

The effects of shrimps on benthic material in a Brazilian island stream

MARCELO L. DE SOUZA AND TIMOTHY P. MOULTON

Departamento de Ecologia, IBRAG, Universidade do Estado do Rio de Janeiro, RJ, Brazil

SUMMARY

1. Shrimps are abundant in many tropical coastal streams. Studies in Central America and the Caribbean have demonstrated the importance of shrimps in removing sediments and altering the composition of the benthos. Previous work in our study area showed that ephemeropterans and not shrimps were important in removing benthic material.
2. Here we used an experimental exclusion to test the hypothesis that shrimps exert strong influence on sediment dynamics with direct and indirect effects on the benthic algal and faunal community at a site where they are the predominant element of macrofauna. We used electricity to exclude *Macrobrachium olfersi* and *Potimirim glabra* from small quadrats (0.135 m²) for 34 days in a stream located at Ilha Grande, Rio de Janeiro state, Brazil. We analysed benthic sediment dynamics and community colonisation during this period on artificial substrates in electrified and not-electrified quadrats.
3. Significantly higher sediment accrual had occurred in the electrified treatment after 14 days and persisted for the 34-day course of the experiment; substrates protected from shrimps contained about four times as much ash-free dry mass (AFDM) as those of the controls. After 34 days, significantly more pennate diatoms were present in the exclusion treatment, but chlorophyll was not significantly different between treatments. Densities of baetid ephemeropteran nymphs were significantly higher in the presence of shrimps.
4. We attribute all these effects to the atyid *P. glabra*, the more abundant and active shrimp observed in the control treatment. Our results suggest that atyid shrimps played an important role related to sediment removal on hard substrate by direct ingestion and 'bioturbation'. They reduced certain components of the periphyton (pennate diatoms) without affecting primary production (chlorophyll *a*). The activity of these shrimps on periphyton affected also faunal components such as baetid ephemeropterans and seems to determine the composition of the benthic community.

Keywords: electrical exclusion, periphyton, *Potimirim glabra*, sediments, shrimps, strong interactor, tropical stream

Introduction

Recently the effect of macrofauna on sediment distribution has been associated with the dynamics and structure of benthic communities as well as the functioning of lotic ecosystems. Perturbation experi-

ments involving exclusion of macroconsumers have shown how individual species can be considered 'strong interactors' (*sensu* Pringle *et al.*, 1993) because they strongly influence the accumulation of organic and inorganic sediments on hard substrates. The actions of such organisms are more than the mere intake of food, and as such have been dubbed 'bioturbation' (Brenchley, 1981; Pringle & Blake, 1994) or 'ecosystem engineering' (Flecker, 1996). The influence of fishes on sediments, algae and invertebrate assemblages in Neotropical streams has been well

Correspondence: Timothy P. Moulton, Departamento de Ecologia, IBRAG, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier, 524, RJ, 20550-013, Brazil.
E-mail: marcelodesouza@aol.com; moulton@uerj.br

documented by studies carried out in Panama (Power, 1990), Venezuela (Flecker, 1996) and Costa Rica (Pringle & Hamazaki, 1997, 1998). Various authors have also reported the role of shrimps on ecological processes as well as its direct and indirect effects on the benthic community (Covich, Palmer & Crowl, 1999; Crowl *et al.*, 2000, 2001; Palmer *et al.*, 2000). Experiments in Puerto Rico and Costa Rica showed that shrimps particularly can exert strong effects on sediments (Pringle & Blake, 1994), benthic fine particulate organic matter (Pringle *et al.*, 1999) and the whole benthic community (Pringle *et al.*, 1993; Pringle, 1996; Pringle & Hamazaki, 1998). Interstream as well as instream differences in the benthos because of different shrimp assemblages reinforce the importance of these macroconsumers as interactors in Puerto Rican streams (Pringle *et al.*, 1999; March, Pringle & Townsend, 2002).

Shrimps have been recognised to be dominant macroconsumers in certain tropical coastal streams (Covich, 1988; Resh & De Szalay, 1995). In Brazil, Atyidae and Palaemonidae are the most common families of shrimps cohabiting in streams along the southeast coast (Moulton & Parslow, 1994; Moulton, 1988). The palaemonid *Macrobrachium olfersi* Wiegmann appears to have a strong effect on the benthic invertebrate assemblage and influences the periphyton directly or indirectly (Moulton *et al.*, 2004). Atyids such as *Potimirim glabra* Kingsley have an increased activity in the fishless reaches and seem to reduce sediment accrual on hard substrates (Visoni & Moulton, 2003). These genera belong to the same families of amphidromous shrimps that interact strongly with the substrate in the Caribbean and in Central America. However, the individual roles of these shrimps and how they interact with biotic and abiotic components of the benthos are still not clear and appear to depend on the rest of the assemblage. Even though the studies quoted above have defined important ecological roles for different species of Caribbean atyids and palaemonids, the same roles should not be extrapolated to the same families in Brazil without considering their specific differences in distribution and structure in Atlantic Forest streams. In apparent contrast to the studies in the Caribbean and Central America, previous studies at our study site in Brazil showed opposite results when shrimps were experimentally excluded – inorganic sediments and ash free dry mass (AFDM), and chlorophyll *a*

decreased (Silveira & Moulton, 2000; Silveira, 2002, Moulton *et al.*, 2004). It appears that ephemeropterans, not shrimps, are the important grazers in this system; this was confirmed by experimental exclusion of ephemeropterans (Silveira & Moulton, 2000; Silveira, 2002, Moulton *et al.*, 2004). Barbee (2005) also found that grazing insects reduced algal biomass in a stream in different part of Costa Rica to that where shrimps and fish had been found to be the principal grazers by Pringle & Hamazaki (1997, 1998).

As increasing demographic pressure threatens hydrological connectivity in coastal areas in southeast Brazil, both amphidromous *M. olfersi* and *P. glabra* can no longer be found in many impacted streams. Many species including the atyid *P. glabra* have been considered an endangered species in the state of Rio de Janeiro (Moulton *et al.*, 2000). Despite the presumed importance of these macroconsumers, their participation in ecosystem processes and the benthic community structure in Brazilian coastal streams remains poorly understood. Therefore, it is increasingly important to understand the role of these shrimps for both management and conservation purposes.

We studied a freshwater stream benthic community of the coastal island Ilha Grande, in the state of Rio de Janeiro, in which both *M. olfersi* and *P. glabra* are predominant elements of the macrofauna (Visoni & Moulton, 2003). We excluded shrimps and studied the responses of the benthic community on the substrate without their activity. Here, the technique of electrical exclusion introduced by Pringle & Blake (1994) was adapted as an alternative to the traditional cages to avoid interferences with light, water flow and sedimentation rates on the experimental substrates (Miller, 1986; Cooper & Dudley, 1988; Peckarsky & Penton, 1990; Dudgeon, 1993). We set up electrified quadrats to induce a press perturbation (*sensu* Bender, Case & Gilpin, 1984) by continuously excluding *P. glabra* and *M. olfersi* from experimental substrates. Our experiment was designed primarily to test the hypothesis that there would be differences in periphyton on the experimental substrates in response to the presence or absence of shrimps. We noted which species of shrimps were more active in the controls and how they affected the main components of the periphyton in comparison with the exclusion treatment. We also examined the response of smaller macroinvertebrates, especially baetid ephemeropterans, to the absence of these shrimps.

Methods

Study area

We conducted the experiment from 17 April to 21 May 2001, in a stream at the island Ilha Grande (23°5′–23°14′S, 44°5′–44°23′W). Ilha Grande is a coastal island of area 193 km² located 12 nautical miles from Angra dos Reis, on the south coast of Rio de Janeiro state, south east Brazil (Fig. 1). The Rio Andorinha flows for about 7 km from the slopes of Papagaio Peak (959 m a.s.l.) to its estuary at Dois Rios village. The whole catchment is surrounded by preserved Atlantic rain-forest of the Tamoios State Park. The mean annual air temperature is 22 °C, the mean annual rainfall is 2390 mm and the rainy season occurs from December to May [Fundação Instituto de Desenvolvimento Econômico e Social do Rio de Janeiro (FIDERJ), 1978]. The Andorinha is considered an oligotrophic stream with low conductivity waters (35–40 µS cm⁻¹) and pre-Cambrian granite gneiss geology. The substrate of the study site was composed mostly of large boulders and well-embedded cobbles.

Our study site was 80 m a.s.l., 1.3 km from the estuary and upstream from a waterfall locally known as Mãe D'água. The Mãe D'água is a barrier for downstream species, particularly for the pelagic pre-

daceous fishes *Bryconamericus microcephalus* Bizerril and Araújo and *Phalloceros caudimaculatus* Hensel. *Characidium japuhybensis* Travassos is the only fish found above the waterfall and it occurred in low densities at the study site. However, the waterfall does not seem to be an obstacle to upstream movement of the amphidromous shrimps *P. glabra* and *M. olfersi*; both shrimps are more abundant above Mãe D'água than downstream. We set up our experiment 300 m upstream from the waterfall where the periphyton and sediment accrual appeared to be reduced compared with downstream reaches, and shrimps, especially *P. glabra*, showed increased activity possibly due the absence of predaceous fishes. Baetid ephemeropterans were the most common benthic insects observed on the hard substrates. Freshwater snails are absent in the Rio Andorinha.

Electrified quadrats and experimental design

We set up eight fixed quadrats divided into two treatments: absence and presence of shrimps. Each quadrat was a frame (30 × 60 cm) made of PVC tube (Ø 1.27 cm) containing six unglazed tiles (15 × 15 cm). Copper wire electrodes were attached to the sides and central axis of the frame (Fig. 2). We set out the eight quadrats in four pairs arranged in a randomised blocks design (Fig. 2). Within blocks, we randomly connected the electrodes of one quadrat to the electrifier to exclude shrimps; the other quadrat of the pair was the control. The approximate distance between electrified and control quadrats within blocks

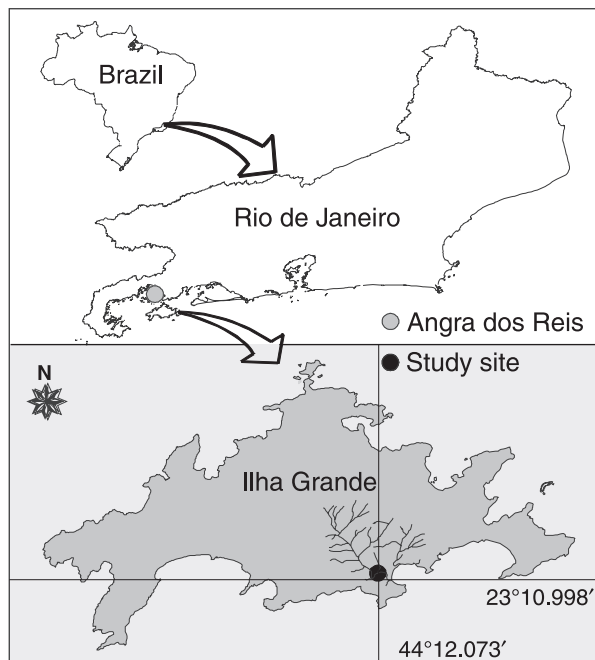


Fig. 1 Location of the study site at the coastal island Ilha Grande, Rio de Janeiro state.

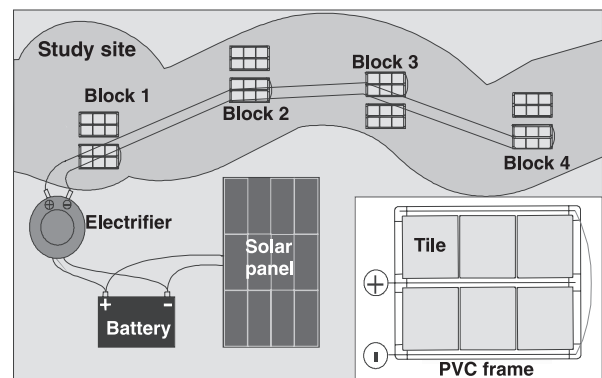


Fig. 2 Schematic representation of the experimental setup and experimental quadrat (bottom right panel) used as control and exclusion treatments.

was 30 cm and the blocks were separated by about 15 m.

We used a commercially-available fence electrifier (Ballerup®, Alfa S.A., São Paulo, SP, Brazil) to produce regular high-voltage electric pulses responsible for the exclusion of shrimps in the electrified quadrats. The four serially connected electrified quadrats worked simultaneously. A battery (12 V, 60 A.h), diurnally recharged by a solar panel (model M65; Siemens, Camarillo, CA, U.S.A.), fed the electrifier during the whole experiment.

We obtained the appropriate strength of electrification by trial-and-error, observing the reaction of the fauna to the pulses and changing the system settings in order to get an effective exclusion of shrimps without affecting other organisms such as ephemeropterans. We manually introduced baetid ephemeropterans and shrimps into the electrified area to test whether the organisms gave a visible twitch at each pulse of electricity. Both shrimps and ephemeropterans were also briefly introduced into the electrified areas during the course of the experiment to confirm that the desired exclusion was maintained. The exclusion effect was proportional to the body size of the animals; only shrimps and, presumably, larger animals such as *C. japyhybensis* were affected by the electricity in the electrified quadrats. Smaller macroinvertebrates such as ephemeropterans showed no reaction when exposed to the electric pulses during the experiment. In contrast, even the smaller shrimps (c. 2.5 cm) when purposely placed on the electrified substrates reacted to the electric pulses and left the electrified quadrats immediately. The electric exclusion seemed to extend no further than 10 cm beyond the limit of the electrified quadrats.

Sampling

The electric fences excluded shrimps continuously for 34 days and the substrates were sampled on days 14, 21 and 34 of the experiment. We sampled one tile from each quadrat on these occasions using a device to retain all benthic material on the tile during its detachment: our sampler was a bottomless plastic box made to retain all sediments, algae, sessile macroinvertebrates and a known volume of water (150 mL). We pressed the bottomless base of the box to the tile, making an effective seal with plastic foam. We then placed the lid on the box and transferred the

tile with its contents to a small tray. We used a syringe, soft paintbrush and then a stiffer brush to gently wash and remove the adhered benthic material from the tile surface using the water contained in the sampler. The samples were transferred from the tray to sealed plastic bags (Whirl Pack; Nasco, Fort Atkinson, WI, U.S.A.) and taken immediately to the laboratory for processing. There we filtered sub-samples (90 mL) using preashed and preweighed glass-fibre filters (GF/F, Ø 47 mm, Whatman). Sessile invertebrates were picked off the filters immediately after filtering using a stereomicroscope (30×) and were preserved in ethanol 80% for later identification. We dried the filters without invertebrates for 24 h at 60 °C, re-weighed them and burnt their organic content in a muffle furnace for 1 h at 500 °C to estimate the AFDM.

Photopigments were extracted from sub-samples (20 mL) filtered onto glass-fibre filters (GF/F, Ø 25 mm, Whatman) in 90% buffered acetone overnight in a freezer. We measured chlorophyll *a* of the extracts in a spectrophotometer at 664 nm using acidification for phaeopigment correction (Nusch, 1980). We calculated the ratio AFDM/chlorophyll *a* or Autotrophic Index to obtain comparable rates of autotrophy of the periphyton (APHA, 1992, Hauer & Lamberti, 1996). We preserved a sub-sample of 6 mL from the last sampling day with 2% formalin for the quantification of algal community composition. Adnate and stalked diatoms were counted and identified to genus and quantified using a Fuchs-Rosenthal slide and a compound microscope at 400× magnification. We scanned the whole content of each sample and estimated the diatom density of the original substrate in cells mm⁻².

The presence of shrimps and visible macroinvertebrates, such as baetid ephemeropterans, in both treatments was quantified by diurnal and nocturnal direct observation, counting the individuals that were present at the instant of observation at eight different dates during the experiment. A spotlight was used at night to count the number of animals before they retreated from the light. We were able to recognise both species of shrimp, but we could not differentiate the ephemeropteran species. It was not possible to carry out these estimates during rain and floods.

Depth and current velocity were measured at each quadrat position at base flow conditions to check the inherent similarity of quadrats with respect to these

parameters and to potentially use them as covariates. We continuously monitored water level at a position 300 m downstream from the experimental areas using a depth logger (Global Water[®], Forestry Suppliers, Jackson, MS, U.S.A.). The logged data were combined with discharge estimates to obtain a stage–discharge relationship using regression methods (Gordon, McMahon & Finlayson, 1992). We also monitored rainfall using a tipping bucket rain gauge (Davis Instruments coupled to Hobo[®] event logger, Onset Instruments, Pocasset, MA, U.S.A.). Water and air temperatures were recorded hourly using a temperature logger (Stowaway[®], Onset Instruments) throughout the experiment. Canopy coverage was assessed for each block with a concave densiometer (Forest Densimeters, Bartlesville, OK, U.S.A.). Conductivity was measured using a conductivity meter model HI 9033 (Hanna Instruments, Leighton Buzzard, U.K.).

Statistical analysis

The parameters analysed were total dry benthic mass, organic mass (AFDM), inorganic mass, chlorophyll *a*, algal density and visually estimated shrimp and ephemeropteran density. We analysed the results of each sampling day separately and performed two-way ANOVA, blocks \times treatment (Sokal & Rohlf, 1981), to test the null hypothesis that the absence/presence of shrimps had no significant effect with respect to the parameters related to sediments and algae. The two-way ANOVAs considered treatment as a two level factor (shrimp exclusion and controls) and blocks as a four level factor (four pairs of electrified quadrats and controls). The interaction term between treatments and blocks was the estimated error. We also performed two-way ANOVA to assess the variation of sediments among

the sampling days within shrimp-present and shrimp-absent treatments. This analysis considered days (three levels) and blocks (four levels) as factors and their interaction term as the error. We analysed the visually assessed benthic fauna using a Repeated Measures ANOVA, blocks \times treatment (Sokal & Rohlf, 1981) of the count from electrified versus non-electrified quadrat. Sampling days in which the exclusion was total in the electrified treatment were removed from the analysis because of their lack of variance. All data were log-transformed to homogenise variance; zero values of abundance data were trapped by adding unity to all data. We used the GLM module of SYSTAT 10.2 (SPSS, Richmond, CA, U.S.A.) for the statistical analysis.

Results

Abiotic factors

The mean current velocity in the exclusion treatments was 0.155 and 0.145 m s⁻¹ in the controls with no significant difference between treatments. Discharge estimated by the stage–discharge relationship showed a spate occurred on day 26 with a peak of 8.52 m³ s⁻¹ (Fig. 3). The experiment was interrupted on day 38 by a second and stronger spate. The base flow discharge during the experiment was 0.23 m³ s⁻¹. Conductivity was 36.9 μ S cm⁻¹. The average water and air temperature during the experiment were respectively 20.6 and 22.9 °C. Canopy coverage among blocks varied between 78 and 82%.

Exclusion

Visual observation confirmed the efficacy of the exclusion; no shrimps were seen inside the exclusion

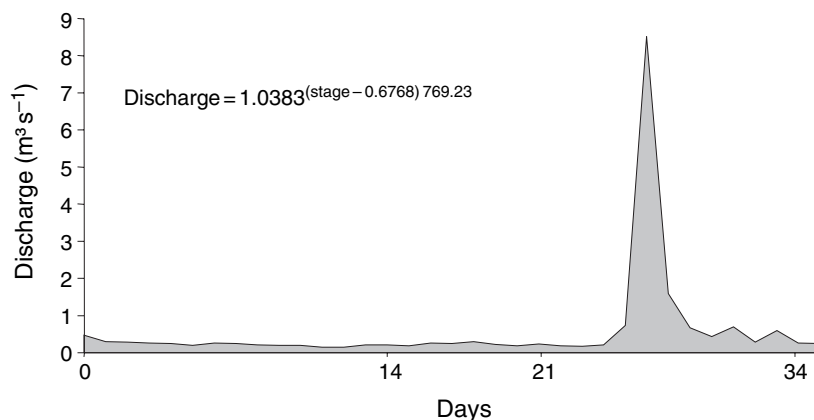


Fig. 3 Estimated discharge at the study site during the 34-day course of the experiment. The equation shows the stage–discharge relation at a site close to the experimental area.

treatment during the experiment (Table 1). The visually assessed density of *P. glabra* in the control was more than 10-fold higher than *M. olfersi*. The highest density was 133.3 individuals m^{-2} of *P. glabra* and 29.6 individuals m^{-2} of *M. olfersi*. We observed no individuals of *C. japyhybensis*, the only local species of fish, in the experimental quadrats.

Sediments

Periphyton and sediment accrual were visually higher in the absence of shrimps after 1 week of exclusion. We detected statistically significant differences in sediments after 2 weeks of continuous exclusion (Table 2); benthic mass was four times higher in the absence of shrimps than in their presence (Fig. 4). The substrates exposed to the activity of shrimps contained a higher ratio of inorganic matter to AFDM (1.49) compared with the exclusion treatment (0.86).

We found an increase of 60% in inorganic sediments in the exclusion treatment and 125% in the controls between days 14 and 21 (Fig. 4). The AFDM remained stable in the controls and increased by 17% in the exclusion. On day 21, there was three times more total benthic mass in the electrified quadrats

than in the presence of shrimps (Table 2). The ratio of inorganic sediment mass to AFDM was 2.42 in the exclusion and 1.66 in the controls.

The last sampling on day 34 was preceded by a spate and the discharge at sampling was still slightly higher than the base flow (Fig. 3). Inorganic sediments increased 2% in the exclusion and 45% in the controls from day 21. We observed an increase of AFDM on day 34 compared with day 21: 167% in the absence of shrimps and 60% AFDM in their presence. The ratio inorganic mass to AFDM decreased to 1.14 in the exclusion and 1.51 in the controls. After 34 days, total benthic mass was four times larger in the absence of shrimps compared with the control treatment (Table 2; Fig. 4). Significant variation among blocks (Table 2) indicated that high flow conditions possibly had different effects on these parameters at different positions in the experimental area. We attribute this block effect to the intrinsic physical differences among positions. These differences were probably related to the sediment dynamics or to the shrimp activity on the substrate during the event.

We found statistically significant differences in AFDM among the three sampling days in the exclusion treatment (Table 3). We attributed these differences to sediment accrual, in particular AFDM, after

Table 1 Densities of macroinvertebrates visually estimated during the experiment ($n = 16$; mean \pm SE, individuals m^{-2})

	<i>M. olfersi</i>		<i>P. glabra</i>		Ephemeroptera	
	Exclusion	Control	Exclusion	Control	Exclusion	Control
Block 1	0.0 \pm 0.0	2.8 \pm 2.8	0.0 \pm 0.0	0.7 \pm 0.7	27.1 \pm 6.2	86.0 \pm 18.9
Block 2	0.0 \pm 0.0	0.7 \pm 0.7	0.0 \pm 0.0	48.6 \pm 11.4	0.7 \pm 0.7	4.2 \pm 2.7
Block 3	0.0 \pm 0.0	0.7 \pm 0.7	0.0 \pm 0.0	8.3 \pm 3.8	1.4 \pm 0.9	7.6 \pm 2.3
Block 4	0.0 \pm 0.0	2.4 \pm 1.7	0.0 \pm 0.0	9.5 \pm 3.1	3.2 \pm 3.2	23.8 \pm 23.8

Table 2 Statistical comparison between treatments (absence/presence of shrimps) of benthic material and chlorophyll *a* after 14, 21 and 34 days of continuous exclusion (two-way ANOVA)

Day	d.f.	14		21		34	
		$F_{1,3}$	<i>P</i>	$F_{1,3}$	<i>P</i>	$F_{1,3}$	<i>P</i>
(a) Total mass							
Treatments	1	78.59	<0.01	10.75	0.04	34.51	0.01
Blocks	3	4.46	0.12	0.19	0.89	10.41	0.04
(b) Inorganic sediments							
Treatments	1	51.81	<0.01	9.21	0.05	38.09	<0.01
Blocks	3	2.35	0.25	0.12	0.94	3.18	0.01
(c) AFDM							
Treatments	1	51.29	<0.01	18.81	0.02	36.09	<0.01
Blocks	3	5.40	0.10	1.12	0.44	5.68	0.09
(d) Chlorophyll <i>a</i>							
Treatments	1	0.92	0.41	0.72	0.46	1.16	0.36
Blocks	3	2.76	0.21	1.84	0.31	0.67	0.62

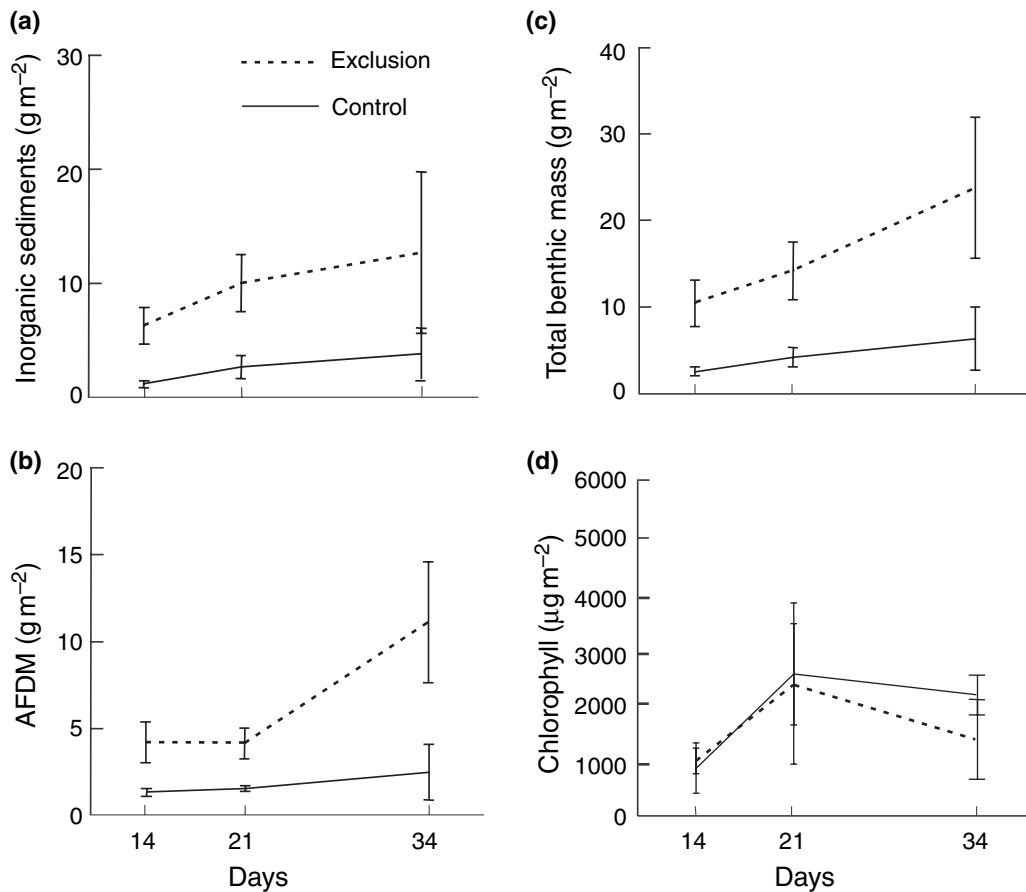


Fig. 4 Amounts of benthic material composed of (a) inorganic; (b) organic; (c) total sediments and (d) chlorophyll *a* ($n = 4$; mean \pm SE) in the presence and exclusion of shrimps on the three sampling days. On day 0 the substrates contained no material.

the spate that occurred between days 21 and 34 (Fig. 4). In contrast, shrimps apparently diminished the AFDM in the controls soon after the spate

resulting in no statistically significant difference among sampling days (Table 3; Fig. 4).

Table 3 Statistical comparisons of benthic material and chlorophyll *a* among the three sampling days within individual treatments (two-way ANOVA)

	d.f.	Shrimp exclusion		Controls	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
(a) Total mass					
Days	2	5.86	0.04	0.63	0.56
Blocks	3	5.57	0.04	1.44	0.32
(b) Inorganic sediments					
Days	2	0.92	0.44	0.85	0.46
Blocks	3	2.49	0.15	1.01	0.44
(c) AFDM					
Days	2	26.44	<0.01	0.36	0.70
Blocks	3	9.62	0.01	2.26	0.18
(d) Chlorophyll <i>a</i>					
Days	2	0.21	0.82	5.04	0.06
Blocks	3	0.59	0.59	1.08	0.43

Periphyton

There were no significant differences in chlorophyll *a* between treatments on any individual sampling day (Table 2; Fig. 4). The average Autotrophic Index was *c.* 9000 in the controls and 37 000 in the exclusion treatment. We also found no statistically significant differences in chlorophyll *a* among sampling days in either treatment (Table 3; Fig. 4). In contrast to the response of chlorophyll, diatoms were significantly more abundant in the absence of shrimps than in the controls after the 34-day course of the experiment (Table 4; Fig. 5). The most abundant taxa comprised motile pennate forms such as *Navicula* and *Nitzschia* (41%) and stalked forms such as *Gomphonema*, *Achnanthes* and *Cymbella* (39%). The blue-green *Rivularia* was the most common microfilamentous

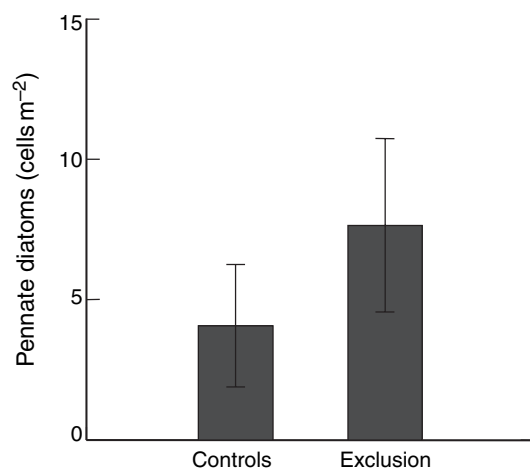


Fig. 5 Motile pennate diatoms such as *Navicula* and *Nitzschia* (41%) and stalked forms such as *Gomphonema*, *Achnanthes* and *Cymbella* (39%) sampled at the end of the experiment in presence and absence of shrimps.

Table 4 Statistical differences of abundance of diatoms after 34 days of exclusion (two-way ANOVA)

	d.f.	F	P
Treatments	1	24.05	0.016
Blocks	3	24.62	0.013

alga in both treatments. We were not able to quantify microfilamentous blue-green algae because of their state of fragmentation in our samples. We observed few macrofilamentous green algae in our samples from both treatments; they were not common at the study site.

Benthic insects

Few invertebrates were found by examining the filters and the numbers of sessile invertebrates such as Chironomidae (Diptera), Lepidoptera and Trichoptera were insufficient for statistical analysis. Ephemeropterans were the most frequent macroinvertebrates visually assessed in the experimental quadrats (Table 1). Their density was statistically higher in the presence than in absence of shrimps ($F_{1,3} = 16.5$; $P < 0.03$).

Discussion

Shrimps and accrual of sediment

Shrimps caused significant removal of sediment from hard substrate at our study site. Benthic material

accumulated to approximately four times the level in controls when shrimps were excluded. The benthic material comprised more inorganic than organic material. Most of the organic material appeared to be not associated with photosynthetic organisms. The ratio AFDM/chlorophyll *a* or Autotrophic Index ranged from *c.* 9000 in controls to 37 000 in electrified quadrats. (The normal range for epilithon consisting mainly of algae is 50–100: APHA, 1992; Hauer & Lamberti, 1996.)

We presume that the atyid *P. glabra*, rather than *M. olfersi*, was the main agent of sediment removal since it was more abundant and active on control substrate. Some atyids, including *P. glabra*, are characterised by their setaceous chelae (Molina, 1987) which they use with their pereopods to manipulate sediments and periphyton. According to Pringle & Blake (1994), atyid activity and water flow play interacting roles in sediment distribution. We observed at least two mechanisms associated with the removal of sediments and algae by *P. glabra*. The first involved the simple resuspension of sediments so they were washed away from the hard substrates with the water flow. The second mechanism was the ingestion of material, and subsequent egestion as faecal pellets.

The results from the electrified quadrats agree with a previous experiment conducted in the Andorinha stream and another nearby stream (Visoni & Moulton, 2003). The experiment showed a significant accrual of sediments on cobbles inside cages from which both *M. olfersi* and *P. glabra* were excluded. The experiment could not, however, identify which was the principal species to be excluded by the cages or which was presumably responsible for most of the removal of benthic material. The atyids here showed an activity similar to that of the larger bodied atyid *A. lanipes* on sediments deposited on hard substrates in Central America and Caribbean streams (Pringle *et al.*, 1993; Pringle & Blake, 1994; Pringle, 1996; Pringle & Hamazaki, 1998; Pringle *et al.*, 1999; March *et al.*, 2002).

Benthic algae

Our results suggest a negative effect of atyid shrimps on the algal community. On the last sampling day, the treatment with no shrimps and significantly greater amounts of sediments also contained significantly more diatoms than the controls. The major taxa

comprised motile biraphid forms such as *Navicula*, *Nitzschia* and stalked forms such as *Gomphonema*, *Achnanthes* and *Cymbella*. The increased surface area and availability of nutrients provided by the sediment accrual probably benefited these diatoms. These algae are adapted to colonise sediments since they are able to trap and stabilise the particles in algal mats composed of siliceous frustules and mucilage and the motile forms are able to keep themselves on the top of the sedimentary layer (Round, 1981; Pringle, 1990; Stevenson, Bothwell & Lowe, 1996; Pringle & Hamazaki, 1998).

Although the density of diatoms was significantly higher in the exclusion treatment, chlorophyll *a* concentration did not follow this tendency. We speculate that this response for chlorophyll was caused by grazer-resistant algae, presumably represented by blue-green microfilaments directly attached to the tiles rather than diatoms associated with sediments. Blue-greens such as *Rivularia*, *Calothrix* and *Lingbya* were apparently more abundant in the controls and may have contributed chlorophyll that obscured any potential difference caused by the chlorophyll from diatoms. Various studies have found that the removal of sediment and associated algae by fishes or shrimps can markedly affect the algal community, favouring well-attached taxa of the lower story of the periphyton (Power, Stewart & Matthews, 1988; Gelwick & Matthews, 1992; Pringle *et al.*, 1993; Flecker, 1996; Pringle & Hamazaki, 1997, 1998). Some studies have reported that atyids were able to promote this shift in algal composition in stretches where shrimps were abundant and fishes occurred in low densities (Pringle *et al.*, 1993; Pringle & Blake, 1994; Pringle, 1996; March *et al.*, 2002).

Interactions among ephemeropterans, palaemonids and atyids and their effects on the benthos

A series of electric exclusions at an open site with shallow bedrock downstream of the current study site showed baetid ephemeropterans to be more effective in removing sediments and reducing chlorophyll *a* when both species of shrimps were excluded (Silveira & Moulton, 2000; Silveira, 2002; Moulton *et al.*, 2004). Baetid ephemeropterans were an order of magnitude more abundant in the absence of shrimps at the downstream site, and this was attributed to the negative effect of *M. olfersi* on the ephemeropterans.

In the present study, however, we observed that the ephemeropterans did not become more abundant when shrimps were excluded. On the contrary, significantly higher densities of baetid nymphs were found in the presence of *P. glabra*, which implies a positive interaction between them. This association between baetids and atyids is typically encountered in the upper reaches of the Andorinha stream and in a nearby stream, where both are not suppressed by actual or potential predators (fishes and *Macrobrachium*) and they occur in high densities. Positive interactions between baetids and atyids have been previously reported in Puerto Rico (Pringle *et al.*, 1993; March *et al.*, 2002). The sediment removal exerted by atyids seems to facilitate the exploitation of periphytic algae (Pringle *et al.*, 1993).

The differences between the present results and those from previous experiments appear to be related to the relative abundance and activity of *P. glabra*, *M. olfersi* and ephemeropterans at the different sites. In the present study, the substrates were in deeper water, slower current and more heterogeneous surroundings compared with the shallow, open bedrock site of the previous experiment (Moulton *et al.*, 2004). Our study adds to the many examples of the importance of site-specificity in stream community interactions (Power, 1992).

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