Strong interactions of *Paratya australiensis* (Decapoda: Atyidae) on periphyton in an Australian subtropical stream

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RUNNING HEAD: EFFECTS OF ATYID SHRIMP ON PERIPHYTON

ABSTRACT

Atyid shrimps are often an abundant component in undisturbed tropical streams. Studies in coastal streams in Puerto Rico and Brazil have demonstrated the importance of this group in removing periphyton and sediment from hard substrates and their effects on the composition and quantity of periphytic algae. We used experimental exclosures to investigate the influence of the small atyid *Paratya australiensis* on periphyton accrual on hard substrates in a coastal stream in the subtropics of Australia. We measured organic and inorganic matter, chlorophyll and algal biovolume in the presence and absence of shrimps on natural and artificial substrates. We found a five-fold increase in the amount of organic matter on natural substrate in the absence of *P. australiensis* and a two to ten-fold increase in total periphyton mass on

artificial substrate. The natural substrates did not show differences in biovolume of algae, however, algal biovolume on the artificial substrates was significantly higher in the exclusion treatment and diatoms were most affected. We conclude that *P. australiensis* can be considered a strongly-interacting element of the stream biota and an important species for monitoring and conservation.

Keywords: biofilm, bioturbation, electrical exclusion, shrimps. .

INTRODUCTION

There is growing evidence that some macroconsumers play a significant role in freshwater ecosystems and can have an effect on benthic community structure and ecosystem processes that is disproportionately large compared to their actual food intake. The phenomenon is not universal, however, and studies have shown a variety of interactions among systems. These range from (i) trophic cascades in which the higher-level consumer adversely affects herbivores or detritivores (Rosemond et al. 1998), (ii) strong negative interactions with the base-level resources, which is often mediated by bioturbation (Creed et al. 2010), to (iii) no apparent effect of macroconsumers on intermediate or base-level resources (Mantel and Dudgeon 2004).

In tropical streams, shrimps and fishes have been shown to influence ecological processes through bioturbation (Pringle and Blake 1994, Pringle and Hamazaki 1998, Cross et al. 2008) and ecosystem engineering (Flecker 1996) with implications for the benthic community and ecosystem processes. Here again the interactions are not necessarily predictable among various systems. For example, in Costa Rica, fish and shrimps were shown to have strong direct effects in reducing basal resources (Pringle and Hamazaki 1998), whereas in Brazil *Macrobrachium* shrimps were shown to have the indirect effect of increasing periphyton by their strong negative effect on intermediate herbivores (mayflies) (Moulton et al. 2004).

The importance of these interactions for ecosystem functioning have led ecologists to link them to environmental impacts (e.g. Greathouse et al. 2006) and to call for research that targets “keystone” and strongly-interacting groups (Power et al. 1995).

Atyid shrimps have been shown to be strong interactors in coastal streams of the Caribbean, Central America, Hong Kong and Brazil because of their effects on the benthic community (Pringle et al. 1993, Crowl et al. 2001, Souza and Moulton 2005, Yam and Dudgeon 2005a, b). Experimental exclusion of shrimps led to significant accretion of material on hard substrates (Pringle et al. 1993, Pringle and

Hamazaki 1998, Silveira and Moulton 2000, Visoni and Moulton 2003, Moulton et al. 2004). This relationship also has been observed through inter-stream comparisons associating sediment and algal mass with the natural densities of shrimps in Puerto Rican (Pringle et al. 1999) and Brazilian streams (Moulton et al. 2010).

In some cases, strong interactions between atyids and algae have also been observed, related to the development of an abundant and diverse algal upper storey community in the absence of atyids (Pringle and Blake 1994, Souza and Moulton 2005). The way in which these shrimps affect periphyton generally results from their manipulation and ingestion of detritus and loosely-attached algae accumulated on hard substrates (Pringle et al. 1993, Pringle and Hamazaki 1998, Souza and Moulton 2005, Cross et al. 2008). Water velocity acts as a second agent removing and displacing downstream the material suspended by shrimps. The action of the shrimps has also been described as algal gardening in which the removal of detritus and filamentous algae favours understory algal groups by increasing their exposure to light and nutrients and promoting stability of periphyton on hard substrates. The trophic basis for this activity appears not to be a straightforward assimilation of the ingested material; evidence from stable isotope analysis places *Atya lanipes* (March and Pringle 2003) and *Potimirim glabra* (Brito et al. 2006) as secondary consumers of algal-consuming prey. Yam & Dudgeon (2005b) found that *Caridina* spp. primarily assimilated algae although allochthonous detritus was more prevalent in the shaded streams that they studied. Thus in our consideration of “role” of atyids in stream ecosystems we need to distinguish their actions of bioturbation and grazing from their ultimate trophic relationships.

Atyid shrimps are widespread in coastal streams in Australia, especially in the sub-tropics and tropics. *Paratya australiensis* (Decapoda: Atyidae) is a small freshwater shrimp which is widespread in eastern Australia (Williams and Altmann 1980, Choy and Horwitz 1995) and is one of the most conspicuous and abundant macroinvertebrates in small headwater streams in southeastern Queensland (Hancock and Bunn 1997). The species has been extensively studied in terms of genetics, dispersal, behaviour and systematics (Hughes et al. 1995, Baker et al. 2004, Fawcett et al. 2010, Bool et al. 2011), but its role in transforming periphyton and sediments has not been studied experimentally.

This study tests the hypothesis that the activity of *P. australiensis* significantly affects benthic material on hard substrates. We expected from previous research on atyids that the interaction would be direct, rather than mediated by other organisms, but our experiment could also detect indirect effects.

Material accrues on hard substrates by active biological processes -- photosynthesis and heterotrophic incorporation of organic matter, and by passive accumulation of fine particulate organic and inorganic material. We could not distinguish the different processes, but measured the mass and inorganic

and organic content of the material and chlorophyll and direct counts of the algal content. We refer to this material as “periphyton”. We assessed the activity of shrimps on periphyton by excluding them using electricity. Similar studies have often used artificial substrates such as unglazed tiles (Pringle and Blake 1994, Pringle and Hamazaki 1998, Souza and Moulton 2005) or paving bricks (Brown et al. 2000), which facilitate sampling. Here we used both artificial substrates (bricks) and the natural cobbles of the stream in an attempt to provide both experimentally advantageous sampling units (the bricks) and potentially more ecologically relevant units (the cobbles). We predicted that the periphyton of the natural cobbles might be adapted to currents and grazing due to its exposure to these factors and thus it might be more resistant to effects of shrimps than the recently-colonized periphyton on the bricks.

METHODOLOGY

Study site

We conducted the experiment from 2 August to 20 September 2002, in Branch Creek (26° 51' 48.41" S, 152° 41' 38.27"), a 3rd order upland stream in the headwaters of the Stanley River, approximately 130 km northwest of Brisbane, Queensland, Australia. This headwater catchment is located in State Forest in the Conondale Range, which divides the Mary and Brisbane river-basins. The geology of Branch Creek consists of igneous formations. Dry sclerophyll forest is locally predominant; moist eucalypt forest dominates the slopes and patches of rainforest occur in the gullies. The climate is sub-tropical with an average annual rainfall of 1500 mm (Young and McDonald 1987) and distinct dry and wet seasons determined by stable high-pressure and low-pressure systems causing respectively drought and flooding (Stanley and Ross 1989). The study was carried out during a prolonged dry spell and the highest daily rainfall during the study period (Australian Bureau of Meteorology, station 040062, 26.81° S, 152.87° E) was 46.5 mm in August 2002. No rain was recorded in September.

The study reach was approximately 50 m long and comprised 3 pools with substrate composed mostly of well-embedded cobbles and boulders. The pools were not wider than 5 m and not deeper than 0.5 m. During almost the entire course of the experiment, the pools had almost no surface connection and water flow was negligible even after two rainy days. We placed our experimental treatments in four blocks along the stretch in which *P. australiensis* was abundant and fish were not found. Densities of *P. australiensis* of up to 250 individuals.m⁻² have been recorded from large pools in neighboring streams (Hancock 1995) but, in smaller pools, the densities of shrimp can be lower (5-20 individuals.m⁻²) (Marshall 2001).

Electric exclusion

We set out 8 quadrats in 4 pairs arranged in a randomized block design along the reach. Each quadrat was a frame made of wood and copper pipes (60×60 cm; 0.36 m^2) with the substrate composed of 5 un-colonized house bricks (23×11 cm) and cobbles from the stream that were naturally colonized by periphyton. The pipes were arranged as 3 parallel electrodes in the center and both sides of each quadrat. Within blocks, we connected the electrodes to the electrifier of only one quadrat randomly selected to exclude shrimps; the other quadrat of the pair was used as a control. The approximate distance between electrified and control quadrats within blocks was 0.3 m. Two blocks within the same pool were separated by 3 m but for others in separate pools, this distance was more than 5 m.

We used a commercially-available fence electrifier (Gallagher®, B160, 1.5 Joule, New Zealand) to produce intermittent high-voltage electric pulses to exclude shrimps in the electrified quadrats. The 4 electrified quadrats were connected in series and worked simultaneously, powered by a deep-cycle battery. We adjusted the effectiveness of the exclusion by changing the system settings and observing the reaction of the most common local macroinvertebrates to the electric pulses. We obtained the appropriate electric intensity by trial-and-error to exclude *P. australiensis* and not affect other animals such as snails, ephemeropterans, chironomids, etc.

We assessed the activity of macroinvertebrates by counting every animal on the bricks on days 12, 18, 19, 27 and 47 of the experiment. Visual assessment of macroinvertebrates on cobbles was not possible because of the dark colour of the cobbles and low visibility of the macroinvertebrates. On days 18 and 19 we carried out observations every hour for the circadian period; on the other days we counted once at between 1100 and 1200 h. We monitored the electric system weekly using a voltmeter, replacing the battery when necessary.

We carried out the experiment in the dry season, for a 47-day period in which there was no apparent water flow between the pools, except for some hours during rain that occurred between days 18 and 19. Mean water temperature was 14.3°C , mean air temperature was 16.6°C and conductivity was $140.7 \mu\text{S cm}^{-1}$ during the experiment.

Sampling

We sampled both substrates on days 6, 12, 20, 27 and 47 of the experiment. We used a small (diameter 21 mm) syringe device (cf. Loeb 1981, Moulton et al. 2009) to sample the periphyton of the

bricks and cobbles of each experimental quadrat. A combined sample of at least 4 syringe samples was taken from each experimental substrate of each treatment on each sampling day. We measured turbidity by nephelometry and in-vivo chlorophyll by fluorescence immediately after taking the samples in the field using a hand-held fluorometer (Aquafluor 8000, Turner Designs, Sunnyvale, USA) (Moulton et al. 2009). This procedure enabled us to assess periphyton total mass and chlorophyll at levels that were too low for conventional weighing (with a balance at 0.1 mg detection) or spectrophotometry. The samples were stored in Whirl Packs® (Nasco, US), kept on ice in the dark, and taken to the laboratory for further analysis.

In the laboratory we extracted photosynthetic pigments in alcohol and quantified chlorophyll *a* (Nusch 1980) of the samples from natural substrate on days 27 and 47 by spectrophotometry. We also filtered, weighed, burnt (550°C, 30 min) and re-weighed the samples to assess the total mass, inorganic mass and Ash Free Dry Mass (AFDM) of periphyton accrued on substrates. These data were also used to calibrate chlorophyll and nephelometric measurements of turbidity obtained in the field with the handheld fluorometer. The *in vivo* measurement derived from fluorescence does not distinguish chlorophyll *a* and *b* and phaeophytin and we refer to it as “chlorophyll”. Turbidity was well correlated to total periphyton dry mass ($R^2 = 0.74$, $n = 45$); we refer to the measurement derived from it as “estimated total mass” to distinguish it from total mass obtained by weighing.

We quantified the main algal groups from both substrates on days 6, 20 and 47. We placed a 50 µL drop of the sample on a microscope slide under a coverslip of known dimensions and observed a known proportion by moving the visual field in least 5 transects of the slide at 400x magnification. We identified and counted algae at the lowest possible taxonomic resolution. We determined biovolume of single and colonial cells using the software BIOVOL 2.1 (Kirschtel 1992, 1996) and measured the length and width of filaments. We grouped the results at the level of Bacillariophyceae (diatoms), Chlorophyceae (green algae) and Cyanobacteria (blue greens).

Statistical analysis

We tested the effects of electrical exclusion on periphyton masses and chlorophyll and macroinvertebrates using two-way ANOVA with one fixed factor (Exclusion of shrimps or Control with presence of shrimps) and the other factor (Days) was a repeated measure. Data were log-transformed to homogenize variances. The adjustments to degrees of freedom of the univariate F test statistics are the Greenhouse-Geisser epsilon and the Huynh-Feldt epsilon. We used SYSTAT 7.0 to perform the analysis.

RESULTS

Exclusion and macroinvertebrates

The effectiveness of exclusion appeared to be proportional to body size with the larger species being more sensitive to the electric pulses. *P. australiensis* was effectively excluded and no shrimps were seen foraging on the electrified substrates (Fig. 1). In the controls, however, these shrimps were the most abundant macroinvertebrates observed during the experiment. The snail *Physa acuta* was the second most conspicuous macroinvertebrate in the quadrats. The electricity did not visibly affect them and the density of snails was higher in the electrified quadrats compared to the controls ($F_{1,1} = 23.4$; $P \leq 0.001$) (Fig. 1). Ephemeropterans were the next-most abundant (visible) macroinvertebrate group; no statistically significant differences in their densities were found between treatments ($F_{1,1} = 2.9$; $P \leq 0.09$). None of the macroinvertebrates was statistically different in density between day and night (Table 1). We infrequently observed the presence of a larger shrimp (most likely *Macrobrachium australiense*) near the experimental substrates.

Periphyton mass and chlorophyll

Natural substrates

We found more periphyton accrued on the natural substrates (cobbles) in the absence of *P. australiensis* (Table 2, Fig. 2). There was a visible difference between the exclusion treatment and the control after 6 days of exclusion and this difference in periphyton became more pronounced as the experiment progressed. The difference was due to the organic content, since the inorganic mass was not statistically different between treatments. On day 6, the organic/inorganic ratio of 0.39 in the presence and 0.9 in the absence of shrimps indicated the predominance of organic mass on the electrified cobbles.

Artificial substrates

Although artificial substrates had about one quarter of the periphyton mass of the natural cobbles, the differences between treatments were more visibly apparent by virtue of the light colour of the bricks. Except for day 27, samples taken by our syringe device contained too little material for the quantification of the mass and its organic and inorganic components by weighing. There was approximately 4.5× more

material on average in the absence of atyids in relation to the control treatments (Fig. 2; Table 3). On day 27, the organic/inorganic ratio was 0.43 for the controls and 1.38 for the exclusion treatment and the organic content was almost 19× higher in the exclusion treatment (14.7 g.m^{-2}) compared with the control (0.79 g.m^{-2}). For days 6, 12, 20, 27 and 47, the periphyton total mass estimated from turbidity was significantly different between treatments (Fig. 2; Table 3).

Chlorophyll and algae

Natural substrates

We found no significant difference in chlorophyll on the natural substrates (cobbles) between treatments (Table 2). Similarly, the total biovolume of algae did not differ between treatments. We grouped algae into green, blue green and diatoms, the principal groups identified by microscopy (Fig. 3). On the cobbles without shrimps, filamentous algae represented 91% of the green algae group and 90% of the blue-green group. The stalked forms composed 61% of the diatoms group. In the cobbles with shrimp, filaments were 66% and 86% of the green algae and blue green algae biovolumes. Stalked diatoms (68%) predominated again in biovolume in comparison to the adnate diatoms within the diatom group.

Artificial substrates

On the artificial substrates, the total biovolume of algae was higher in the exclusion treatment in comparison to the controls (Table 4). The same occurred individually with the diatoms (Table 4). The stalked forms were more predominant in the controls (82%) compared to the exclusion (65%) in terms of biovolume for the diatom group. Very little biovolume of green algae could be found in the brick samples of day 6. On days 20 and 27, however, the filamentous forms were 84% of all green algae in terms of biovolume in the absence of shrimps and 60% in their presence. The blue-green filamentous algae represented 80% and 91% of their group in biovolume in the absence and presence of *P. australiensis*, respectively. We did not observe a difference in length of filaments of filamentous blue-green algae between treatments (data not presented), but on bricks that we brought to the laboratory we could clearly observe the presence of longer filaments in the electrified bricks compared to those exposed to shrimp. The sampling made with the syringe did not preserve the integrity of these filaments and, thus, differences in length were not measured. The analysis of chlorophyll also did not show overall differences between

treatments although for certain of the sampling days there was higher chlorophyll on the bricks without shrimp (Table 3, Fig. 2).

DISCUSSION

Paratya and bioturbation

The atyid *P. australiensis* was the most abundant macroinvertebrate observed in the control treatment, and no shrimps were seen foraging in the electrified quadrats during the experiment. The amount of periphyton mass accumulated in the presence of *P. australiensis* was significantly lower compared to the exclusion treatment for both natural and artificial substrates. Thus, based on these general results, we conclude that *P. australiensis* effectively reduced the amount of periphyton mass in our experiment. A similar functional role to that here attributed to *P. australiensis* was found for the similarly-sized atyid *Potimirim glabra* in a coastal Brazilian stream (Souza and Moulton 2005, Moulton et al. 2009, Moulton et al. 2010) as well as for the larger atyid *Atya lanipes*, in Caribbean streams (Pringle et al. 1993, Pringle and Blake 1994, Pringle et al. 1999, March et al. 2002, Cross et al. 2008), although previous research on *P. australiensis* in the Conondale Range did not show such an effect (Marshall 2001) (Table 5).

We believe that the differences in periphyton mass in the absence of atyids among different studies may be related to physical conditions and/or manipulative methods. Pringle *et al.* (1993) set up their manipulation in a situation in which there was much higher accrual of periphyton, which could explain the higher periphyton biomass in the absence of atyids than observed in our study (*ca.* 100 g.m⁻²). In the Australian streams, we speculate that the reason for which the results of Marshall (2001) diverge from ours is related to the manipulative approach utilised to exclude shrimps. His first attempt employed a pulse perturbation removing *P. australiensis* from the experimental pools by electro-shocking at the commencement of the manipulation. He was quite confident about the effectiveness of the exclusion and pointed to various alternative explanations for the negative result such as water temperature, density and body size of the atyids, sedimentation rates and water flow. However, none of them seemed to be sufficient to explain the increased periphyton mass in the presence of *P. australiensis* and the experiment was interrupted by a high-flow event which altered the depositional environment and possibly allowed shrimps into the exclusion.

One likely reason for the low rate of accrual of periphyton mass observed on substrates in our study was the extremely low base flow and terrestrial run-off throughout the study period, which probably

reduced the rate of deposition. In a similar manipulation carried out in Brazil, Souza and Moulton (2005) put forward two mechanisms involved in the periphyton removal by the atyid *Potimirim glabra*. The first was the re-suspension of the periphyton by the shrimps with the waterflow playing a secondary role of washing the re-suspended material downstream. The other mechanism was the ingestion of the benthic material by *Pot. glabra* and the consequent egestion as faecal pellets. All the previously-cited manipulations involving atyids, periphyton and bioturbation led us to believe that the abiotic force represented by the current was fundamental for the process. In the present study in the absence of water movement, we can offer two possibilities: (i) We sampled the upper surfaces of the bricks and cobbles; material was possibly moved by the shrimps such that it fell off the sides of the substrates to the stream bed. (ii) Possibly the egestion and consequent pelletisation of periphyton are sufficient by themselves to cause bioturbation, as in the case of simuliid filter feeders (Wotton 2003). Nevertheless, we presume that the amount of sediment removal could be much higher under higher flow conditions in which the water movement carried away the manipulated material. Certainly we can speculate that a large part of the material that was removed from the surface was not ingested by the shrimps, as was seen in a study of *Atya lanipes* (Cross et al. 2008).

Effect of *Paratya* on periphyton composition

The organic content of the periphyton of the natural substrates was significantly higher in the absence of *P. australiensis*. The periphyton accumulated in the exclusion treatment was predominantly organic and the organic/inorganic ratios were higher than those of the control. With no differences in chlorophyll between treatments, the increased content of organic matter sampled in the exclusion treatments was apparently not associated with more autotrophic production. Presumably it represents active heterotrophic incorporation of dissolved organic matter into the periphyton and passive sedimentation of fine particles, but we cannot differentiate between these processes.

In concordance with the result for chlorophyll, there were no differences in the total algal biovolume between treatments for the natural substrate (cobbles). The algal composition of the cobbles was predominantly green and blue-green filamentous algae.

In spite of the increased biovolume of diatoms found in the bricks of the shrimp-exclusion compared to controls, no overall differences in chlorophyll were observed. (In the isolated results of days 12 and 27, chlorophyll was significantly higher in the electrified treatment.) The chlorophyll of the other groups of algae may have partially masked the contribution of the diatoms, or the discrepancy might lie within the range of experimental error. The algal composition was clearly distinct between artificial and natural substrates, particularly in the samples of days 6 and 20 when filamentous green algae were not

observed on the artificial substrates. The periphyton architecture seems to be also affected by the atyids; we observed longer blue green filaments on the substrates from the electrical exclusions (data not presented). Here, we suggest the possibility of an algal “gardening” exerted by *P. australiensis*. In this process, shrimps modify the structure of the blue green turf influencing other algal groups. An example of shrimps modifying the periphyton structure was reported by Pringle *et al.*, (1993) and March *et al.*, (2002); shrimps of the genera *Atya* (Atyidae) and *Xiphocaris* (Xiphocarididae) favored the enhancement of understorey periphyton by removing the sediment cover and exposing the substrates. Hart (1985) showed that a territorial caddisfly defended an area of increased algal productivity; in the case of non-territorial shrimp the argument is much less persuasive that this behaviour of the shrimp is purposive and directed towards gaining higher quantity and quality of dietary algae.

The dietary preferences of *P. australiensis* appear to depend on the local availability of resources, and cyanobacteria, as well as detritus, have been reported to be important. Bunn and Boon (1993) attributed 30% of the *P. australiensis* biomass in billabongs to the assimilation of macrophytes and leaf litter, the rest was mostly epiphytes and bacteria. Burns and Walker (2000) observed that filamentous cyanobacteria represented up to 83% of the autotrophic component of the foregut contents of *P. australiensis* in the River Murray. The isotopic signature, however, indicated that macrophytes and allochthonous fine particulate organic matter (FPOM) were the most probable items assimilated by *P. australiensis*. On the other hand, Piola *et al.* (2008) demonstrated that *P. australiensis* assimilated cyanobacterial accumulations in a lake environment. Marshall (2001) observed that the gut contents of *P. australiensis* in the upland streams of the Conondale Range were composed mostly of FPOM and its isotopic signature indicated that detritus of terrestrial origin is the main primary source of carbon assimilated by the atyid.

Other studies involving the trophic relationships of atyids have shown that their primary food source is algal. Although the gut contents of *Potimirim glabra* in a Brazilian coastal stream were mostly FPOM, the carbon stable isotope ratios ($\delta^{13}\text{C}$ values) showed that this atyid assimilated carbon of microalgal origin and the ^{15}N values indicated that it was a secondary consumer of prey that consumed microalgae (Brito *et al.* 2006). Similar patterns occurred in the study of March and Pringle (2003) in Puerto Rico with atyids, *Atya* spp. and the xiphocarid shrimp *Xiphocaris elongates*. Yam and Dudgeon (2005b) in Hong Kong found that *Caridina cantonensis* and *Caridina serrata* were principally herbivorous. We found no evidence to consider *P. australiensis* a secondary consumer. On the contrary, investigations involving stable isotopes of ^{13}C and ^{15}N have shown no intermediaries between *P. australiensis* and its source of autotrophic carbon (Bunn and Boon 1993, Burns and Walker 2000).

Snails and ephemeropterans were seen in both experimental treatments. The electric exclusion apparently did not affect the snails. They were seen mostly in the exclusion treatment of the artificial substrates, in the absence of *P. australiensis*. We speculate that the snails were attracted to the increased quantity and, perhaps, quality of the periphyton. Alternatively, they might have responded directly to the absence of *P. australiensis*. Although in some cases we could see trails of diminished periphyton caused by the snails, the capacity of snails in reducing benthic material and cleaning the substrate was apparently much less than that of the shrimps, since the exclusion treatment had significantly more periphyton. The snails were considerably less abundant than the shrimps, in contrast to a study in Puerto Rico where snail effects apparently dominated those of shrimps at low-altitude sites (March et al. 2002). The effect of macroconsumers on other fauna has been shown to vary among streams and to have different consequences for basal resources: *Macrobrachium olfersi* was shown to inhibit ephemeropterans which provoked a trophic cascade and increase in periphyton in a Brazilian stream (Moulton et al. 2004), whereas the actions of the atyid *Potimirim glabra* reduced the amount of periphyton and apparently attracted ephemeropterans in another part of the same stream (Souza and Moulton 2005). Streams within a region were shown to have large differences with respect to top consumers and trophic cascades, apparently without strong relationship with herbivore traits (Kurle and Cardinale 2011).

The reactions of periphyton on the artificial (brick) substrate and the natural (stream cobble) substrate were basically similar – periphyton mass, particularly organic mass, increased in the absence of shrimps. Algae apparently increased more on the artificial substrates compared to the natural and this was probably because the stream cobbles started with the natural levels of attached benthic algae (Fig. 2 & 3). We have no explanation of why the algae apparently increased during the first 20 days of the experiment on both shrimp-excluded and control substrates (Fig. 2). The bricks were convenient for visual sampling of macroinvertebrates and provided a uniform substrate for periphyton colonization; the stream cobbles provided a necessary comparison with natural substrate.

Our study demonstrates that *P. australiensis* can substantially reduce the quantity of periphyton on hard substrata in the coastal, sub-tropical stream that we studied. This places the species in the group of strongly-interacting macroconsumers that are considered important for ecosystem functioning (Pringle et al. 1999, Palmer et al. 2000). *Paratya australiensis* is not amphidromous and is not likely to suffer the effects of downstream impacts that affect the amphidromous shrimps *Atya lanipes* (Greathouse et al. 2006) and *Potimirim glabra* (Moulton et al. 2007). However its apparent importance in the stream ecosystem implies that it should be carefully monitored in programs of stream assessment and conservation.

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Figure 1. Abundance of *Paratya* shrimps and *Physa* snails on artificial (brick) substrate in electrical exclusions and controls. No shrimps were seen in the electrified exclusions. Error bars are ± 1 s.e.

Natural (cobble) substrate

Artificial (brick) substrate

Figure 2. Periphyton mass and chlorophyll on natural (cobble) and artificial (brick) substrates, in exclusion and control quadrats. Estimated total mass was derived from the turbidity of the sample. Chlorophyll was measured by *in vivo* fluorescence. Organic and inorganic mass were weighed. Error bars are ± 1 s.e.

Natural substrate

Artificial substrate

Figure 3. Algal composition (%) of natural and artificial substrates on days 6, 20 and 47 of the experiment.