

Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream

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Synopsis

We experimentally manipulated fish grazing pressure to determine whether fish herbivory played an important role in the structure of a Costa Rican stream. Non-planktonic plant matter represented a significant percentage ($\geq 25\%$) of the diet of 77% of the 17 fish species in the community. We prevented fish grazing on macrophytes, tree leaves, and periphyton using fish exclusion cages. Fish grazed *Panicum* sp., used as a generalized aquatic macrophyte, to the stems after 6 days in control areas, and consumed all or much of *Ficus insipida* and *Monstera* sp. leaves when placed in the stream after 48 hours. Plants and leaves experimentally protected by cages remained intact. In periphyton studies, fifty percent more ash free dry weight occurred on 25×25 cm floor tiles protected from fish grazing by cages than on tiles in roofless controls exposed to fish grazing for 19 days, suggesting a reduction in periphyton biomass. These results demonstrate that fish herbivory affects macrophyte abundance, and impacts the amount of leaf litter in the stream. Fish herbivory may also have an important effect on overall periphyton biomass. Herbivorous fish species generally represent a larger proportion of the total fish community in tropical compared to temperate streams; thus fish grazing is more likely to have an important influence on plant and animal abundances and distributions in tropical streams.

Introduction

Ecologists are often interested in identifying characteristics of communities that aid in predicting those species that play an important role in the function of ecological systems. One possible indicator of differences in community function is a change in the trophic structure of the community. For example, in north-temperate streams, typically 0–25% of fish species eat significant amounts of plant material (algae, macrophytes or fallen leaves, Table 1). In contrast, typically 25–100% of fish

species in tropical streams have diets that include a large plant component. Although many tropical fish species feed on plant material (Table 1, see also Lowe-McConnell 1975, 1987, Goulding 1980, Goulding et al. 1988), only one experimental study has been conducted to examine how fish grazing affects the abundance and composition of plant material in tropical streams (Power 1981, 1983).

Observations of large streams and rivers in the Atlantic lowlands of Costa Rica yield some striking qualitative floristic differences from many streams in North America: macrophytes are rare or absent

from even large rivers, and often algae in these communities consist only of a short (1–2 mm) turf. Growth-saturating levels of nitrogen and phosphorus (Pringle et al. 1990) suggest that nutrient limitation does not result in low plant standing crops, and the low abundance of herbivorous stream invertebrates (Stout & Vandermeer 1975) indicates that plant standing crops are not limited by insect grazing. In contrast, the differences in fish trophic structure in tropical relative to temperate streams, fish herbivory seems to support a hypothesis that fish grazing promotes the relatively low abundance of plants in these Costa Rican streams. Here we present experiments assessing some of the impacts of fish grazing on the aquatic plant community,

including leaves, macrophytes, and algae in a Costa Rican stream, and discuss possible consequences for overall community structure.

Methods and study site

We conducted the study in the Quebrada el Sabalo, a fourth-order stream bordering the La Selva biological field station of the Organization of Tropical Studies (OTS), located in Heredia Province, Costa Rica (10° 26' N, 83° 59' W). The stream, about 15 m wide and 0.5 m deep, bordered primary tropical forest on one side, pasture on the other. Direct sunlight reached the experimental sites from

Table 1. Percentage of fish whose diets contain one quarter or more macrophyte material or algae (excluding phytoplankton and detritus) in temperate and tropical stream communities.^a

Location (n)	% S	% N	Source
<i>Temperate streams^b</i>			
California (1)	25.0	29.4	Moyle & Vondracek (1985)
Illinois (1)	11.5		Schlosser (1982)
Indiana (4)	14.3–22.2		Gorman & Karr (1978)
Indiana (3)	0–7.7	0–4.3	Grossman et al. (1982)
Kentucky (4)	0–16.7		Kuehne (1962)
Kentucky (3)	0–14.2		Lotrich (1973)
Kentucky (2)	14.3–22.2	5.0–8.7	Small (1975)
New York (6)	0–13.0		Sheldon (1968)
North Carolina (3) ^c	5.9–16.7		Gatz (1979)
North Carolina (1) ^c	7.4–8.7		Hall (1972)
Oklahoma (2)	11.8–21.4	8.9–10.6	Ross et al. (1985)
Wisconsin (1)	20.7		Mendelson (1975)
<i>Tropical streams^b</i>			
Brazil (3)	37.5–61.0	37.6–48.3	Knoppel (1970)
Brazil (10)	6.0–46.0		Goulding et al. (1988)
Costa Rica (2)	52.6–80.0	24.0–76.7	Burcham (1985)
Costa Rica (1)	76.5		This study
Costa Rica (2)	26.7–41.7		Winemiller (1983)
Nigeria (1) ^c	48.2		Adebisi (1988)
Panama (9)	33.3–75.0		Angermeier & Karr (1983)
Panama (1)	47.4		Gorman & Karr (1978)
Panama (1)	42.9		Power (1981)
Panama (2)	36.0–40.0	17.4–37.3	Zaret & Rand (1971)
Sri Lanka (6)	60.0–100		Wikramanayake & Moyle (1989)
Uganda (1) ^c	83.3–100		Welcomme (1969)

^a %S—percentage of species, n—number of streams sampled, % N—percentage of individuals (# individuals × % of diet). % N only presented for studies presenting both species abundances and detailed diets.

^b Temperate values limited to a literature survey of *Ecology*, *Ecological Monographs*, and *The American Naturalist*. Tropical values from a more comprehensive literature survey.

^c Incomplete available diet information. Ranges represent minimum and maximum percentages.

2.7 to 7.3 hours per day, encompassing a range of light regimes found from primary forest to open pasture. The Sabalo consists of pools with a silt and sand bottom alternating with cobble-bottomed riffles. The present study was conducted in two cobble areas (mean flow rate = $0.41 \pm 0.09 \text{ m s}^{-1}$ during the study, average cobble size approximately 7 cm in diameter) which could potentially provide natural attachment sites for periphyton. Cobbles covered about 300 m² at one site, 75 m² at the second site 40 m away. Burcham (1985) describes the study stream in detail, and Pringle et al. (1990) characterize its nutrient regime.

We sampled the stream fish community in January and March of 1987, during the driest portion of the year at La Selva, to determine the fish species composition, and to supplement diet data of Burcham (1985). Fish composition in seine samples was similar throughout the study. We used a combination of seining during the late morning, and snorkeling observations throughout the day to determine species composition. We captured fish with a seine net (1.2 × 2.4 m), and immediately transported them to the laboratory for dissection and diet analysis. We estimated the proportion of the diet consisting of filamentous algae, diatoms and terrestrial plant material by dissecting out the stomach of the freshly-caught fish, visually estimating the proportion of the volume of various food categories. Fish were identified according to Bussing (1987).

To determine the effects of fish herbivory on a generalized macrophyte and on fallen leaves in the stream, we constructed 5 cages (25 × 25 × 15 cm) made of 0.5 cm mesh hardware cloth. The mesh was small enough to exclude most adult fish, but large enough to minimize current effects and allow access by any invertebrate grazers. Five square areas (25 × 25 cm) with 10 cm high upstream fences made of 0.5 cm mesh hardware cloth served as controls for any current reduction due to upstream clogging of the mesh. In each replicate we tied to the cage or control wall 5 stems of *Panicum* sp., a grass that commonly grows along the stream bank and is often submerged during floods, to serve as a representative macrophyte, because no aquatic macrophytes were available. We also tied by the

petiole a large, single fresh leaf of *Ficus insipida* and *Monstera* sp. in each replicate to test for the effects of fish grazing on fallen leaf inputs into the stream. Cages were cleaned daily to prevent the build-up of trapped leaves. Herbivory was measured as % leaf area lost from the tree leaves, and from the top three blades from each *Panicum* stem. We only examined the top three blades from *Panicum* because lower leaves would often be affected when we bundled stems together and tied them to the cage or control wall.

We assessed the effect of fish herbivory on algal standing crop with additional cage experiments. Floor tiles (25 × 25 cm) served as substrates for algal attachment. We excluded fish from grazing on experimental tiles by surrounding each tile with a cage of 0.5 cm hardware cloth, 6 cm high on each side. Control tiles, each paired with an adjacent caged tile, resided in roofless cages so that interference of the current by upstream cage walls occurred in both treatments. Each day, and immediately prior to sampling, we cleared trapped leaves from the sides of the cages and controls, and removed trapped sediments in both treatments by creating water turbulence by hand 7–8 cm above the tiles for 5 seconds in order to minimize any sedimentation effects caused by the cages and any leaves trapped on them. Removal of loose accumulated sediments was justified because rocks in the adjacent area remained clear of silt.

Fish grazing intensity in control treatments probably was lower than the natural intensity. Fish avoided the tiles to some extent, perhaps because of their light color relative to the surrounding substrate, which might have increased the risk of kingfisher (*Ceryle torquata*, *C. alcyon*, *Chloroceryle americana*, and *C. amazona*) predation, and because access to the tiles meant swimming over an elevated fence (T. Wootton personal observation). Behavioral observations suggested that fish preferred to remain close to the bottom, where water flow is slower. To reduce this problem, we removed two 3 cm sections of the control fences on the downstream sides to allow easier access. Despite these problems, we frequently observed fish foraging on the control tiles.

We placed the periphyton tile experiments out

on 28 February 1987, and collected accumulated biomass on one half of each tile after 9 days. We obtained algae and other components of the biofilm for biomass measurements by carefully scraping each half tile with a razor blade and collecting the removed algae on dried, pre-weighed filter paper. We then replaced the tiles in the stream. After 10 days, we collected biomass separately from both the previously-sampled and undisturbed halves of each tile. Thus we obtained three separate biomass samples (after 9, 10 and 19 days of growth). The duration of our experiments was chosen to keep periphyton in growth phase and to reduce errors due to sloughing of a more mature periphyton community. To derive measures of algal biomass, we dried samples for 24 hours at 70°C, and weighed them. Then we burned a subsample of known weight in a muffle furnace at 500°C for 4 hours and weighed the ash to determine ash free dry weights.

Results

Fish community composition

Seventeen species occurred at the study site during the experiments, representing 4 families (Table 2). The diet of 13 of the 17 species (76.5%) contained a substantial (arbitrarily designated as more than one quarter of the diet) non-planktonic plant component. Although the sampling techniques did not allow a quantitative estimate of fish species abundances, the six dominant species, in order of abundance, were *Astyanax fasciatus*, *Alfaro cultratus*, *Poecilia gillii*, *Melaneris chagresi*, *Cichlasoma septemfasciatum*, and *C. alfari*. We regularly observed other *Astyanax*, *C. nigrofasciatum*, and *C. nicaraguense* grazing on the control tiles, and *C. tuba*, *C. alfari*, and *Brycon guatemalensis* grazing macrophytes and leaves.

Macrophyte experiments

Fish grazing adversely affected macrophytes. After 7 days, fish grazed most *Panicum* blades to the stem in control areas, while caged plants exhibited little

or no leaf loss (Fig. 1). A significantly higher percentage of caged *Panicum* blades exhibited no damage compared to controls (Mann-Whitney U-test, $p < 0.02$), and although no blades were completely removed in cages, 69.8% of *Panicum* blades were completely grazed in controls (Mann-Whitney U-test, $p < 0.02$). We directly observed fish feeding on the leaves, and also found fish bite marks on plants with portions of the blade remaining at the end of the experiment, as well as on plants during the duration of the experiment.

Leaf grazing

Fish proved to be voracious leaf consumers. After 48 hours, fish had removed nearly all or at least substantial amounts of leaf area from both plant species used, whereas leaves protected from fish remained completely intact (Mann-Whitney U-tests, both $p < 0.02$, Fig. 2). We directly observed

Table 2. Fish community of the Quebrada el Sabalo, Costa Rica January–March 1987.^a

Species	Diet
Characidae	
<i>Astyanax fasciatus</i>	Omnivore ^b
<i>Brycon guatemalensis</i>	Omnivore ^b
<i>Bryconamericus scleroparius</i>	Omnivore ^b
<i>Roebooides guatemalensis</i>	Insectivore/Fish Scales
Antherinidae	
<i>Melaneris chagresi</i>	Omnivore ^b
Cichlidae	
<i>Cichlasoma dovii</i>	Carnivore/Insectivore
<i>C. tuba</i>	Omnivore ^b
<i>C. alfari</i>	Omnivore
<i>C. septemfasciatum</i>	Omnivore ^b
<i>C. nigrofasciatum</i>	Omnivore ^b
<i>C. nicaraguense</i>	Omnivore ^b
<i>Neetroplus nematopus</i>	Omnivore ^b
Poeciliidae	
<i>Poecilia gillii</i>	Herbivore
<i>Brachyrhaphis parismina</i>	Omnivore
<i>Alfaro cultratus</i>	Insectivore
<i>Neoheterandria umbratilis</i>	Omnivore ^b
<i>Priapichthys annectens</i>	Insectivore

^a Fish indicated as omnivorous have a diet comprised of $\geq 25\%$ periphyton and vascular plant material, but also feed on insects.

^b Diets contain $> 50\%$ plant material.

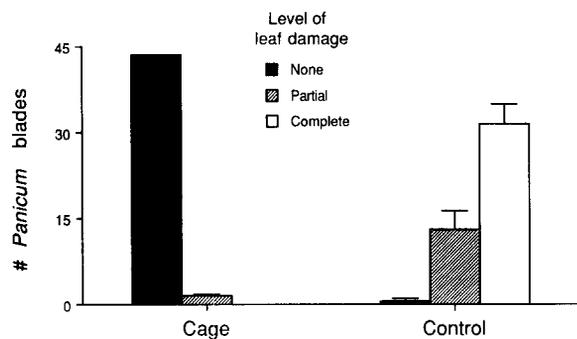


Fig. 1. Mean (\pm SE) number of *Panicum* blades in different leaf damage categories (no loss, partial loss, complete loss) in cage and control treatments. $n = 5$.

Cichlasoma tuba, *C. alfari* and *Brycon guatemalensis* feeding on leaves. Fish also exhibited distinct preferences for particular plant species. *Ficus* leaves were completely grazed to the midrib, most within 24 hours, and in one instance within 10 minutes. In contrast, more than 50% of *Monstera* leaf area remained intact after 48 hours. Fish consumed higher amounts of *Ficus* than *Monstera*, whether expressed as leaf area consumed or percent leaf area consumed (Mann-Whitney U-tests, $p < 0.02$, Fig. 2).

Periphyton effects

Fish bite marks were clearly visible in the algae turf on control tiles. Ash free dry weight increased significantly under cages compared to controls (Fig. 3, paired t -tests, all $p < 0.005$); by the end of the experiment, ash-free dry weight in cages was 50% higher than in controls. Ash free biomass increased through time, but over the final 10 days of the study, accumulated at a significantly higher rate on the side of the tile scraped at nine days (i.e. no initial biomass) than on the undisturbed side, with algae from 9 days of previous growth, in both cage and control treatments (Fig. 4, paired t -test, $p < 0.0001$). The difference in standing biomass between the 10 and 19 day samples was significantly higher in cage treatments than controls (paired t -test, $p < 0.03$). Biomass accumulated at a significantly lower rate in the 9-day samples than for the

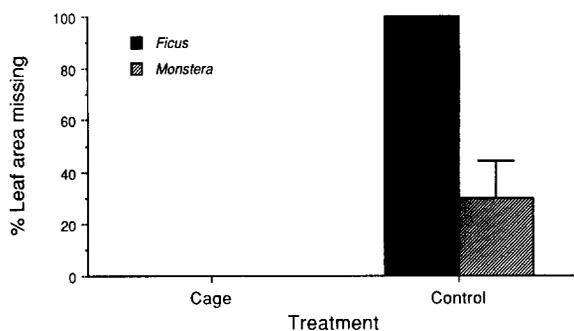


Fig. 2. Mean (\pm SE) percentage of leaf area lost after 48 hours in cage and control treatments for leaves of two terrestrial plant species. Dark bars-*Ficus insipida*, light bars-*Monstera* sp.

10-day samples in both cage and control treatments (paired t -test, $p < 0.005$).

Discussion

Fish grazing clearly has an important impact on the standing crop of all types of plant material in the Quebrada el Sabalo. The heavy grazing on the grass *Panicum* over a 6 day period demonstrates that fish may cause severe damage to or removal of riparian vegetation when it is inundated. Furthermore, fish herbivory may explain the overall lack of rooted aquatic macrophytes in this stream and others throughout much of the tropics.

Fish appear also to have an important impact on fallen leaves in the stream. Fish readily consumed leaves placed in the stream within two days. Because the same fish that consumed leaves in our experiments also had ready access to whatever natural background level of leaf biomass was present in the stream, our results indicate that fish probably reduce the total biomass of available fallen leaves in the stream. The levels of herbivory may have been over-estimated to some degree in the experiments because the leaves we used may have been more palatable to fish than naturally-shed leaves. However, it seems clear from the speed that fish found and consumed our leaves that fish routinely sample leaves to assess their palatability, and therefore are likely to eat leaves on a regular basis.

Differences in leaf area lost between the two

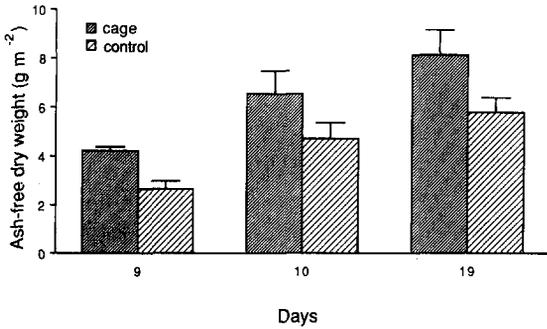


Fig. 3. Mean (\pm SE) ash free dry weights at different sampling times in cage (dark bars) and control (light bars) treatments. $n = 8$.

plant species we used indicate selective foraging by the fish. The basis for this selectivity is currently unknown, but might relate to leaf toughness, olfactory or taste cues, or the prevalence of chemical defenses aimed at deterring terrestrial herbivores. Similarly, shredding insects also exhibit selectivity for different leaf species, demonstrating increasing impacts with declines in levels of defensive chemistry in the leaf (Stout 1989). Because of the selectivity exhibited by fish, those leaves that remain in tropical streams (e.g. Angermeier & Karr 1983) may represent the subset of those that enter but are unsuitable for grazing by fish or invertebrates.

Fish may also limit total algal standing crop. Ash free biomass data suggest an effect of fish grazing. In just 19 days, 50% more biomass accumulated on tiles protected from grazing than on grazed areas. The decline in biomass accumulation rates over time indicates that the rates had started to stabilize by the end of the experiment. The comparison of 10 and 19 day samples also shows that biomass reached stabilization levels more quickly in grazed than caged plots, hence the differences between treatments would probably become even more pronounced in longer term experiments. Differences in the 9 and 10 day samples suggest an effect of a lag in algal colonization; higher rates of biomass accumulated on 10 day tiles that were previously colonized than on 9 day tiles that were newly added to the river. The ash free biomass data therefore lends support to the hypothesis that fish grazing explains, at least in part, the low algal abundance observed in

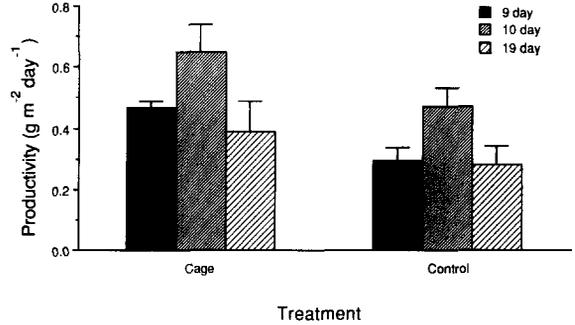


Fig. 4. Mean rate of ash-free dry weight accumulation (\pm 1 SE) for different treatments and sampling dates. Rates for 19 day samples derived only for the last 10 days of the experiment by calculating the difference between the 19 and 9 day biomasses for each tile. Note that 9 day tiles were initially uncolonized by algae, while 10 day tiles were.

this stream. However, some caution must be exercised in interpreting these results. Organic sediments may have contributed to differences in the ash-free dry weight component between our treatments, despite our protocol to remove sediments from our tiles, the presence of an upstream cage wall affecting currents in controls as well as cages, and our failure to visually observe differences in organic detritus between treatments. If organic matter contributed to the differences in ash-free dry weight, then fish may also have reduced organic detritus either by directly consuming it, or dislodging it while grazing on algae (see also Power 1990).

Our conclusions for periphyton are supported by observations from other experiments designed to test for nutrient limitation of productivity in other streams at La Selva; in these experiments, fish grazing tended to obscure any differences between nutrient treatments (C. Pringle personal communication). Experiments in a warm water Oklahoma stream (Power et al. 1985) and algal transplants in Panama (Power 1981, 1983) also demonstrate that grazing fish can have an effect on periphyton standing biomass.

The grazing activities of fish could also explain the overall scarcity of stream insects, particularly herbivores, in tropical relative to temperate streams (Stout & Vandermeer 1975). The lack of palatable plant material that results from fish graz-

ing represents a loss of both shelter and food for grazing invertebrates. Therefore fish, rather than insects, may be the most important leaf processors in this system, particularly if fish consume palatable leaves before invertebrates have an opportunity to eat them. The overall reduction in numbers and biomass of grazing invertebrates in turn may affect the abundance of invertebrate predators that feed upon them.

If differences in trophic structure of fish communities between tropical and temperate streams (Table 1) reflect differences in the importance of fish grazing to general stream community processes, then it would be useful to know why there are more herbivorous fish in the tropics. One hypothesis suggested by our results, that ecological conditions are more favorable to maintaining herbivorous populations in tropical streams because of relatively constant plant growth and continual leaf fall, is not supported by patterns of fish diets in strongly seasonal tropical forests. Comparing streams in wet tropical forests (Table 1) with streams in dry tropical forests (Table 3), indicates that the fish communities of dry forest streams have an equally large herbivorous component. Because streams in dry tropical forests, like temperate streams, experience strongly seasonal leaf fall, the failure to find differences in the trophic structure of fish communities rejects the hypothesis that a stable leaf supply promotes fish herbivory. Similarly, seasonality in leaf input has not prevented the evolution of leaf-

shredding insects in temperate streams (e.g. Stout & Vandermeer 1975, reviewed in Stout 1989). Physiological interactions, perhaps based on the interaction of temperature, food supply, and digestive efficiency, may provide a source for future study. Interestingly, herbivorous fish are also a larger component of the total fish community in tropical compared to temperate marine communities (Randall 1961, Ogden & Lobel 1978, Paine 1980, Menge & Lubchenco 1981, Gaines & Lubchenco 1982, Hay 1984, Carpenter 1986, Lewis 1986). Thus, the explanation may be common to both systems.

In conclusion, herbivorous fish can greatly reduce the total biomass of aquatic macrophytes and of terrestrially-derived leaves through grazing activity, and may affect the biomass of periphyton either as a direct or indirect consequence of their actions. By reducing in-stream energy sources and the physical structure provided by plants in the stream, effects of fish herbivory might cascade through other members of the aquatic community, possibly dramatically affecting abundance patterns of aquatic insects. The consistent differences in trophic structure observed for tropical and temperate stream fish communities suggest that these effects may be more widespread. We predict that other tropical streams will be more strongly influenced by grazing fishes and thus may exhibit lower resident plant and reduced aquatic insect biomass than are typically found in temperate streams.

Table 3. Proportion of fish species with $\geq 25\%$ plant material in the diet from 9 Costa Rican dry forest river communities. Data from Bussing (1987).

River	% Herbivorous	# Species
Rio Tempesque	46	13
Rio Diria	42	12
Rio Liberia	40	5
Rio Blanco (Guanacaste Province)	25	12
Rio Nosara	50	8
Rio Morole	60	10
Rio Guacimal	80	5
Rio Trojas	67	6
Junction-Rio Tarcoles & Rio Virilla	60	5

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