to examine nutrient limitation. We chose to integrate approaches because each method has its own set of strengths and limitations (see Pringle and Triska 1996). Our approaches included the following: (1) nutrient enrichment of flow-through channels, (2) comparisons of nutrient uptake lengths of N and P, and (3) in situ nutrient-diffusing substrates. Moreover, nutrient-diffusing substrates, set up in both the presence and absence of herbivorous fishes, allowed us to address whether nutrient limitation varied as a consequence of differential grazing pressure.

Flow-through channel enrichments

The potential for N and P limitation of periphyton growth was initially tested by nutrient enrichment in a series of flow-through channels (Peterson et al. 1983, Pringle and Triska 1996) placed directly in Rio Las Marias. Units of four flow-through channels built side by side were constructed of clear Plexiglas (0.63 cm thickness). Each channel was 90 cm long by 9.5 cm wide by 8 cm high, and a series of baffles at the upstream end ensured complete mixing of water and nutrients as they entered the channels. Fish were excluded from the channels by affixing screens constructed of plastic netting (mesh, 6 mm) to both ends of the channels. Experiments were set up as a randomized complete block design with four treatments: (1) unenriched control, (2) N enrichment, (3) P enrichment, and (4) simultaneous N and P enrichment. One replicate of each treatment was placed randomly in each of two blocks, with a four-channel unit comprising a block (i.e., two blocks × four channels yielding eight channels total). Nutrients were added at a constant rate to the upstream ends of channels by dripping concentrated solutions from 2-L Mariotte bottles (Webster and Ehrman 1996). Our goal was to increase nutrients above ambient concentrations by an order of magnitude. For N enrichments, we aimed to increase both NO_3 levels and NH_4 levels ~300 μg/L above ambient concentrations, using $NaNO_3$ and NH_4Cl, respectively. For P enrichments, KH_2PO_4 was used to increase PO_4 levels ~100 μg/L above ambient concentrations. Our rationale in choosing these enrichment concentrations was to increase nutrient availability sufficiently to alleviate nutrient limitation, yet not at levels that could be toxic to algae.

Unglazed ceramic tiles (8.5 × 8.5 cm) were used for assessing responses of periphyton to the nutrient treatments, with each channel containing 10 tiles. Two experiments were conducted; responses to the experimental treatments were rapid, and trials were run for short durations appropriate for determining nutrient limitation of algal growth rates (see Downing et al. 1999b). The first experiment was performed for five days, after which three tiles were randomly selected from each channel and sampled for periphyton. The second experiment was run for eight days, and periphyton was sampled from three tiles in each channel on days 4 and 8. Periphyton was collected by scraping the

TABLE 2. Mean chlorophyll ± 1 SE from monthly surveys of riffle and run habitats in Rio Las Marias, Venezuela, conducted during the 1999 dry season.

Date (1999)	Habitat	Chlorophyll (mg/m^2)
8–9 Jan	riffle	16.8 ± 1.1
8–9 Jan	run	10.6 ± 0.3
8–10 Feb	riffle	11.4 ± 0.4
8–10 Feb	run	8.4 ± 0.4
15 Mar	riffle	22.7 ± 4.4
15 Mar	run	16.7 ± 2.4

Note: On each survey date, chlorophyll samples were collected from three stones from each of five riffles and 10 runs.

entire upper surface of a tile with a razor blade. A subsample of the algal slurry was collected for chlorophyll analysis by pipetting a known volume of slurry onto a small glass fiber filter (Gelman A/E, 25 mm diameter) and immediately placing it on ice in the dark. The remaining slurry was preserved in ~3% formalin for subsequent determination of algal assemblage composition. At the field site, chlorophyll was extracted in 90% ethanol for ~24 h (Nusch 1980). All chlorophyll extractions were begun almost immediately after sample collection, and chlorophyll *a* concentrations were determined using a Turner AU-10 fluorometer (Turner Designs, Sunnyvale, California, USA). We chose not to grind algal samples for chlorophyll extractions due to potential hazards of sample loss with grinding; therefore, we may have underestimated concentrations of pigments associated with cyanobacteria (Steinman and Lamberti 1996). Cell counts were made in the laboratory for algal samples collected at the end of the second experiment. We used a Palmer-Maloney counting chamber and for each sample identified a minimum of 300 cells or algal units to genus at 400× (Lowe and LaLiberte 1996). Algal assemblage data were expressed as biovolumes based on measurements of 30 cells for each algal taxon present in the samples using an ocular micrometer.

All data were log-transformed to correct for problems associated with nonhomogeneity of variances. Algal responses to the nutrient treatments, as measured by chlorophyll, were analyzed separately for each of the two experiments. Experiment 1 was analyzed as a randomized complete block ANOVA with nutrient as the main factor, whereas Experiment 2 was analyzed as a randomized complete block design with repeated measures. The response of different algal taxa to the nutrient treatments was analyzed using a randomized block MANOVA with block as a random effect. Subsequently, ANOVAs were performed on individual algal groups (cyanobacteria, filamentous green algae, and diatoms). All chlorophyll and cell count data were analyzed using the PROC GLM procedure of SAS statistical software (SAS Institute 1989).

Nutrient releases

In situ experimental channels were used to conduct a series of short-term nutrient enrichments and to compare the relative uptake lengths of nitrogen and phosphorus. Our rationale was that uptake lengths of nutrients in limited supply should be relatively shorter than nutrients in abundance. On three dates (4, 11, and 15 February 1999) nutrient uptake lengths were measured for NO_3, PO_4, and NH_4 using short-term enrichments of experimental channels. Channels were constructed of polyvinyl chloride (PVC) rain gutter (diameter, 15 cm) suspended near the surface of Rio Las Marias and were 30 m in length with plastic mesh (6 mm) ends to exclude fish. Stones with a live periphyton layer were placed throughout the bottom of each chan-

nel and were allowed to incubate in the stream over a 14-d period. Releases were performed on Days 14, 21, and 25 of the experiment.

In each channel, two separate releases were performed in series to minimize the complication of nitrification interfering with NO_3 uptake measurements. A solution of $NaNO_3$, KH_2PO_4, and NaCl was used for the first release, followed by a solution of NH_4Cl and NaBr. Goal concentrations for each solute were 7 mg/L Cl, 50 μg/L NO_3-N, and 20 μg/L for PO_4-P, NH_4-N, and Br. Goal concentrations were selected on the basis of analytical precision and the ratios between nutrient availability from 1998 Las Marias concentration data. We attempted to add as little nutrient as we could reasonably detect downstream in order to minimize enrichment impacts. Constant inflow was maintained by pumping the solution with a battery-powered Watson Marlow peristaltic pump (model 504S; Watson-Marlow Bredel, Falmouth, UK). Conductivity was continuously monitored with a YSI conductivity meter (model 10, YSI, Yellow Springs, Ohio, USA) throughout the first release. We sampled eight sites along each channel after a plateau in conductivity was reached at the downstream end of the channel (generally within 30–60 min). The second release (NH_4 and Br) was started immediately after sampling the first release, and samples were taken after the time to plateau interval determined from the first release. Samples were filtered in the field through rinsed glass fiber filters (Gelman type A/E; pore size, 1 μm), stored in new polyethylene bottles (rinsed with deionized water) and immediately preserved with 0.4% chloroform. Samples were then stored in the dark at room temperature for one to two weeks before they were transported to the United States for analysis.

Water samples were analyzed for NH_4 using a modification of the phenol–hypochlorite (Solorzano 1969) technique on an Alpkem analyzer (OI Analytical, College Station, Texas USA). NO_3, PO_4, Cl, and Br concentrations were determined for all samples using a Dionex Ion Chromatograph (model DX 500 IC with an AS4A anion column; Dionex, Sunnyvale, California, USA). Analyses were performed by the analytical laboratory at the Institute of Ecosystem Studies, Millbrook, New York, USA, within one month of sampling.

Nutrient uptake lengths were determined for each release by calculating the slope of the line relating nutrient concentrations to downstream distance, using the linear form of the exponential uptake equation:

$$\ln N_x = \ln N_0 - k_x$$

where N_0 is the background concentration, N_x are the concentrations at x meters downstream from the release site (0 m), and k is the per meter uptake rate (Newbold et al. 1981). The uptake length of a nutrient (S_W), or the average downstream distance traveled by a nutrient molecule prior to removal from the water column, is calculated as k^{-1}. To correct for dilution, nutrient con-

centrations were divided by the concentration of Cl (for NO_3, and PO_4) or Br (for NH_4), our conservative tracers (Webster and Ehrman 1996). In several instances, the experimental channels were not long enough to determine phosphate uptake lengths; for these cases, conservative estimates of the phosphate uptake length were computed based on nonsignificant regression equations. Uptake rates (U) of nutrients per square meter of substrate were calculated using the following equation:

$$U = (QN_0)/(S_W w)$$

where Q is stream discharge (measured in cubic meters per hour) and w is wetted channel width (measured in meters) (Newbold et. al. 1981). Estimates of the uptake length of nitrogen, S_N, regardless of its form, were calculated by standardizing the uptake length of both NH_4 and NO_3 by their respective portions of the total nitrogen uptake:

$$S_N = \left[S_{NO_3} \left(\frac{U_{NO_3}}{U_{NO_3} + U_{NH_4}} \right) \right] + \left[S_{NH_4} \left(\frac{U_{NH_4}}{U_{NH_4} + U_{NO_3}} \right) \right].$$

Uptake length data were analyzed as a two-factor (nutrient and block) randomized complete block ANOVA, in which dates were considered blocks. Subsequently, orthogonal contrasts were performed to compare S_{PO_4} vs. S_N, with NH_4 and NO_3 weighted by their respective proportions.

Nutrient-diffusing substrates

To examine the relative importance of top-down vs. bottom-up limitation of periphyton, nutrient levels and grazing fish were manipulated simultaneously using nutrient-diffusing substrates. Nutrient-diffusing substrates were made from clay flowerpots (diameter, 8.5 cm; height, 8 cm; volume, 225 ml) filled with nutrient-rich agar and sealed with petri dishes on the bottom (see methods described in Fairchild et al. [1985], Pringle and Triska [1996], Scrimgeour and Chambers [1997]). Agar (20 g/L H_2O) was spiked with $NaNO_3$ and NH_4Cl for N and NaH_2PO_4 for P enrichment, which slowly diffused through the flowerpots. Four nutrient treatments were established: (1) unenriched control (agar only), (2) N addition, (3) P addition, and (4) N and P addition. To remove residual nutrients, flowerpots were initially soaked in filtered stream water for 7 d. Nutrients were manipulated by adding 12.0 g NaH_2PO_4/L agar for P enrichment; 42.5 g $NaNO_3$ and 26.75 g NH_4Cl per liter agar for N enrichment; and 42.5 g $NaNO_3$ and 26.75 g NH_4Cl plus 12.0 g NaH_2PO_4 per liter agar for combined N and P enrichment to produce a 10 N:1 P treatment (1 mol/L N:0.1 mol/L P).

To tease apart the importance of nutrients and herbivores on algal standing crops and species composition, we placed one flowerpot of each nutrient treatment in fish exclusion and open cages. Fish exclusions (dimensions, 1×1 m) were constructed of 6-mm plastic mesh and effectively prevented herbivory by fishes, whereas open cages contained mesh only on the upstream end and were fully accessible to grazing fishes. Fishes were frequently observed grazing flowerpots in open cages, particularly the epibenthic feeders *Parodon* (Parodontidae), *Prochilodus* (Prochilodontidae), and *Ancistrus* (Loricariidae). Cages were placed in runs and were anchored with rebar stakes in each corner. Treatments were arranged in a split-plot randomized block design, with grazer and grazer exclusion treatments as whole plots and the four nutrient treatments as split plots. Each grazer–nutrient treatment was replicated in eight blocks for a total of 64 flowerpots. The four flowerpots were spaced 10–15 cm apart across the middle of each cage. Cages were brushed once each day to remove debris, and flowerpots were lightly shaken to reduce sediment accumulation and confounding effects of differential sediment accrual among grazer treatments.

Experiments were conducted three times (February 1998, February 1999, and March 1999). Each experiment was run for 14–18 d, and algae were sampled from flowerpots on two to three dates. Attached algal cells were removed with a toothbrush from a 6.15-cm^2 circle delineated with an acetate template. Algal samples were placed immediately on ice and chlorophyll was extracted in 90% ethanol within 24 h, and subsequently analyzed fluorometrically. On Day 12 of the February 1999 experiment, algal samples were also collected for cell counts. These samples were preserved in ~3% formalin, and transported to the United States for processing in the laboratory using methods similar to those described for the flow-through channel enrichment.

Chlorophyll data were log-transformed and divided by the number of days of the experiment to standardize for differences in their duration. Algal response to nutrients and grazing fishes, as measured by chlorophyll *a*, was analyzed for the combined experiments as a split-plot design with eight randomized complete blocks, two subplots with factors fish or no fish, and four split plots within subplots, with factors nitrogen and phosphorus. Each split plot had either two or three repeated measurements. The design was unbalanced due to unequal numbers of sampling dates in the replicates, as well as the loss of four samples. For this reason, Kenward-Roger approximate F tests and estimated degrees of freedom were used for testing (Kenward and Roger 1997, SAS Institute 1999), which can result in fractional degrees of freedom in the F tests. Analyses of chlorophyll *a* data were conducted using the PROC MIXED procedure of SAS Version 8.1. The response of different algal groups to nutrients based on cell counts was analyzed using a split-plot randomized complete block MANOVA with block as a random effect. As for chlorophyll, cell count data were log-trans-

formed. Cell count analyses were conducted using the PROC GLM procedure of SAS (SAS Institute 1989).

Response indices of consumer vs. resource limitation

We combined the data from the three nutrient-diffusing substrate experiments to evaluate the magnitude of the response of algal biomass to limiting nutrients (i.e., nitrogen; see *Results*) and grazing fishes, both alone and together. For graphical display of relative magnitude, responses to nitrogen and grazers were determined by calculating the log ratio of the treatment, divided by the ungrazed, unenriched controls, and standardized by experiment duration in days (i.e., nitrogen = log([nitrogen, no fish]/[no nitrogen, no fish])/days; fish = log([no nitrogen, fish]/[no nitrogen, no fish])/days; fish + nitrogen = log([nitrogen, fish]/[no nitrogen, no fish])/days). This "dynamic index" (cf. Berlow et al. 1999) quantifies an effect size that is theoretically derived from the discrete-time version of dynamics described by Lotka-Volterra equations (see Osenberg and Mittlebach 1996, Wootton 1997, Berlow et al. 1999). For statistical analyses, we performed a split-plot repeated-measures ANOVA for a randomized complete block design, with fish, nitrogen, block, and experiment as factors. Planned comparisons on the log-transformed chlorophyll data were used to test whether a given treatment (i.e., nitrogen, fish, or nitrogen + fish) differed significantly from the unenriched, no-fish control. Analyses were run using the PROC MIXED procedure of SAS.

A second response analysis was conducted on the combined data of the nutrient-diffusing substrate experiments to evaluate whether grazing fishes influenced the magnitude of nutrient limitation. For graphical display, we computed indices of nutrient limitation for substrates accessible to fish and compared these to similar indices computed for substrates from the fish exclusions. Nutrient limitation indices were determined for both fish and no-fish treatments by calculating the log ratio of algal standing crop in N-enriched substrates divided by standing crops of the unenriched controls and standardized by the duration of the experiment (i.e., fish = log([fish, nitrogen]/[fish, no nitrogen])/days; no fish = log([no fish, nitrogen]/[no fish, no nitrogen])/days). For statistical analysis, we tested for a significant fish × nitrogen interaction term based on a split-plot repeated-measures ANOVA for a randomized complete block design, with fish, nitrogen, experiment, and block as factors. This analysis was performed on log-transformed chlorophyll data from the three combined nutrient-diffusing substrate experiments using the PROC MIXED procedure of SAS.

RESULTS

Flow-through channel enrichments

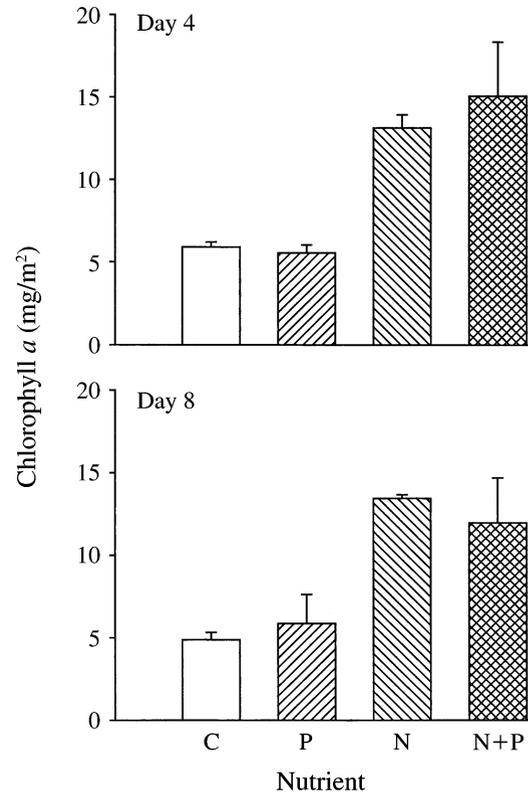Striking differences in algal accrual were quickly observed among the different nutrient channels. Nitro-

FIG. 1. Algal standing crop (chlorophyll *a* in mg/m²) from the four nutrient enrichment treatments of flow-through channel Experiment 2. Chlorophyll *a* was measured after four and eight days. Means + 1 SE are shown.

gen enrichment of flow-through channels resulted in highly significant stimulation of algal growth (Experiment 1, $F_{1,3} = 355.5$, $P < 0.0003$; Experiment 2, $F_{1,3} = 46.2$, $P < 0.0065$), whereby chlorophyll increased 2–3-fold relative to the unenriched controls (Fig. 1). In contrast, no effects were observed due to the addition of P alone. Moreover, there was no significant interaction between N and P (Experiment 1, $F_{1,3} = 3.55$, $P < 0.156$; Experiment 2, $F_{1,3} = 0.86$, $P < 0.422$). Thus, chlorophyll concentrations in channels with both N and P addition were indistinguishable from channels in which N was added alone, suggesting that observed increases in chlorophyll, relative to controls, were solely due to the effects of N (Fig. 1).

Cell count data revealed that algal biovolumes significantly increased in response to N enrichment (MANOVA Wilks' lamda $F_{3,1} = 311.88$, $P < 0.0416$). Among the major algal groups, significantly greater biovolumes of cyanobacteria ($F_{1,3} = 172.25$, $P < 0.001$) and diatoms ($F_{1,3} = 42.86$, $P < 0.0072$) were observed in the nitrogen treatment (Fig. 2). Cyanobacteria displayed a dramatic response to N addition, with biovolume increasing by more than an order of magnitude. Interestingly, the cyanobacterial group was
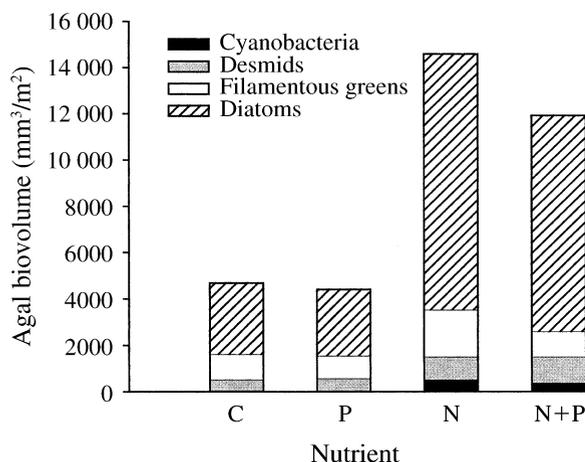
FIG. 2. Algal community composition from the four nutrient enrichment treatments in flow-through channels. Data are from Day 8 of Experiment 2. Bars show means of algal biovolumes (mm^3/m^2).

dominated by the N-fixer *Anabaena*, and chains of this alga contained an abundance of heterocysts.

Nutrient releases

Estimates of uptake lengths suggested N limitation in Rio Las Marias. Uptake lengths varied among nutrients and were shortest for NH_4, intermediate for NO_3, and longest for PO_4 (Table 3). When N was considered irrespective of form, uptake length of N (mean $\pm$ 1 SE, 48.3 $\pm$ 6.8 m) was significantly shorter than the uptake length of PO_4 (mean $\pm$ 1 SE, 88.3 $\pm$ 2.5 m; $F_{1,4} =$ 848.37, $P < 0.0001$). These relative differences in uptake among nutrients were highly consistent, as in 11 of the 12 sets of releases the uptake length ratio for N vs. P (i.e., $S_N:S_P$) was less than one (mean $\pm$ 1 SE, 0.59 $\pm$ 0.09). For three of the releases, our channel length was not long enough to calculate a PO_4 uptake length, whereas this was never the case for NH_4 or NO_3.

Uptake rates were significantly higher for the two forms of dissolved inorganic N than for PO_4 (Table 3). Nutrient uptake rates were greatest for NO_3, even though NH_4 displayed shorter nutrient uptake lengths.

Nutrient-diffusing substrates: grazer nutrient manipulations

We observed highly significant main effects on chlorophyll *a* of both grazing fishes ($F_{1,6.11} = 19.52$, $P < 0.0043$) and nitrogen ($F_{1,6.72} = 23.85$, $P < 0.002$), as well as a highly significant fish $\times$ nitrogen interaction ($F_{1,5.79} = 12.41$, $P < 0.0133$). Similar to the flow-through enrichment experiments, N was the only nutrient that stimulated algal accrual; we found no significant response to the addition of P alone or evidence of colimitation by N and P (Fig. 3). Likewise, algal biovolumes based on cell counts displayed highly significant main effects of grazing fish (MANOVA Wilks' lambda $F_{4,4} = 36.98$, $P < 0.002$) and nitrogen enrichment (Wilks' lambda $F_{4,11} = 3.47$, $P < 0.0456$), and a significant interaction between grazers and nutrients (MANOVA Wilks' lambda $F_{4,11} = 3.49$, $P < 0.0451$) (Fig. 4). Among the major algal groups, significant reductions in biovolume were observed on substrates accessible to grazing fishes for filamentous green algae ($F_{1,7} = 9.82$, $P < 0.0165$), desmids ($F_{1,7} = 16.89$, $P < 0.0045$), cyanobacteria ($F_{1,7} = 5.57$, $P < 0.0503$), and diatoms ($F_{1,7} = 118.92$, $P < 0.0001$) (Fig. 4). Fishes also modified the composition of algal assemblages; in particular, the grazer-resistant alga *Stigeoclonium* (Chlorophyta) comprised a larger proportion of algal assemblages on substrates accessible to grazing fishes compared to fish exclusions. Interestingly, cyanobacteria were the only taxon in which N addition caused a significant increase in biovolume ($F_{1,14} = 8.96$, $P < 0.0097$), and the greatest responses were observed when fishes were excluded resulting in a highly significant fish $\times$ nitrogen interaction ($F_{1,14} = 9.05$, $P < 0.0094$).

TABLE 3. NO_3, PO_4, and NH_4 uptake lengths (S_W) and uptake rates from experimental channel releases. Uptake weighted S_W for total inorganic nitrogen ($NH_4 + NO_3$) and ratios of N and P uptake lengths and uptake rates are also given.

Date (1999)	Channel	S_W (m)				Uptake length ratio $S_N:S_P$	Uptake rate ($mg \cdot h^{-1} \cdot m^{-2}$)				Uptake rate ratio N:P
		NO_3-N	PO_4-P	NH_4-N	Total N		NO_3-N	PO_4-P	NH_4-N	Total N	
4 Feb	1	28.8	47.4	14.4	22.8	0.48	33.33	9.32	24.09	57.42	6.16
	2	29.1	63.9	13.6	21.8	0.34	32.99	6.71	29.51	62.50	9.31
	3	53.4	124.3†	31.0	43.6	0.35	13.48	3.13	10.45	23.93	7.65
	4	72.6	98.0†	28.5	50.4	0.51	11.24	3.67	11.37	22.61	6.15
11 Feb	1	68.5	97.4†	71.6	69.1	0.71	13.97	4.70	3.36	17.33	3.69
	2	66.8	47.1	63.5	66.0	1.40	14.56	13.04	4.96	19.53	1.50
	3	53.4	124.3†	31.0	42.3	0.34	7.19	3.60	7.01	14.20	3.94
	4	72.6	98.0†	28.5	45.9	0.47	4.63	4.41	7.09	11.71	2.66
15 Feb	1	88.8	128.3	36.9	66.6	0.52	5.81	2.68	4.33	10.14	3.78
	2	83.4	118.4	43.7	68.9	0.58	6.45	2.55	3.70	10.14	3.97
	3	43.0	47.8	15.7	27.4	0.57	9.21	8.28	12.33	21.53	2.60
	4	59.2	64.6	47.1	54.5	0.84	8.00	7.33	5.15	13.14	1.79

† The regression from which S_W was calculated was *not* significant at $P < 0.05$; in these cases we made a conservative estimate of PO_4 uptake from a nonsignificant regression.
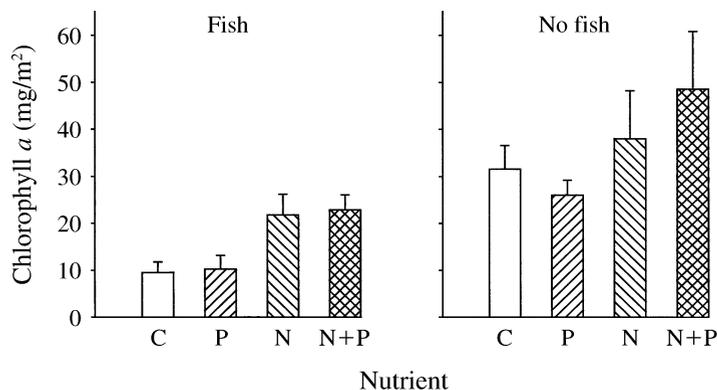
FIG. 3. Algal standing crop (chlorophyll *a*) from the three nutrient-diffusing substrate experiments conducted in 1998 and 1999. "No fish" treatments excluded grazing fishes and other fish trophic groups. "Fish" treatments were open cages accessible to the natural fish assemblage. Means + 1 SE are shown for the three experiments combined.

Response indices of consumer and nutrient limitations

Response indices of the nutrient-diffusing substrate experiments revealed consistent patterns of resource and consumer limitation (Fig. 5). Although effects of both nitrogen addition and grazing fishes were observed, the strength of the algal response to grazers was considerably greater than the response to nutrients. Relative to the unenriched, no-fish control, the magnitude of the reduction in algal standing crops due to fishes (mean ± 1 SE, 0.1086 ± 0.0167, $t_{7.82}$ = 5.39, P < 0.0007) was nearly three times greater than the increase in algae due to N enrichment (mean ± 1 SE, 0.0364 ± 0.0128, $t_{10.4}$ = −2.54, P < 0.028) (Fig. 5). Interestingly, algal biomass did not differ significantly from the unenriched, no-fish control when grazers and nutrients were added simultaneously (mean ± 1 SE, 0.0150 ± 0.0182, $t_{10.9}$ = 0.91, P < 0.38) (Fig. 5).

Finally, the relative degree of nutrient limitation was significantly greater for substrates exposed to grazing fishes compared to substrates where grazers were excluded (Fig. 6). In other words, the increase in algal biomass with nitrogen addition was much greater in the presence of grazing fishes resulting in a significant fish × nitrogen interaction term ($F_{1, 5.79}$ = 12.41, P < 0.0133). We observed that the indices of nutrient limitation for grazed substrates (log([fish, nitrogen]/[fish, no nitrogen])/days) averaged (mean ± 1 SE, 0.0936 ± 0.0128) more than 2.5 times the index value observed in the absence of grazing fishes (log([no fish, nitrogen]/[no fish, no nitrogen])/days; mean ± 1 SE, 0.0364 ± 0.0128). Thus, it appeared that grazing fishes strongly exacerbate nutrient limitation in addition to causing severe reductions in algal standing crops.

DISCUSSION

Our findings provide evidence that both grazing fishes and nutrients can represent important simultaneous limitations on primary producers and that such bottom-up and top-down forces interact in tropical Andean streams during the dry season. We observed consistent evidence of nitrogen limitation across an array of studies using several different approaches. At the same time, the presence of grazing fishes strongly reduced algal biomass and modified the response of algae to nitrogen addition. Interestingly, our findings suggest that consumers might play an important role by influencing nutrient demand, which contrasts with other studies that have focused on the influence of consumers in affecting nutrient supply.

Resource limitation: effects of nitrogen

Multiple lines of evidence suggest that algal accrual in Rio Las Marias was limited by N availability. Con-
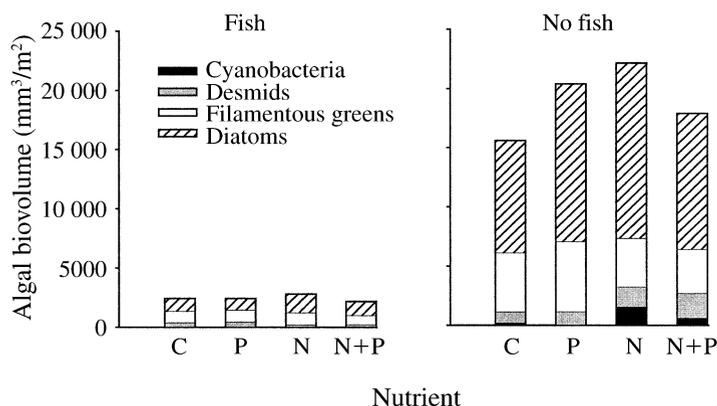

FIG. 4. Composition of algal assemblages from Day 12 of the nutrient-diffusing substrate experiment conducted in February 1999. Bars show means algal biovolumes (mm³/m²).
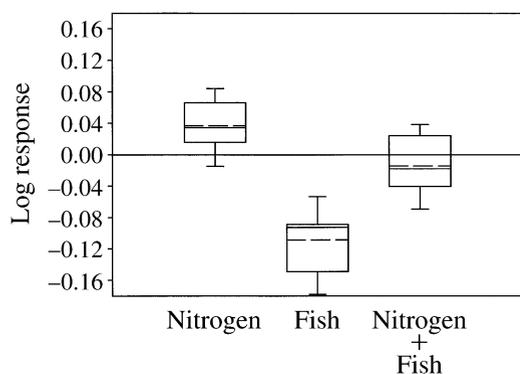
FIG. 5. Comparison of the relative strength of consumer vs. resource limitation from the nutrient-diffusing substrate experiments. For graphical display of relative magnitude, algal responses to nitrogen and grazers were calculated as follows: nitrogen = log([nitrogen, no fish]/[no nitrogen, no fish])/days; fish = log([no nitrogen, fish]/[no nitrogen, no fish])/days; fish + nitrogen = log([nitrogen, fish]/[no nitrogen, no fish])/days. For statistical analyses, planned comparisons were made between each treatment (i.e., nitrogen = nitrogen, no fish; fish = no nitrogen, fish; fish + nitrogen = nitrogen, fish) vs. the control (no fish, no nitrogen) (see *Methods: Response indices of consumer vs. resource limitation* for details). Box plots are for the log response of combined data of the three nutrient-diffusing substrate experiments. The response index of zero depicted by the horizontal line represents log(chlorophyll) for the control, and box plots represent deviations between experimental and control treatments. Box plots show the mean (dashed line), median (solid line), 10th (bottom error bar), 25th (box bottom), 75th (box top), and 90th (top error bar) quartiles. Mean log(chlorophyll) $\pm$ 1 SE standardized by days for the different treatments are as follows: control, 0.3231 $\pm$ 0.04771; nitrogen, 0.3595 $\pm$ 0.04771; fish, 0.2145 $\pm$ 0.04771; fish + nitrogen, 0.3081 $\pm$ 0.04773.

centrations of dissolved inorganic nitrogen (i.e., NO_3-N, NH_4-N) were moderately low, and consistently measured <100 μg/L (Table 1), the concentration below which examples of N limitation have been reported in temperate streams (Borchardt 1996). In addition, N:P ratios in Rio Las Marias were relatively low (1998 dry season mean, 15.4:1; 1999 dry season mean, 8.5:1). Our field experiments corroborated these initial observations, as algal accrual was stimulated by N enrichment.

Our experiments were short in duration, so it is important to bear in mind that we addressed questions about limitation, rather than the regulation or control of primary producers (Osenberg and Mittelbach 1996). Assessing the most appropriate time frame for experimental studies is interesting fodder for debate, and depends in part on the system and the particular question being addressed (Osenberg et al. 1999). For investigating nutrient or grazer limitation, experiments should be sufficiently brief that system feedbacks do not interfere with estimates of limitation (Osenberg and Mittelbach 1996, Downing et al. 1999b). In contrast, for studies of population regulation, feedbacks may be precisely the question of interest. Indeed, the nature of

nutrient enrichment can vary over time with temporal changes in ambient concentrations and the relative importance of different nutrient sources. For example, Peterson and Grimm (1992) examined the effects of nitrogen enrichment in a desert stream over an 89-d period and observed that strong responses of enrichment on early successional algal biomass were greatly reduced in later stages of succession. This was attributed to the eventual development of a thick algal mat in the absence of disturbance, thus resulting in a more pronounced role of internal nutrient recycling as a major supplier of nutrients to benthic algae. Likewise, multiyear phosphorus fertilization of an Arctic stream has resulted in a series of interesting feedbacks that could not be anticipated based on short-term studies of nutrient limitation (Peterson et al. 1993).

Results from the nutrient enrichment experiments were consistent with observed differences in nutrient demand at a larger spatial scale based on nutrient uptake. Since these whole-system releases measure the relative demand for nutrients by the entire benthic community, they indicate that not only algae but also the full benthic assemblage, including heterotrophs, has a higher demand for N than P. Ratios of the weighted nitrogen uptake to phosphate uptake were less than one in all but a single case. Previously, uptake ratios less than one for NH_4 and PO_4 have been used to indicate greater ecosystem efficiency in retaining nitrogen (Martí and Sabater 1996). We computed a ratio that takes into account the downstream transport of both forms of N, which gives us a more complete estimate of the ecosystem demand for N. Release data were consistent with several other recent studies that have shown that uptake lengths are shorter for limiting nutrients (Munn and Meyer 1990, Martí and Sabater 1996, Martí et al. 1997).

Despite the consistent patterns of shorter uptake lengths for N than for PO_4, our estimates need to be interpreted within their appropriate context. Experi-
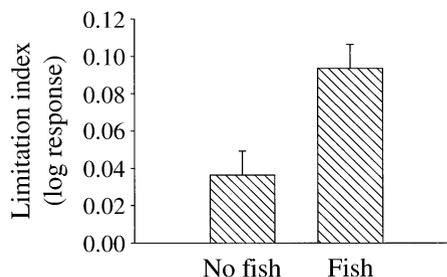

FIG. 6. Degree of nutrient limitation in the presence vs. absence of grazing fishes. Nutrient limitation indices were calculated by comparing algal biomass as measured by chlorophyll *a,* from enriched and unenriched substrates in fish exclusions (log([nitrogen, no fish]/[no nitrogen, no fish])/days) and from open cages accessible to grazing fishes (log([nitrogen, fish]/[no nitrogen, fish])/days). Bars represent mean + 1 SE limitation indices from the three nutrient-diffusing substrate experiments.

ments were designed specifically to examine relative differences in uptake within artificial channels, rather than provide absolute estimates for uptake in the natural stream. Our reported uptake lengths are relatively short, which may be in part due to higher algal standing crop in channels (chlorophyll *a,* mean ± 1 SE, 36.9 ± 4.0 mg/m²) in the absence of fish compared to the natural stream (February survey chlorophyll *a*: riffle mean ± 1 SE, 11.4 ± 0.4 mg/m²; run mean ± 1 SE, 8.4 ± 0.4 mg/m²; Table 2) where grazers were abundant. However, nutrient demand may be underestimated using nutrient enrichment methods if the ambient community becomes saturated, thereby leading to a reduction in the proportion of nutrient removed (Mulholland et al. 1990). For our releases, both PO_4 and NH_4 were added at the same concentration (20 μg/L), whereas greater amounts of NO_3 (50 μg/L) were added. The effect of greater nitrate enrichment, if any, would be to underestimate NO_3 uptake; however, we observed that NO_3 uptake was greater than PO_4, even with this potential bias.

Our results provide some interesting contrasts with work from elsewhere in the neotropics. Although N limitation has been described for some temperate streams (e.g., Gregory 1980, Grimm and Fisher 1986, Hill and Knight 1988, Tate 1990, Lohman et al. 1991), it is not well known for tropical running waters. Lewis et al. (1995) suggested that known inorganic N concentrations for streams and rivers of tropical South America were generally higher than would be expected for N-limited systems. In contrast, Downing et al. (1999*a*) posited that tropical freshwaters are often N limited based on low ambient N:P ratios, but acknowledged that there are too few data to predict how tropical freshwaters will respond to altered nutrient supplies. The few published experimental studies of nutrient limitation in neotropical streams provide no indication of N limitation (Pringle et al. 1986, Pringle and Triska 1991). Thus, N in a pair of lowland forest tributaries in Costa Rica was apparently at growth-saturating concentrations; experiments using nutrient-diffusing substrates revealed either P limitation (Pringle and Triska 1991) or no response to N and P enrichment (Pringle et al. 1986, Paaby-Hansen 1988, Pringle and Triska 1991).

Shifts in algal assemblage composition were observed in response to N addition, although the magnitude of the response by specific taxa to nitrogen differed between experiments (Figs. 2 and 4). Methodological differences in enrichment source and experimental duration may have contributed to the varied responses, as the precise nature of the nutrient supply to specific taxa can be difficult to partition in many enrichment experiments (Borchardt 1996). Curiously, one of the most striking responses we observed to N enrichment was the order-of-magnitude increase in the N_2-fixing cyanobacteria *Anabaena.* We anticipated that in a N-limited ecosystem, the greatest abundance of N_2

fixers would occur in treatments where N availability was low (i.e., controls and P additions), presuming N_2-fixing cyanobacteria have a competitive advantage when N is limiting (Tilman et al. 1982, Howarth et al. 1988). One possibility is that the time frame of the experiment may have been simply too short to allow a sufficient trajectory of algal succession, and in the short term N may have provided a "jump start" to an initially established algal assemblage that included cyanobacteria.

Dual effects of top-down and bottom-up influences on primary producers

We observed that resources (nitrogen) and consumers (grazing fish) simultaneously limited the accrual of algal biomass (Fig. 5). The relative magnitude of the response to these dual processes differed substantially, whereby the decrease in primary producers associated with grazing was considerably greater than the stimulatory effect of N addition. One caveat when interpreting these results is that the nature of our manipulations was not entirely equivalent for grazers (i.e., no fish vs. many fish) and nitrogen (i.e., some nitrogen vs. more nitrogen), and it is unclear whether such differences might have influenced the relative strength of algal responses to the manipulations. Nonetheless, strong and highly significant reductions in algal accrual by grazers were largely mitigated by the addition of N. Thus, algal biomass in the treatment with both fish and nitrogen was not significantly different from the unenriched, no fish control (Fig. 5).

Such concurrent limitation of consumers and nutrients on periphyton may be a common feature of many stream systems, although there have been too few studies to allow for satisfying generalization (Lamberti 1996). Experiments from temperate streams vary in the extent to which they demonstrate responses to enrichment among different grazer treatments (Stewart 1987, McCormick and Stevenson 1991, Hill et al. 1992, Rosemond 1993, Rosemond et al. 1993, Forrester et al. 1999). For example, Stewart (1987) compared the effects of algivorous minnows (*Campostom*a) in unenriched pools of a prairie margin stream to other pools in which fertilizer was added. Although nutrient enrichment increased primary productivity, grazing fishes strongly depressed epilithic algal biomass and were able to keep pace with algal growth stimulated by fertilization. Likewise, in a small headwater stream in Tennessee, snails displayed a strong numerical response to fertilization and maintained a thin epilithic layer of grazer-resistant algae regardless of nutrient enrichment; however, once grazing snails were excluded, algal biomass increased with nutrient addition (Hill et al. 1992). In contrast, McCormick and Stevenson (1991) observed strong responses to nutrient amendment when substrates were accessible to grazing invertebrates, which is consistent with our findings for

Rio Las Marias (Fig. 6, see *Discussion: Interactions between top-down and bottom-up processes*).

Several investigators have attempted to measure the magnitude of limitation by consumers and nutrients. In an elegant set of studies, Rosemond (1993) and Rosemond et al. (1993, 2000) manipulated nutrients and herbivorous snails simultaneously in a two-trophic-level system. The relative strength of top-down vs. bottom-up limitations varied among experiments, and strong interactive effects were apparent. Interestingly, nutrients generally had greater effects than grazers on chlorophyll *a,* although grazers had stronger effects on chlorophyll-specific productivity. Their findings contrast sharply with our observations of a greater effect of grazers than nutrients when examined separately, and a greater degree of nutrient limitation on algal standing crops when grazing fishes were present. Forrester et al. (1999) reported both top-down and bottom-up effects among three trophic levels in a Sonoran Desert stream. Benthic algae were stimulated by nitrate addition, whereas decreases in algal standing crops were associated with the removal of insectivorous fishes, presumably due to the corresponding release of grazing invertebrate populations. Effects of nutrient addition were still considerably greater in magnitude than the influence of insectivorous fishes cascading through the food web.

In Rio Las Marias, the fish assemblage is composed of a broad suite of trophic groups, in addition to herbivores (Flecker 1992, 1996). Nevertheless, algal standing crops were consistently low when substrates were accessible to the natural fish assemblage, suggesting that abundant populations of predators and omnivores do not preclude a strong trophic link between grazers and primary producers. In this regard, our results contrast with Forrester et al. (1999), as well as Brett and Goldman's (1997) conclusions from their meta-analysis of resource vs. consumer limitation for pelagic food webs. Brett and Goldman assembled studies involving three trophic levels that manipulated both nutrients and planktivorous fishes. They found top-down and bottom-up limitations of phytoplankton community biomass operating simultaneously; however, their analysis suggested that some degree of trophic uncoupling occurred at the zooplankton–phytoplankton link resulting in only a moderate degree of consumer limitation of phytoplankton. In contrast, tight limitation of phytoplankton biomass was associated with nutrient addition. Unlike such pelagic systems, we posit that the biomass of grazing fish may be so substantial in many midsized tropical streams that simple resource limitations on algal standing crops are overshadowed by the presence of consumers.

Interactions between top-down and bottom-up processes: do consumers modulate nutrient limitation?

Models of food web limitation have paid considerable attention to the role of consumers and ecosystem productivity in influencing the standing crops of different trophic levels (Power 1992). However, there has been relatively little focus on the influence of consumers in modifying the magnitude of resource limitation (but see DeAngelis [1992]). Interestingly, we observed that the degree of N limitation was more than 2.5 times greater on substrates grazed by fishes compared to substrates inaccessible to macroherbivores (Fig. 6), suggesting that grazers may modulate the nature of nutrient cycling by primary producers (Steinman 1996). These findings are not entirely unique to Rio Las Marias. Studies in an ephemeral Kentucky stream reported that grazers modified algal responses to nutrient enrichment (McCormick and Stevenson 1989, 1991). When grazing snails were present in experimental mesocosms, grazer-resistant algae (e.g., *Stigeoclonium*) increased with nutrient enrichment, yet the addition of nutrients had little effect in the absence of herbivores. Such top-down enhancement of nutrient limitation could occur if grazers stimulate rates of primary production and thus increase in situ nutrient uptake rates. Empirical research from terrestrial systems (McNaughton et al. 1988, Pastor et al. 1988, Knapp et al. 1999) and mathematical models (DeAngelis 1992) suggests that grazing can increase rates of nutrient cycling; however, evidence using enzyme alkaline phosphatase as an indicator of phosphorus limitation suggests to the contrary that grazing by invertebrates alleviates rather than enhances nutrient limitation in streams (Mulholland et al. 1991, Rosemond et al. 1993). Thus, studies from streams and terrestrial systems may provide conflicting evidence on the role grazers play in enhancing nutrient cycling rates, which as Steinman (1996) points out may be in part confounded by the need to distinguish between system-level vs. in-situ cycling in running waters.

A number of studies of benthic grazer–algal interactions indeed support the notion that herbivores increase per capita productivity of grazer-resistant taxa (Lamberti 1996, Steinman 1996). Several mechanisms may account for herbivores stimulating primary producers and these may lead to different predictions about whether grazers should facilitate nutrient limitation (Lamberti et al. 1987, Stewart 1987, McCormick and Stevenson 1989). First, herbivores and other consumers recycle nutrients via excretion, thereby augmenting rates of nutrient supply (Sterner 1986, Vanni 1987, 1996, Grimm 1988, Elser 1992, Hood 2000). Although this could explain McCormick and Stevenson's (1991) results from closed experimental microcosms, it is unlikely to account for our findings in an open system such as Rio Las Marias in which the availability of nutrients recycled by fishes would not have been localized to specific experimental treatments. Alternatively, grazers may influence the nature of the supply of limiting nutrients to understory algae by removing overlying senescent cells that can diminish nutrient transport rates into even a thin periphyton layer (Mc-

Cormick and Stevenson 1991; but see Steinman et al. [1995]), as well as selecting for rapidly dividing algal taxa (Hill et al. 1992). Perhaps more importantly, epibenthic grazers in tropical streams play a key role in clearing rapidly deposited sediments from benthic substrates (Power 1984, 1990, Flecker 1992, 1996, Pringle and Blake 1994, Pringle and Hamazaki 1997). Thus, in the absence of grazers, heavy sediment deposition may limit light to algal cells in the lower strata of periphyton mats, thereby reducing rates of photosynthesis. Indeed, sediment removal by armored catfish in Panama increased primary productivity compared to ungrazed substrates not exposed to grazers (Power 1990). Although all flowerpots in our experiments were lightly shaken daily to reduce sediment accrual (see *Methods: Nutrient-diffusing substrates*), a sediment layer accumulated nonetheless when fish were excluded potentially limiting light availability to understory primary producers.

In summary, grazing fishes and nutrients were shown to simultaneously limit primary producers of a tropical Andean stream. Consumers not only reduce algal standing crops, but also increase the degree to which primary producer biomass increases with the addition of limiting nutrients. Whereas other studies have shown consumers affecting nutrient supply in ecosystems, our findings suggest that consumers can play an important role in influencing nutrient demand. These results reinforce the notion that ecological processes are highly interactive and their study cannot be decoupled from the appropriate ecological context. Understanding the role of consumers and resources in tropical streams becomes ever more important as fish populations and nutrient inputs in many poorly studied regions of the tropics are increasingly influenced by human-accelerated environmental change.

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