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Patterns of periphyton are determined by cascading trophic relationships in two neotropical streams

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Abstract. Indirect foodweb interactions often determine the dynamics of aquatic ecosystems. Predators may reduce the activity of herbivores, which, in turn, may cause basal resources to increase. We studied the patterns of distribution of periphyton (organic and inorganic mass and chlorophyll) on rocks in pools in two Atlantic rainforest coastal streams that varied with respect to the presence or absence of fish. A steep waterfall apparently prevented most fish species from colonising the upper parts of one stream; the other stream was apparently naturally without most species of fish. When fish were present, atyid shrimps and baetid mayflies were less abundant compared with parts of the streams without fish. Concomitant with this, the quantity of periphyton organic and inorganic masses was much greater in the presence of fish. Previous experiments showed that atyid shrimps (*Potimirim glabra*) and baetid mayflies could reduce the quantity of periphyton by grazing and bioturbation. We deduce that fish inhibit the grazing and bioturbing activities of *Potimirim* and baetid mayflies, which resulted in larger quantities of inorganic and organic mass of periphyton in parts of streams with fish. Cascading interactions may be common in Atlantic coastal forest streams.

Additional keywords: atyid shrimp, baetid ephemeropteran, bioturbation, epilithon, freshwater fish, grazing, *Macrobrachium*, predator avoidance.

Introduction

For many years, there has been a great deal of interest in the study of interactions within food webs and how they affect the properties of the ecosystem in which they occur (Pace *et al.* 1999; Thébault *et al.* 2007). There has been a growing interest in applying such knowledge to questions of ecosystem conservation and management (Power *et al.* 1996) and restoration (Lake *et al.* 2007). In streams and rivers, periphyton is often the most important source of energy for the food web, and recent research has shown this in small shaded tropical streams (March and Pringle 2003; Mantel *et al.* 2004; Brito *et al.* 2006; Davies *et al.* 2008). Thus, food-web interactions that determine periphyton growth are particularly important to stream ecosystem properties.

The distribution of periphyton in streams is determined by physical and chemical factors such as current velocity, light and nutrients – the so-called bottom-up controls. It is also determined by grazing and bioturbation – top-down control (Biggs 1996; Hillebrand 2002). The controlling factors may vary in different parts of a stream and may interact (Rosemond *et al.* 1993). Food-web interactions may modify the top-down control. Predators may negatively affect herbivores and release periphyton from the control of herbivores – the so-called trophic cascade (Power *et al.* 1985; Woodward *et al.* 2008).

In certain neotropical streams and rivers, top-down effects have been shown to be important. Fish were shown to have a large effect by processing periphyton and sediments in piedmont

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rivers of Venezuela (Flecker 1996) and rivers of Panama (Power 1990*a*). Shrimps, and particularly the atyid *Atya lanipes*, were important in removing periphyton and sediments in Puerto Rico (Pringle 1996; March *et al.* 2002; Cross *et al.* 2008) and shrimps and fish were important in Costa Rica (Pringle and Hamazaki 1998). In other neotropical streams, insects can be significant grazers and bioturbing agents of periphyton (Moulton *et al.* 2004; Barbee 2005). The non-consumptive removal of periphyton, or bioturbation, has been shown to be larger than the ingestion by grazing in certain cases (Krsulović 2004; Cross *et al.* 2008).

Potential trophic cascades may be suppressed by various factors. If the predator also acts on the basal resource, the potential action of intermediate herbivores can be masked. This was apparently the case in a Costa Rican stream where exclusion of fish and shrimp omnivores did not provoke a trophic cascade (Pringle and Hamazaki 1998). In contrast, in our study stream, exclusion of *Macrobrachium* shrimp revealed a trophic cascade where baetid ephemeropterans were the herbivores of the periphyton (Moulton *et al.* 2004). Mathematical modelling revealed that the existence of a trophic cascade is critically dependent on the strength of the interaction between the top omnivore and the intermediate herbivore (Silveira and Moulton 2000).

In our study streams, we observed obvious differences in the quantity of periphyton and sediments on hard substrates in different streams and in different parts of the same stream. We initially attributed this to different rates of sedimentation and different physical and chemical factors. But further observations indicated that the patterns might be related to the distribution of fish – the parts of the stream with fish had visibly more sediment and periphyton on boulders in pools. In upstream sites, exclusion experiments showed that the atyid shrimp *Potimirim glabra* removed periphyton and sediments from hard substrates (Visoni and Moulton 2003; Souza and Moulton 2005). At another upstream site, electrical exclusion experiments revealed a trophic cascade in which the shrimp *Macrobrachium olfersi* inhibited the baetid mayflies that were important grazers of periphyton (Moulton *et al.* 2004). We postulated that fish could be inhibiting grazing and bioturbation of periphyton at downstream sites.

For practical reasons, we could not carry out cage or electrical exclusion experiments to test this hypothesis directly because the scale was too large and the putative grazers (*Potimirim* and mayflies) were not immediately available. Instead, we used the natural exclusion of fish from upstream sites and their absence in another stream to provide the treatments of the experiment. We expected that periphyton abundance would change abruptly across the natural barrier of the waterfall. We also predicted that sites at similar altitudes in the streams with and without fish would have different abundance of periphyton. Moreover, we expected that the putative grazers (*Potimirim* and baetid mayflies) would change concomitantly with the periphyton.

Materials and methods

Study area

Córrego da Andorinha and Rio Barra Pequena are small streams in well-preserved dense Atlantic rainforest within the State Park of Ilha Grande Island (23°04′ to 23°14′S and 44°05′ to 44°23′W) in Rio de Janeiro State, Brazil (Fig. 1). The total catchment of Córrego da Andorinha is ~1410 ha in area and the highest point is 1030 m asl. Rio Barra Pequena has a catchment of 566 ha. For the majority of their courses, the streams have a steep bed slope (2–10%) and they discharge into small tidal estuaries without a meander or transition zone. The substrate is generally well embedded, with large boulders and some sandy stretches. The geology is principally Pre-Cambrian granite; the water chemistry is oligotrophic (total-N $= 180\ \mu g\ L^{-1}$, total-P $= 10\ \mu g\ L^{-1}$, pH = 6.6, conductivity $= 25\ \mu S\ cm^{-1}$). Discharge at base flow is $\sim 200\ L\ s^{-1}$ in Córrego da Andorinha and $130\ L\ s^{-1}$ in Rio Barra Pequena.

Córrego da Andorinha has fish in its lower parts (*Bryconamericus microcephalus*, *Phalloceros anisophallos*, *Rhamdioglanis transfasciatus*, *Awaous tajasica*, *Eleotris pisonis*). They are apparently excluded from the upper parts of the stream by a steep waterfall immediately below the site 'Mae D'agua' (site 3 of this study). One fish species, *Characidium japuhybense*, occurs above the waterfall, but in low density, and it is absent or very rare below the waterfall. Rio Barra Pequena has *Characidium* at low density and very rare at the sites we sampled, although it is more common at higher elevations. For convenience of nomenclature, we consider sites to be 'without fish' if they had no fish except the potential presence of *Characidium.* We did not observe *Characidium* at these 'fishless' sites during the present study apart from a very rare presence at site 2.

The shrimp *Macrobrachium olfersi* is common at all sites; other *Macrobrachium* species (*M. heterochirus*, *M. acanthurus*, *M. carcinus*) occur more infrequently at principally lower sites. All these species are catadromous; one not-catadromous species, *M. potiuna*, occurs in some swampy areas separate from the main streams and we observed it very rarely in the main streams. The atyid shrimp, *Potimirim glabra*, is common in upper parts of both streams; it is catadromous (Smalley 1963; Lima *et al.* 2006).

Study site selection and procedure

In Córrego da Andorinha, we selected three sites above the waterfall and five sites below the waterfall; sites 4 and 5 were immediately below the waterfall and site 5 was in the main channel of the stream, whereas site 4 was to the side, in a part that was apparently not accessible to fish. (We searched thoroughly for fish and found none at this site, and we concluded that fish did not enter because of the configuration of the stream at this point.) We selected four sites in Rio Barra Pequena. At each site, there was a well-defined pool (Table 1). The pools in both streams comprised almost the entire available habitat of this type in the stretches we visited.

Details of the periphyton and organic matter along the gradient of Córrego da Andorinha are found in Brito *et al.* (2006) and Moulton *et al.* (2009). Exclusion experiments have been performed at site 3 (Moulton *et al.* 2004; Souza *et al.* 2007) and a short distance above site 1 (Souza and Moulton 2005) and in both streams at sites 1, 3, 10 and 12 (Visoni and Moulton 2003). The study was conducted from 2000 to 2006, with five field visits. Different sites were sampled on different occasions and some sites were sampled more than once (Table 1).

At each site, we haphazardly selected submerged boulders that had sufficient near horizontal surface for our sampling –

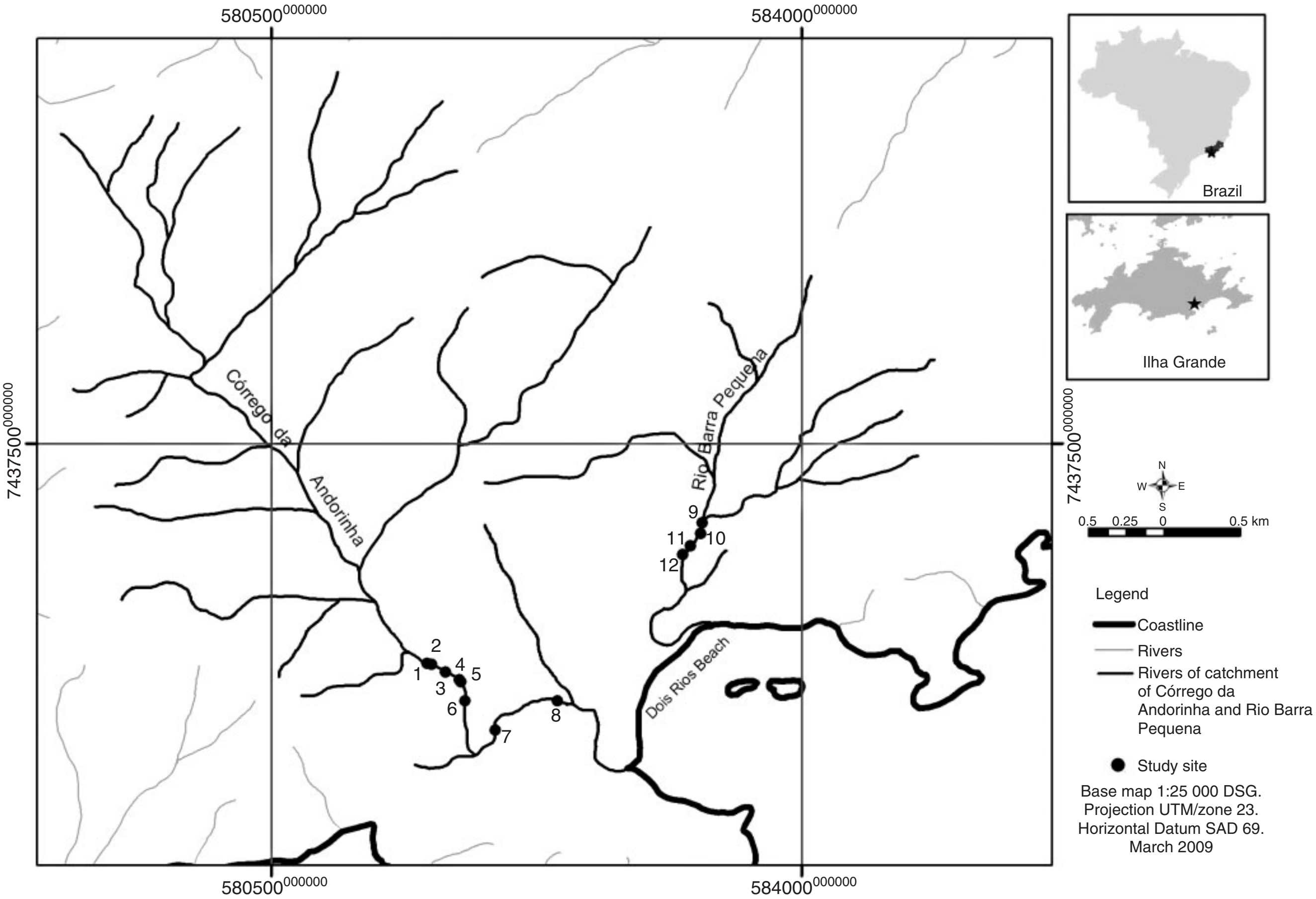

Fig. 1. Map of the study site at Ilha Grande, Rio de Janeiro. Site 4 overlaps site 5 at this scale. The barrier waterfall passes between sites 3 and 5.

they varied from 0.2 to 2.5 m^2. The boulders were in pools with low water current. We visually counted the number of shrimps and other obvious fauna on each boulder. This gave a semiquantitative estimate of *Potimirim*, which is diurnal and appeared not to take cover when observed. *Macrobrachium* is more nocturnal and particularly the larger animals seek refuges during the day, thus the count would likely to have been an underestimate. After the visual count, we sampled macroinvertebrates with a Surber apparatus (30 × 30 cm; 200 μm mesh) – one sample per boulder. We sampled periphyton using an apparatus consisting of a kitchen sink plunger with a brush attached to the handle inside the plunger cup and a 60-mL plastic syringe inserted into the side of the plunger (cf. Loeb 1981). We collected samples by pressing the plunger firmly to the substrate, scrubbing the substrate with the brush, and filling the syringe with the contents of the plunger cup. The volume of the syringe was larger than that of the plunger, so all of the material suspended by scrubbing was retrieved. The plunger sampled 40.6 cm^2 of the rock surface. We took four syringe samples per boulder and combined them.

At each sampling point, we measured the water current at the rock surface with a meter (Teledyne Gurley 'Pygmy', Troy, New York) and canopy cover using a concave-mirror spherical densiometer (Forest Densiometer, Bartlesville, OK, USA). We measured the depth and dimensions of the sampled boulder.

We observed the presence of fishes and shrimps by placing baited traps. *Macrobrachium* was readily caught in traps; *Potimirim* entered traps less readily and possibly was inhibited by *Macrobrachium*. The fish rarely entered traps, apart from *Phalloceros* and *Rhamdioglanis*. We also observed fish directly and caught them in hand nets for identification. We did not quantify the abundance of the fish. Shrimp abundance was obtained from their numbers on the sampled boulders (above). Fish were too rare and fugitive for this method.

Field and laboratory analyses

We measured fluorescence and turbidity of the sample at the time of sampling using a hand-held fluorometer (Aquafluor 8000, Turner Designs, Sunnyvale, CA, USA). We calibrated the *in vivo* fluorescence readings to *in vitro* extracted chlorophyll in a separate experiment (Moulton *et al*. 2009). We calibrated turbidity to dry mass of the sample with samples from other experiments, which were carried out at site 4 (Krsulović 2004; Moulton *et al*. 2009). We used total dry mass, which included inorganic material, rather than ash-free dry mass because inorganic particles as well as organic particles would be expected to contribute to turbidity.

In the laboratory (near the field sites), we filtered periphyton samples onto pre-ashed and weighed glass fibre filters (GF/D,

Table 1. Characteristics of the sample sites

Means and ranges are of the sampled boulders. Dates were: 1, October 2000; 2, January 2001; 3, June 2001; 4, July 2004; 5, April 2006. Data for boulders of sites 1, 10 and 11 are missing

Stream	Site no.	Site name	Distance from mouth (m)	Altitude (m asl)	No. boulders sampled (and dates)	Water current ($m\ s^{-1}$)		Canopy cover (%)		Depth (cm)	
						Mean	Range	Mean	Range	Mean	Range
Córrego da Andorinha	1	Silvia	1298	91	4 (3)						
	2	Characidium	1240	83	4 (2, 4)	0.19	0–0.37	45	20–70	30	12–43
	3	Mãe D'água	1117	70	10 (1, 3, 4, 5)	0.014	0–0.11	9.9	3–26	40	7–76
	4	Bagre (side)	1046	56	4 (2)	0.07	0–0.17	16	5–30	39	23–72
	5	Bagre	1046	56	4 (2)	0.105	0–0.29	24	0–50	48	33–75
	6	Lambari	913	43	2 (1)	0	0	3	1–5	34	33–34
	7	Capivara	497	36	5 (1, 3, 4)	0.14	0–0.29	12	7–20	30	12–41
	8	Lontra	98	13	8 (2, 5)	0.16	0–0.37	0.5	0–2	40	14–80
Rio Barra Pequena	9	Vini (above)	519	39	4 (2)	0.07	0–0.18	28	2–50	29	17–39
	10	Vini	481	37	2 (1)	0.03	0.03	24	8–39		
	11	Ponte (above)	291	34	4 (2)						
	12	Ponte	236	30	6 (1, 5)	0.23	0–0.7	66	14–86	26	20–31

Whatman, Maidstone, Kent, UK), dried the filters at 60°C for 24 h and weighed them, then combusted the filters at 550°C for 30 min and reweighed them to obtain ash-free dry mass (AFDM) and inorganic mass. We preserved the macroinvertebrate samples in 80% EtOH and sorted them under a stereo-microscope at the field laboratory. We identified macroinvertebrates to family level and baetid ephemeropterans to genus.

Statistical analysis

We tested the main hypothesis by comparing sites with different status with respect to fish. We grouped sites into three categories: (1) sites without fish of Córrego da Andorinha (sites 1, 2 and 3 above the waterfall and site 4 on the fishless side arm); (2) sites with fish of Córrego da Andorinha (sites 5, 6, 7 and 8); and (3) sites without fish of Rio Barra Pequena (sites 9, 10, 11 and 12). We tested differences in the means of variables among categories of sites using one-way ANOVA. Periphyton measurements (dry mass, AFDM, inorganic mass and chlorophyll) were transformed by log; macroinvertebrate abundances were transformed by $\log(x+1)$ to stabilise variances. We sought alternative explanations for periphyton distribution on boulders by testing periphyton chlorophyll and dry mass for relationships with depth, current and cover as covariables and sites as fixed factors, using ANCOVA. We used SYSTAT (ver. 10, Systat Software, San José, CA, USA) for the analyses.

Results

Periphyton mass and chlorophyll were distributed quite differently in the different parts of the streams; in the sites with fish below the waterfall in Córrego da Andorinha, periphyton mass (dry mass determined by turbidity, AFDM and inorganic mass) was greater than in fishless sites in Córrego da Andorinha and in Rio Barra Pequena (Table 2, Fig. 2). Chlorophyll, however, was highest at site 12 and not statistically different between Rio Barra Pequena and below-waterfall sites of Córrego da Andorinha (Table 2, Fig. 2*a*). Inorganic mass was higher than organic (AFDM) in Córrego da Andorinha, but the opposite was seen in Rio Barra Pequena (Fig. 2*b*). Periphyton chlorophyll and mass were highly different between sites (Table 3). Chlorophyll was positively correlated with water current within sites, as indicated by ANCOVA (Table 3). Periphyton mass was generally not correlated with current, shading or depth within sites, although AFDM was almost significantly correlated positively with current.

We observed fish at all sites below the waterfall in Córrego da Andorinha. *Bryconamericus microcephalus* was particularly obvious at sites 6 and 7 and was observed at site 8. There was no barrier to its occurrence at site 5, immediately below the waterfall, but it probably could not reach the side arm of the stream where site 4 was sampled. The catfish *Rhamdioglanis transfasciatus* was caught in traps at this site. *Awaous tajasica* was seen at sites 7 and 8, and *Eleotris pisonis* at site 6. *Phalloceros anisophallos* was common at site 7. None of these fish species was seen in Rio Barra Pequena, although this stream runs to the sea at the northern end of the same beach as Córrego da Andorinha (Fig. 1). We observed *Characidium* upstream of the sample sites in Rio Barra Pequena, but not at the sample sites during the study or at other times. It was seen at site 2 above the

Table 2. Means (±s.e.) of sites with and without fish for periphyton measurements, shrimps and macroinvertebrates

Each category had four sites except for chlorophyll and dry mass (three sites with fish). Differences between means were analysed by one-way ANOVA of log-transformed data (periphyton parameters) or $\log(x + 1)$ (shrimps and macroinvertebrates). For all F values, d.f. = 2,9 except for chlorophyll and dry mass (d.f. = 2,8). Values with the same uppercase letter are not significantly different (Tukey's test, $P > 0.05$). Site codes are as in Table 1. Discrepancy between dry mass and the sum of ash-free dry mass (AFDM) and inorganic mass is due to the different methods used for each

Parameter or abundance	C. da Andorinha		R. Barra Pequena	*F*	*P*
	Sites without fish (1, 2, 3, 4)	Sites with fish (5, 6, 7, 8)	Sites without fish (9, 10, 11, 12)		
Chlorophyll ($\mu g\,m^{-2}$)	0.57 ± 0.24	1.79 ± 0.23	1.88 ± 0.68	2.6	0.1361
Dry mass ($mg\,m^{-2}$)	$2.71^{B} \pm 0.77$	$16.60^{A} \pm 2.22$	$1.59^{B} \pm 0.50$	19.1	0.0009
AFDM ($mg\,m^{-2}$)	$1.31^{B} \pm 0.39$	$10.30^{A} \pm 3.05$	$0.62^{B} \pm 0.19$	23.6	0.0003
Inorganic mass ($mg\,m^{-2}$)	$2.46^{B} \pm 0.86$	$16.80^{A} \pm 5.51$	$0.25^{C} \pm 0.13$	50.4	<0.0001
Potimirim (per boulder)	$6.99^{A} \pm 5.73$	$0.56^{B} \pm 0.43$	$11.70^{A} \pm 2.18$	11.2	0.0040
Macrobrachium (per boulder)	$4.61^{AB} \pm 3.11$	$2.14^{B} \pm 1.11$	$13.00^{A} \pm 8.31$	8.8	0.0080
Baetid mayflies (per sample)	$24.50^{A} \pm 7.70$	$4.43^{B} \pm 2.57$	$9.53^{AB} \pm 2.57$	5.4	0.0292
Chironomids (per sample)	21.3 ± 16.9	105.4 ± 18.8	29.1 ± 24.3	3.7	0.0661

waterfall during the study and one individual was seen at site 3 outside the study. It could easily be present at site 1, but we did not see or trap it.

Potimirim shrimps were rare in the sites below the waterfall (Table 2, Fig. 2*c*). They were abundant in sites above the waterfall and particularly abundant in the sites of Rio Barra Pequena. *Macrobrachium* was found at all sites and was particularly abundant in Rio Barra Pequena (Table 2, Fig. 2*c*).

Chironomids were abundant at the below-waterfall sites (Table 2, Fig. 2*d*). They were generally less abundant at the above-waterfall and Rio Barra Pequena sites, although sites 2 and 11 did not conform to this trend. Baetid mayflies, however, were relatively rare in samples from sites 5, 7 and 8 and more abundant in above-waterfall and Rio Barra Pequena sites (Table 2, Fig. 2*d*). *Cloeodes* sp. was the most common baetid and dominated these trends; the anomalously high abundance at site 6 was due principally to *Americabaetis* sp. Other macroinvertebrate groups were not common enough to analyse at all sites.

Discussion

Periphyton organic and inorganic masses per unit area were higher in parts of the stream in which fish were present and *Potimirim* shrimps and baetid mayflies were in relatively low abundance. We take this as strong inferential evidence for a trophic cascade based on potentially predaceous fish, which inhibit two organisms that would otherwise graze and bioturb periphyton and sediments. *Potimirim* shrimp was shown to have a strong effect in removing periphyton at a site 120 m upstream of site 1 in experiments that excluded them from small areas of substrate (Souza and Moulton 2005). Baetid mayflies were also shown to have a strong negative effect on substrate at site 3 (Moulton *et al.* 2004) and, moreover, were subject to inhibition by *Macrobrachium* shrimps (Silveira and Moulton 2000). The evidence for the cascading effects of fishes is inferential because we have not performed manipulations that would experimentally prove the interaction. Such experimental manipulation might be difficult, however, in the case of investigating the hypothesised trophic cascade of fish on *Potimirim*; an exclusion of fish might not provoke an immediate response of an increase in *Potimirim* and their activity. In the case of baetid mayflies and *Macrobrachium* at site 3, the mayflies were present at the site but apparently fugitive of the shrimps (Moulton *et al.* 2004). In the below-waterfall sites, *Potimirim* does not appear to be hiding in refuges from the fish and hence would not be expected to appear immediately after the exclusion of fish.

Alternative explanation based on sedimentation

An alternative explanation for the observed distribution of periphyton and sediments is that different parts of the streams have intrinsically different rates of accumulation of periphyton and sediments. This seems unlikely because the change in periphyton organic, inorganic and total masses occurs abruptly at the position of the waterfall, which is the barrier to the fishes. Córrego da Andorinha does not appear to change in any characteristic that could be associated with periphyton accumulation in the reaches above and below the waterfall – no tributaries enter, the surrounding land use does not change and the immediate conditions of the sampled points was not different (Table 1). The downstream sites in Córrego da Andorinha were quite open, with little shading of the sampled points, but this was not different to the very unshaded upstream site 3, and the openness of the sites was not associated with greater periphytic algal growth, as seen in the pattern of chlorophyll (Fig. 2*a*). Indeed, the more shaded sites of Rio Barra Pequena had the highest levels of chlorophyll and the within-sites results showed no relationship of chlorophyll with shading (Table 3). The pattern of higher periphyton mass associated with presence of fish persisted throughout the 7 years and in the different months of the study.

Biology of the grazers

The observed results are congruent with the observed distribution of *Potimirim* and our interpretation of its biology. As well as removing large amounts of periphyton, *Potimirim* was found to act particularly on the inorganic component and the organic component not associated with algae (Souza and Moulton 2005). Thus, in the sites of Rio Barra Pequena where *Potimirim* was particularly abundant, the periphyton organic and inorganic masses

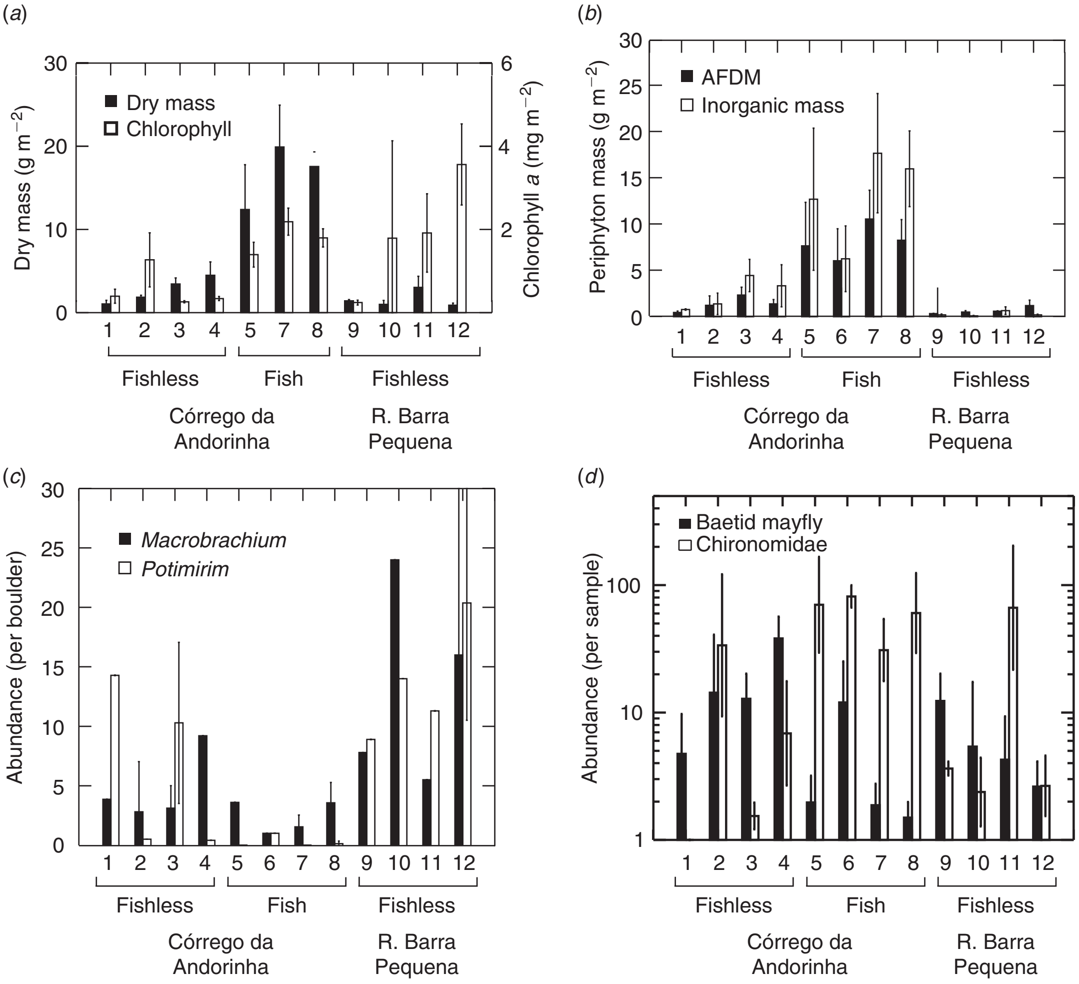

Fig. 2. Periphyton, shrimps and macroinvertebrates (±1 s.e.) in the sampled sites. (*a*) Periphyton dry mass and chlorophyll measured by turbidity and *in vivo* fluorescence, (*b*) periphyton ash-free dry mass and inorganic mass, (*c*) visual estimates of shrimps per sampled boulder, (*d*) abundance of mayflies and chironomids per sample area of 30 × 30 cm. Sites are coded 1 to 12 as in Table 1 and categorised with respect to the presence of fish.

were low but chlorophyll was relatively high (Table 2, Fig. 2*c*). Baetid mayflies were also found to act more strongly on the periphyton mass than on periphyton chlorophyll (Moulton *et al.* 2004). Modification of the algal community and interactions with sediments have been observed for the activities of other shrimps (*Atya lanipes* in Puerto Rico (Pringle 1996; Pringle *et al.* 1999) and fishes (Power 1990*b*; Flecker 1996)). Woodward *et al.* (2008) provide an interesting case in which the cascading interactions of a fish in a complex stream food web did not affect the standing stock of periphyton, even though the abundant snail herbivore was reduced.

Other macroinvertebrates of the benthos appeared to respond positively to the increase in periphyton mass. Chironomids in particular were abundant in the downstream sites of Córrego da Andorinha (Fig. 2*d*). An apparently similar phenomenon occurred in an experiment at site 3 where chironomids responded positively to the exclusion of mayflies and the subsequent increase in periphyton mass (Souza *et al.* 2007). Other small macroinvertebrates, such as cryptostigamatid mites, appeared more common in the thicker periphyton of the downstream sites compared with the upper sites of Córrego da Andorinha and sites of Rio Barra Pequena (T. P. Moulton, unpubl. data).

Behaviourally mediated trophic cascade

We describe the predation of fish on *Potimirim* and mayflies as 'potential' because we have not observed it in the field. Indeed, dietary studies of *Bryconamericus* (Rezende and Mazzoni 2006) and *Phalloceros* (R. R. S. Araújo, pers. com.) at Córrego da Andorinha did not show *Potimirim* in the gut contents and mayflies were rarely found. When *Bryconamericus* and *Potimirim* are placed together in an aquarium, the fish eat the shrimp voraciously and the shrimp huddle in refuges. Because *Potimirim* is catadromous, the juveniles must pass the lower parts of Córrego da Andorinha to reach the upper parts where we observe them in high densities (Fig. 2*c*). In Rio Barra Pequena, *Potimirim* occurs in high density in the sites that we sampled close to the estuary (Fig. 2*c*). We presume that *Potimirim*

Table 3. ANCOVA of periphyton chlorophyll and mass with sites, water current, sample depth and shading

Dry mass was estimated by turbidity. Sites were 2, 3, 4, 5, 7, 8, 9 and 12. Chlorophyll and masses were log-transformed

Source	Sum of squares	d.f.	Mean square	*F*	*P*
Chlorophyll					
Site	4.818	7	0.688	25.61	<0.001
Current	0.222	1	0.222	8.258	0.008
Shading	0.016	1	0.016	0.608	0.44
Depth	0.006	1	0.006	0.217	0.65
Error	0.645	24	0.027		
Dry mass					
Site	15.354	7	2.193	25.69	<0.001
Current	0.212	1	0.212	2.48	0.13
Shading	0.014	1	0.014	0.169	0.68
Depth	0.000	1	0.000	0.003	0.96
Error	2.049	24	0.085		
AFDM					
Site	12.764	7	1.823	30	<0.001
Current	0.246	1	0.246	4.042	0.06
Shading	0.181	1	0.181	2.975	0.10
Depth	0.004	1	0.004	0.073	0.79
Error	1.459	24	0.061		
Inorganic mass					
Site	18.546	7	2.649	20.96	<0.001
Current	0.304	1	0.304	2.407	0.14
Shading	0.032	1	0.032	0.256	0.62
Depth	0.018	1	0.018	0.145	0.71
Error	2.781	22	0.126		

migrates rapidly through the lower reaches of Córrego da Andorinha where it senses the danger of predation by fish. Similar deductions have been made for the atyid shrimp *Atya lanipes* in Puerto Rico (Pringle 1996; Pringle *et al.* 1999; March *et al.* 2002) in its migration from the estuary, through parts of the river with abundant predatory fish, to upper reaches inaccessible to fish. Likewise, we deduce the inhibition of baetid mayflies by fish from their observed behaviour at site 3 with *Macrobrachium*; predator evasion is well-documented for mayflies and fish (McIntosh and Townsend 1996; Peckarsky 1996) and the phenomenon of predator-mediated non-consumptive effects is well-documented (Peckarsky *et al.* 2008; Preisser and Bolnick 2008). *Bryconamericus* and *Phalloceros* readily consume mayflies in captivity (T. P. Moulton, unpubl. obs.).

We propose a behaviourally mediated trophic cascade of fish inhibiting grazing and bioturbing *Potimirim* and baetid mayflies that remove periphyton. The situation is apparently different to that of the Costa Rican streams studied by Pringle and Hamazaki (1998) in which omnivorous fishes and shrimps acted in concert to remove periphyton, and the authors postulated that a trophic cascade did not operate in their system because of the omnivory of the principal organisms (fishes and shrimps). Apparently in our system, the fishes are predaceous and do not significantly bioturb the substrate. The fish fauna is depauperate compared with similar streams on the nearby mainland and there is conspicuous absence of the catfish families Loricaridae and Callichthyidae, which are usually present and speciose in Brazilian streams and which can act as grazers and detritivores that modify the substrate (see also Power 1990*b*).

It is interesting that this is the second postulated trophic cascade in Córrego da Andorinha; the other involves *Macrobrachium*, which acts negatively on baetid mayflies that are strong grazer-bioturbers at site 3 (Silveira and Moulton 2000; Moulton *et al.* 2004). Again, this interaction appears different to the situation with similar organisms in other neotropical streams (e.g. March *et al.* 2002), and a possible explanation for this is that *Macrobrachium* acts strongly as a predator (Silveira and Moulton 2000; Silveira 2002). Certainly all of the fishes and shrimps of Córrego da Andorinha were placed as secondary consumers by stable isotope analysis (Brito *et al.* 2006).

Consequences for stream assessment

Our results imply that we should be careful when making rapid assessments of stream condition. The sites of this study occur in streams with close to pristine conditions of water quality. The large differences in periphyton chlorophyll and mass were apparently caused by biotic interactions and not by external environmental impacts or other bottom-up effects. A superficial or rapid stream assessment would be unlikely to perceive this. Although it is obviously impractical to perform exclusion experiments and detailed sampling at every point of a stream survey, shrimp and baetid mayflies are conspicuous components of the fauna. We suggest that stream assessment in our region should take into account such potential biotic interactions and, indeed, that catadromous species and their effects on the environment can be useful indicators of stream connectivity (Moulton 2001; Moulton *et al.* 2007).

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