Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream

JAMES G. MARCH, CATHERINE M. PRINGLE, MATT J. TOWNSEND*
and AMANDA I. WILSON†
Institute of Ecology, University of Georgia, Athens, GA, U.S.A.

SUMMARY

1. In tropical island stream ecosystems freshwater shrimps are often the dominant macroconsumers and can play an important role in determining benthic community composition. However, most studies of the ecological role of shrimps are limited to high-altitude shrimp-dominated sites where other biota (fishes and snails) are absent or significantly less abundant than at lower altitudes.

2. We examined how effects of different shrimp assemblages on benthic communities changed along an altitudinal gradient in a tropical island stream in Puerto Rico. We used electroshocking and observations to quantify abundance and taxonomic composition of shrimp assemblages at three sites (300, 90 and 10 m a. s. l) along the Río Espíritu Santo. We also experimentally manipulated access of shrimps to the benthic environment simultaneously at each site using electric fences over a 35-day period.

3. At the high-altitude site, exclusion of shrimps (predominantly *Atya* spp. and *Xiphocaris elongata*) resulted in significantly greater accrual of organic and inorganic material, chlorophyll *a* and algal biovolume. In the absence of shrimps, the algal community was dominated by filamentous green algae (Chlorophyta: *Oedogonium* and *Rhizoclonium*). Excluding shrimps did not affect total insect biomass but significantly increased sessile chironomids (Diptera: Chironomidae). We observed similar treatment effects at the mid-altitude site where shrimps (primarily *Macrobrachium* spp. and *X. elongata*) occurred at lower densities. In contrast, at the low-altitude site there were no treatment differences in organic and inorganic material, chlorophyll *a*, algal biovolume, algal assemblage composition and insects.

4. The lack of treatment differences at the low-altitude site was probably because of very high densities of grazing snails (*Thiara granifera* and *Neritina* spp.) which reduced organic and inorganic resources and obscured potential shrimp effects.

5. This study demonstrates that freshwater shrimps can play an important role in determining benthic community composition; however, their effects vary and appear to depend on the presence of other biota. This study suggests that loss of shrimps as a result of anthropogenic disturbances will have different effects on the stream community depending upon location along the altitude gradient.

Correspondence: James G. March, Institute of Ecology, University of Georgia, Athens, GA 30602, U.S.A.

E-mail: march@sparc.ecology.uga.edu

*Present address: Department of Fisheries and Wildlife, Utah State University Logan, UT, 84322, U.S.A.

†Present address: Department of Biology, University of North Carolina at Greensboro, Greensboro, NC 27402, U.S.A.

Introduction

Studies in marine (e.g. Paine, 1974), lacustrine (e.g. Carpenter *et al.*, 1987) and lotic ecosystems (e.g. Power, 1990) have demonstrated that strong top-down effects of individual species or species assemblages can be important in determining community composition. Further research in these different ecosystems has shown that species effects vary depending on the biotic and abiotic environment (Power, 1992; Kitchell & Carpenter, 1993; Menge *et al.*, 1994). Accordingly, ecologists have been encouraged to determine those environmental conditions in which species assume key roles (Hunter & Price, 1992; Polis *et al.*, 1996; Power *et al.*, 1996).

To do this, Polis *et al.* (1996) stressed the importance of adopting a 'comparative experimental' approach where experiments are simultaneously performed at multiple sites along physical or biological gradients (e.g. Menge *et al.*, 1994). Lotic ecosystems provide an ideal setting in which to use this approach. They provide a natural gradient from headwaters to mouth in which species assemblages change along with stream structure and function (Vannote *et al.*, 1980). Yet, to our knowledge, no *in situ* experimental studies have been run that simultaneously manipulate biota at different sites along a stream gradient (March *et al.*, 2001).

In this study we examined the top-down effects of freshwater shrimps simultaneously at three sites, *in situ*, along an altitudinal gradient in a tropical island stream. In tropical island streams, freshwater shrimps are often the dominant macroconsumers (e.g. Resh & De Szalay, 1995; Covich, 1988) and also inhabit reaches along the entire river continuum (Bhajan *et al.*, 1978). Previous research in Puerto Rico has shown that shrimps affect insect and algal community composition (Pringle *et al.*, 1993, 1996), quantity and quality of fine benthic organic matter (Pringle *et al.*, 1999), sediment cover (Pringle & Blake, 1994), and rates of litter processing (Crowl *et al.*, 2001; March *et al.*, 2001). However, all of these studies have been conducted in high-altitude streams above waterfalls that restrict fishes and snails to lower reaches (but see Pringle *et al.*, 1999; March *et al.*, 2001). The effects of shrimps may be different at lower altitudes where they interact with predatory fishes and algivorous snails. Predatory fishes could reduce shrimp abundance or alter their beha-viour while algivorous snails may themselves have strong effects on the benthic community (e.g. Jacoby, 1985; Steinman *et al.*, 1987; Rosemond, Mulholland & Elwood, 1993) and thus decrease the relative effects of shrimps. Shrimp effects may also be different at lower altitudes because of changes in shrimp assemblage composition. In many tropical island streams, atyid shrimps dominate high-altitude sites while *Macrobrachium* shrimps are more abundant at lower altitudes (e.g. Hunte, 1978; Marquet, 1991; Fièvet, Tito de Morais & Tito de Morais, 1996). Differences in feeding behaviour among shrimp taxa may potentially result in different effects on the benthic community.

Understanding the role that shrimps play in determining community composition and how that role varies along an altitudinal gradient also has resource management implications. Recent anthropogenic disturbances such as damming and water withdrawal, as well as stream poisonings, have increased larval and adult shrimp mortality and resulted in the removal of shrimps from entire reaches (Holmquist, Schimdt-Gengenbach & Yoshioka, 1998; Benstead *et al.*, 1999). Location of anthropogenic disturbance along the altitudinal gradient may be an important factor when predicting their consequences and designing mitigation and regulation programmes.

In this study, we used a comparative experimental approach to examine if the role of shrimps changes along an altitudinal gradient in a tropical island stream. We predicted that the presence of other biota (fishes and snails) in lower altitude reaches would result in decreased shrimp effects on the benthic environment (accrual of organic and inorganic matter, insect and algal abundance and composition) compared with high-altitude shrimp-dominated sites.

Methods

Study sites

We conducted this study in the Espíritu Santo river system which drains the northern part of the Luquillo Experimental Forest (LEF) and surrounding lowlands in north-eastern Puerto Rico. The Río Espíritu Santo is representative of Caribbean montane rivers in that it has a very flashy hydrograph (Ahmad, Scatena & Gupta, 1993); discharge can increase more than 10-fold in less than an hour (Covich & McDowell,

1996). The LEF does not experience marked wet and dry seasons as do some tropical areas. Mean annual precipitation (3460 mm) is evenly distributed throughout the year, except for a slightly drier period from January to April (Waide & Reagan, 1996).

The physical structure of the Río Espíritu Santo changes dramatically from high-altitude headwaters to the river mouth. High-altitude tributaries (> 200 m a.s.l) are characterised by steep gradients with alternating pools and cascades. Substrata consist of large boulders with interstitial cobble and gravel. A large waterfall (> 10 m), at approximately 200 m a.s.l., separates the high- and mid-altitude sites and acts as a barrier to most fishes. At mid-altitude sites (70–200 m a.s.l) the channel widens and the gradient decreases. Small cascades are less frequent, and riffles composed of small boulders and cobble are common. This trend of decreasing gradient and substrata size continues to low-altitude sites (< 70 m a.s.l), resulting in mostly large runs and cobble/gravel riffles.

Land use also changes along this altitude gradient. Tabonuco forest is the dominant vegetative zone in the LEF and is characterised by *Dacryodes excelsa* Vahl. (Burseraceae). This vegetative zone extends below 600 m a.s.l. to the forest boundary, located at approximately 90 m a.s.l. Below the LEF boundary, land use changes dramatically to mostly urban and pasture; however, the riparian zone is predominantly forested.

Biota

Ten species of omnivorous freshwater shrimps inhabit rivers of LEF, representing three families: Palaemonidae, Atyidae and Xiphocarididae. The palaemonid shrimps *Macrobrachium carcinus* (L), *M. faustinum* (De Saussure), *M. crenulatum* Holthuis, *M. acanthurus* (Wiegmann), and *M. heterochirus* (Wiegmann) consume algae, macrophytes, decomposing leaf litter, insects, molluscs, small fish and other shrimps (Covich & McDowell, 1996). The atyid shrimps, represented by *Atya lanipes* Holthuis, *A. scabra* (Leach), *A. innocous* (Herbst), and *Micratya poeyi* (Guérin-Méneville), consume periphyton, small sessile insects, and leaf material by brushing with their cheliped fans (Pringle *et al.*, 1993, 1996; Pringle & Blake, 1994). They use these same cheliped fans to filter feed when flow conditions are suitable (Covich, 1988). *Xiphocaris elongata* (Guérin-Méneville) consumes leaf matter, periphyton, insects, small flowers and fruit using tiny pincers. All of these shrimp species undergo extended larval development and are amphidromous (Covich & McDowell, 1996; Johnson *et al.*, 1998); adult females release planktonic larvae that drift downstream to the estuary (March *et al.*, 1998). Larvae spend 50–110 days in the estuary before migrating back upstream as metamorphosed postlarvae (Chace & Hobbs, 1969; Benstead, March & Pringle, 2000). Adult shrimps differ in their distribution along the altitudinal gradient (March *et al.*, 2001). High-altitude sites above the waterfall are dominated by atyid shrimps (mostly *A. lanipes*) and *X. elongata*. *Macrobrachium* spp. and *X. elongata* comprise the majority of the shrimp assemblage at lower altitude sites.

The fish community in the Espíritu Santo is made up of seven species. The green stream goby, *Sicydium plumieri* (Bloch), grazes periphyton and is the only fish found in high-altitude streams. *Agonostomus monticola* (Bancroft), *Gobiomorus dormitor* Lacepede, *Eleotris pisonis* (Gmelin), *Awaous banana* (Valenciennes), *Anguilla rostrata* (LeSeur) and the introduced *Xiphophorus helleri* (Heckel) all occur below the waterfall at 200 m a.s.l. *Agonostomus monticola* is omnivorous, but consumes mostly insects as well as shrimps (Aiken, 1998). Less is known about diets of the remaining fishes, but they are thought to consume primarily insects and shrimps.

The remainder of the aquatic fauna consists of insects, snails and one species of crab. The insect assemblage is depauperate when compared with continental tropical streams (Buzby, 1998) and is dominated by sessile chironomids and mobile baetid and leptophlebiid mayflies (Pringle *et al.*, 1993; Buzby, 1998). Three species of freshwater snails, *Neritina punctulata*, *N. clenchi* and *Thiara granifera* inhabit mid- and low-altitude sites and graze periphyton.

Experimental details

In this study we established three sites along an altitude gradient. The high-altitude site was located at 300 m a.s.l. in the Sonadora, a second-order tributary of the Río Espíritu Santo. The mid-altitude site was located approximately 3.1 river km downstream at 90 m a.s.l. in a third-order mainstem reach of the Espíritu Santo. The low-altitude site was a side channel of the fourth-order mainstem at 10 m a.s.l, approximately 4.2 river km downstream from the mid-altitude site.

We conducted this field experiment from 8 July to 19 August, 1997. At each site, five pairs of quadrats (i.e. one electric and one control) were placed close to the bank of the stream along a 100-m reach. The two quadrats within each pair were positioned at least 0.5 m apart and were anchored to the stream bottom using cable ties. Quadrats were square frames (45 × 45 cm) made of 19.05 mm chlorinated poly vinyl chloride (cpvc) tubing, with an inner and outer square of uninsulated 12-gauge copper wire held to the cpvc frame with plastic cable ties. A flip of a coin determined which one would be electrified (shrimp exclusion) or a control (shrimp access). Each shrimp exclusion replicate was connected to a solar-powered fence charger (Parker-McCrory® 12-volt, Parker-Mc Crory Mfg. Co, Kasas City, MO, USA) by attaching 12-gauge copper wire from the inner square to the power source and from the outer square to the ground. This method excluded fishes and shrimps but not insects and snails (see Pringle & Blake, 1994; and Pringle & Hamazaki, 1998 for a description of using electricity to exclude fishes and shrimps). To maintain a strong consistent electrical charge we changed batteries in each charger every 3 days. We also checked each replicate daily to ensure chargers were working properly.

In each quadrat, we tethered eight unglazed ceramic tiles (7 × 15 cm) with cable ties and binder clips. One tile was sampled from each quadrat every 5 days from day 10 to day 35. To examine the rate of recovery of the benthic community we turned off the electricity at all sites on day 37 and sampled again on days 38 and 42.

We sampled each tile by cutting cable ties and raising the tile out of the water within a fine mesh hand net to prevent loss of insects. Care was taken not to disturb accrued sediments on the tiles. Tiles and the contents of the hand net were immediately placed into zip-lock bags and transported to the laboratory in a cooler. In the laboratory, we scraped the top surface of the tile with a razor blade and scrubbed it thoroughly with a toothbrush. This resulted in a homogenate of sediment, periphyton, and insects. Insects were removed and preserved in 70% ethanol for later identification. We measured the volume of the homogenate and subsampled for organic/inorganic material, chlorophyll *a*, and algal species composition and biovolume. To measure the organic (ash free dry mass) and inorganic (dry mass – ash free dry mass)

content of the homogenate, we filtered a subsample of known volume onto a combusted and preweighed glass fibre filter (0.7 μm). Filters were dried at 60 °C for 24 h, weighed to the nearest 0.001 g, burned at 500 °C for 3 h, and re-weighed. Differences (between treatments and among sites) of both the inorganic and organic content of homogenate were compared using a two-way repeated-measures ANOVA on $\log_{10}$-transformed data. If there was a significant site–treatment interaction, we examined each site separately using a one-way repeated-measures ANOVA.

We measured chlorophyll *a* on tiles for days 20, 25, 30 and 35. A subsample of the homogenate was filtered onto a glass fibre filter (0.7 μm). To prevent chlorophyll *a* degradation, we added 0.15 mL of a 1% $MgCO_3$ solution to the subsample during filtration (Axler & Owen, 1994). We then placed the filter in an aluminium foil envelope and froze it until we returned to the laboratory in Georgia. Chlorophyll *a* was measured using a Turner Designs fluorometer (Turner Designs, Inc., Sunnyvale, CA, USA) (model 10AU) following standard methods (APHA, 1985). Differences in chlorophyll *a* between treatments and among sites were analysed using a two-way repeated measures ANOVA on $\log_{10}$-transformed data. If there was a significant site–treatment interaction, we examined each site separately using a one-way repeated-measures ANOVA. We excluded day 25 from statistical analysis because of missing values for a replicate at the low-altitude site.

Algal community composition and biovolume was quantified on day 35 only. To do so, we subsampled 20 mL from the homogenate and preserved it with 2% formalin in a scintillation vial. To determine algal biovolume, each sample was concentrated to a known volume, a 0.1-mL aliquot was pipetted into a Palmer cell and scanned at 400× magnification until 500 cells containing chloroplasts were identified. The number of fields of view scanned was recorded. Pennate diatoms that could not be identified to species at 400× magnification were identified as naviculoids. To determine relative abundances of pennate species, permanent mounts were made with Hyrax mounting medium from a cleaned (Carr, Hergenrader & Troelstrup, 1986) aliquot of each replicate sample and were scanned at 1000× until the same number of cells in the Palmer cell count were identified. The first 10 individuals of each taxon were measured for length, width and depth. To determine biovolumes,

the average of these measurements was used in an equation that best described the geometric shape of the cell (Gruendling, 1971). The total algal biovolume for each sample was calculated by summing all biovolumes of diatoms and filaments. Total algal biovolume was compared among sites and between treatments using a two-way ANOVA on $\log_{10}$-transformed data. The absolute biovolume ($\log_{10} + 1$ transformed) and percent biovolume (arcsin square-root transformed) of the major taxa were also compared using two-way ANOVAS.

Insects found on tiles were identified to family or genus (Merritt & Cummins, 1984), and measured to the nearest mm using 1 mm grid paper. Insect biomass per m^2 was calculated using published family level length–mass relationships (Benke *et al.*, 1999). If a length–mass relationship was not available for a family, we used one from a taxon with a similar shape. Statistical comparisons were performed using a two-way, repeated measures ANOVA on either $\log_{10} + 1$ or square root transformed data for total insect biomass and the biomass of the most common taxa, Chironomidae and Ephemeroptera. Differences in snail abundance on tiles between treatments and sites were compared with a two-way repeated measures ANOVA on $\log_{10} + 1$ transformed data.

To identify fishes, shrimps and snails present at each site we conducted 1.5 min observations of each treatment replicate on nine dates during the day and on six dates at night. We conducted observations both during day and night because shrimp activity and habitat use varies between night and day (Johnson & Covich, 2000). Total observation time was 112.5 min per treatment at each site (67.5 diurnal, 45 nocturnal). Observations were conducted from the stream bank or from nearby large boulders. We used red filters on flashlights to conduct nocturnal observations. Shrimps were usually identified to genus; however, when visibility was low because of ripples on the water surface, increased turbidity, or when shrimps were too small (< 2 cm), they were recorded as unidentifiable. Snails were identified to genus.

In addition to our observations, we electroshocked a known area (mean = 8.5 m^2) around four replicate pairs at each site at the conclusion of the experiment. Shrimps were identified to genus (Note: *Micratya poeyi* was lumped with *Atya* spp.) and the carapace length

(CL) was measured to the nearest mm. Shrimp abundance was converted to biomass using length–mass relationships (March, 2000).

Water temperature at each site was measured every 15 min throughout the experiment using submerged temperature data loggers. Discharge values were obtained from USGS gauges located at the high-altitude site and between the mid- and low-altitude sites. Total suspended solids were quantified on 32 dates during the experiment. Water (2 L) was sampled from the entire water column and filtered through precombusted and preweighed glass fibre filters that were dried at 60 °C for 24 h and re-weighed. Water temperature and total suspended solids over the entire period were compared among sites with one-way ANOVAS on $\log_{10}$ transformed data. If site was significant in the ANOVA, we tested for differences between individual sites with Tukey–Kramer HSD tests.

We measured water depth and velocity in each treatment replicate on three occasions during base flow. Depth was measured to the nearest cm from the middle of the quadrat to the water surface with a ruler. We measured water velocity with a Marsh-McBirney® (Marsh-McBirney Inc., Frederick, MO, USA) electromagnetic flow meter at four locations in each quadrat. Percent canopy cover was estimated above each quadrat with a spherical densiometer. Differences in water depth, water velocity, and canopy cover between treatments and among sites were compared using two-way ANOVAS on $\log_{10}$-transformed data for water depth and velocity and on arc-sin square root transformed data for canopy cover. If site was significant in the ANOVA, we tested for differences between individual sites with Tukey–Kramer HSD tests. All statistical analyses were performed using JMP 3.1.5 (SAS Institute Inc., 1994).

To examine the rate of recovery of the benthic community after the main experiment, we turned off the electricity on day 37 and sampled the remaining tiles on days 38 and 42. Insects, chlorophyll *a*, inorganic and organic matter were quantified as above. Three shrimp exclusion replicates at each site were observed constantly for a 60-min period immediately after turning off the electricity. The 60 min were divided into 20 3-min periods and the number of shrimps and snails observed on the tiles and in the quadrat (shrimps only) were recorded.

Results

The freshwater shrimp assemblage was dramatically different among sites along the altitude gradient in terms of taxonomic composition, total abundance, total biomass and size within each taxon. The high-altitude site had the greatest total shrimp abundance and biomass of the three sites (Table 1). *Xiphocaris* and *Atya* were dominant while only three *Macrobrachium* were sampled at this site. No small [carapace length CL < 12 mm] *Macrobrachium* were found at this site. At the mid-altitude site, total shrimp abundance and biomass were less than at the high-altitude site (Table 1). *Atya* was absent and the assemblage was composed of *Xiphocaris* and *Macrobrachium* (Table 1). Mean CL of each taxon was less than at the high-altitude site (Table 1). At the low-altitude site, total shrimp abundance and biomass were low relative to the upper two sites and the only adult shrimps present were *Macrobrachium*. All of the *Atya* and *Xiphocaris* found at this site were small (CL < 6 mm) juveniles. Fishes were rarely seen in shallow habitat near the experimental quadrats. Electroshocking resulted in only one eel (*Anguilla rostrata*) at the low-altitude site and two gobies (*Sicydium plumieri*) at the mid-altitude site.

Physical parameters also varied along the altitude gradient (Table 2). Mean water depth significantly increased with altitude while temperature signifi-cantly decreased. Mean water velocity was slower at the high-altitude than at the lower two sites. Canopy cover was significantly less at the mid-altitude site than at the other two sites. Total suspended solids were not significantly different among sites. There were no differences in water depth, water velocity and canopy cover between treatments.

Discharge during the study was typical of the river and fluctuated greatly during the 42-day experiment. The range in mean daily discharge was 0.03–0.65, 0.35–5.74 and 0.81–13.29 $m^3 s^{-1}$ at the high-, mid- and low-altitude sites, respectively. Large spates occurred on days 13, 33 and 41. Despite these spates, the electric exclusion technique proved effective. However, we did lose one replicate at both the low- and mid-altitude sites during the day 13 storm and loss of ceramic tiles resulted in only two replicates remaining at each site on days 38 and 42. Shrimps were effectively excluded at all sites with two exceptions. On day 16, two shrimp were observed in a shrimp exclusion treatment at the mid-altitude site. Batteries were immediately changed and shrimps were subsequently excluded. On day 15, at the high-altitude site, a fence charger was turned off, but for less than 4 h. We verified that shrimps were excluded from each treatment replicate daily, and these were the only exceptions during the entire study.

Observations on 14 dates over the study period showed that shrimp taxa feeding on tiles were repre-

Table 1 Abundance (# m^{-2}), biomass in parentheses (g wet weight m^{-2}) and carapace length in brackets (mm) of shrimps at each site obtained via electroshocking. Data are mean ± 1 SE

Site	Total shrimp	*Atya*	*Macrobrachium*	*Xiphocaris*
High-altitude	5.43 ± 0.81 (9.95 ± 2.96)	1.96 ± 0.32 (4.03 ± 1.12) [11.1 ± 0.6]	0.17 ± 0.07 (2.64 ± 1.92) [23.0 ± 5.6]	3.30 ± 0.52 (3.28 ± 0.62) [10.0 ± 0.2]
Mid-altitude	3.40 ± 1.10 (2.22 ± 0.76)		1.31 ± 0.44 (1.35 ± 0.48) [9.1 ± 0.6]	2.09 ± 0.69 (0.87 ± 0.30) [7.4 ± 0.2]
Low-altitude	1.87 ± 0.21 (1.31 ± 0.34)	0.48 ± 0.15 (0.02 ± 0.01) [4.2 ± 0.1]	1.37 ± 0.19 (1.29 ± 0.35) [8.9 ± 0.4]	0.02 ± 0.02 (0.00 ± 0.00) [5.0 ± 0.0]

Table 2 Physical parameters at each site. Data are mean ± 1 SE

Site	Water depth (cm)	Water velocity (m s^{-1})	Water temp. (°C)	Canopy cover (%)	Suspended solids (mg L^{-1})
High-altitude	31.2 ± 1.4*	0.02 ± 0.002*	23.07 ± 0.01*	80.8 ± 3.8*	7.19 ± 1.81*
Mid-altitude	20.9 ± 1.0†	0.07 ± 0.013†	25.22 ± 0.02†	24.8 ± 7.3†	4.73 ± 0.73*
Low-altitude	16.0 ± 1.1‡	0.12 ± 0.021†	26.98 ± 0.03‡	58.1 ± 14.2*	5.41 ± 0.92*

Different symbols show statistical differences ($P < 0.05$).

sentative of the overall shrimp assemblage at each site (Table 3). At the high-altitude site, shrimps observed on tiles were predominately *Atya* and *Xiphocaris*. At the mid-altitude site, *Macrobrachium* and *Xiphocaris* were observed on tiles in similar proportions. Shrimps on tiles were primarily *Macrobrachium* at the low-altitude site. The total number of shrimps observed on tiles increased with altitude (Table 3). Snails were absent from the high-altitude site and few were observed at the mid-altitude site. In contrast, snails were very abundant at the low-altitude site and were consistently observed on tiles in both shrimp exclusion and control treatments. Fishes were never observed on tiles but were seen in deeper mid-channel habitats or large pools. Observations conducted during the first hour after the electricity was turned off showed similar trends among sites (Table 4). At the high-altitude site, high numbers of shrimps immediately began feeding in previously electrified treatment. *Xiphocaris* shrimps arrived in large numbers followed by *Atya*. The number of shrimps entering the previously electrified treatment was low at the mid-altitude site relative to the high-altitude site and were mostly *Macrobrachium* and some *Xiphocaris*. At the snail-dominated low-altitude site, few shrimps entered the previously electrified treatment.

The effect of the shrimp assemblage on accrual of inorganic and organic (AFDM) matter varied significantly along the altitude gradient (Table 5). At the high-altitude site, the shrimp assemblage maintained relatively 'clean' tiles in controls (Figs 1 and 2). When shrimps were excluded, significantly more inorganic matter ($F_{1,4} = 64.79$, $P = 0.0013$, Fig. 1) and organic matter ($F_{1,4} = 42.15$, $P = 0.0003$, Fig. 2) accrued. When the electricity in the shrimp exclusion treatment was turned off, shrimps removed inorganic and organic matter to levels similar to controls within 24 h (Figs 1 and 2). Results were similar at the mid-altitude site (Figs 1 and 2). Greater amounts of inorganic ($F_{1,3} = 725.07$, $P = 0.0001$) and organic ($F_{1,3} = 51.43$,

Table 5 Repeated measure ANOVAs on inorganic and organic (AFDM) material and chlorophyll *a* on tiles. *P*-values are presented and bold values indicate statistical significance

Source	Inorganic dry mass			Chlorophyll *a*	
	d.f.	*P*-values	AFDM	d.f.	*P*-values
Treatment	1	**0.0001**	**0.0001**	1	**0.0002**
Site	2	**0.0001**	**0.0001**	2	**0.0337**
Treatment × site	2	**0.0001**	**0.0004**	2	**0.0142**
Pair (site)	10	**0.0001**	**0.0021**	10	0.9838
Error	10			10	

Table 3 Number of shrimps and snails observed per tile during 1.5 min observation periods. Data are mean ± 1 SE

Site	Treatment	Total shrimps*	*Atya*	*Macrobrachium*	*Xiphocaris*	Snails
High-altitude	Control	0.502 ± 0.059	0.221 ± 0.041	0.006 ± 0.003	0.238 ± 0.035	0.000 ± 0.000
	Shrimp exclusion	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Mid-altitude	Control	0.295 ± 0.054	0.000 ± 0.000	0.150 ± 0.044	0.104 ± 0.028	0.051 ± 0.022
	Shrimp exclusion	0.006 ± 0.006	0.000 ± 0.000	0.006 ± 0.006	0.000 ± 0.000	0.008 ± 0.004
Low-altitude	Control	0.066 ± 0.017	0.000 ± 0.000	0.033 ± 0.012	0.002 ± 0.002	2.082 ± 0.335
	Shrimp exclusion	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	3.306 ± 0.467

*Total shrimps observed include unidentifiable shrimps.

Table 4 Number of shrimps and snails observed entering the quadrat and per tile per 3 min observation during the first hour after electricity was turned off

|	Total shrimps	*Atya*	*Macrobrachium*	*Xiphocaris*	Total snails
Quadrat					
High-altitude	28.86 ± 12.96	1.10 ± 0.67	0.22 ± 0.20	26.93 ± 12.86	Not counted
Mid-altitude	3.44 ± 1.52	0.00 ± 0.00	1.77 ± 0.62	1.63 ± 0.87	Not counted
Low-altitude	0.95 ± 0.74	0.00 ± 0.00	0.64 ± 0.49	0.10 ± 0.10	Not counted
Tile					
High-altitude	3.14 ± 1.30	0.08 ± 0.03	0.02 ± 0.02	3.03 ± 1.29	0.00 ± 0.00
Mid-altitude	0.33 ± 0.24	0.00 ± 0.00	0.23 ± 0.17	0.09 ± 0.06	0.00 ± 0.00
Low-altitude	0.10 ± 0.07	0.00 ± 0.00	0.01 ± 0.01	0.03 ± 0.03	5.07 ± 1.62
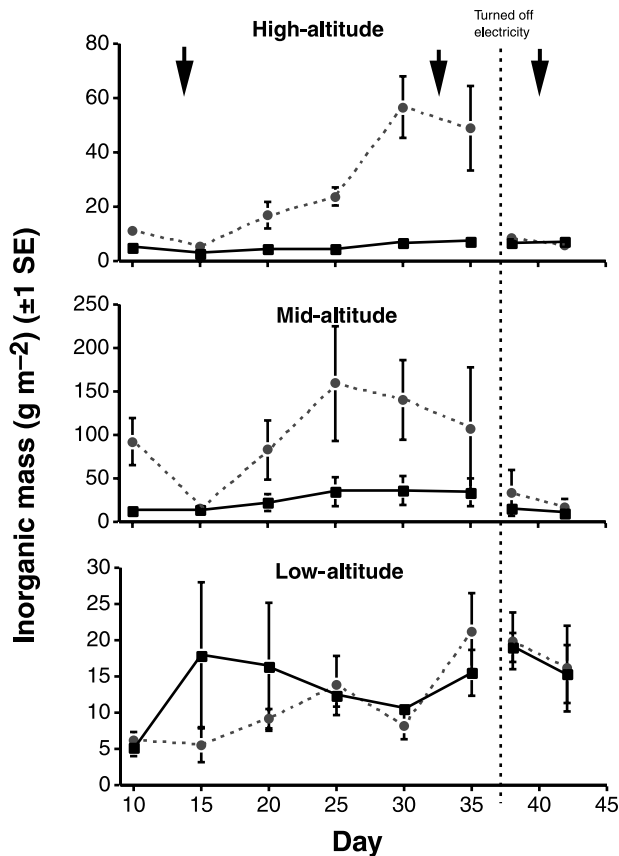
Fig. 1 Differences in inorganic sediment mass on tiles between treatments at each site. Dashed lines with circles represent the shrimp exclusion treatment. Solid lines with squares represent the control treatment. Arrows indicate the occurrence of large spates. Electricity was turned off on day 37 and tiles were sampled again on days 38 and 42.

Fig. 2 Differences in organic material (AFDM) on tiles between treatments at each site (symbols described in Fig. 1).

$P = 0.006$) matter accrued in the absence of shrimps and when the electricity was turned off shrimps removed the inorganic and organic matter on tiles within 24 h. In contrast to the upper two sites, at the low-altitude site there was no difference in inorganic ($F_{1,3} = 0.29$, $P = 0.63$) or organic ($F_{1,3} = 0.04$, $P = 0.86$) matter between treatments and no sudden changes occured when the electricity was turned off. Despite large variation in shrimp effects among sites, mean levels of organic matter in controls were similar among sites (high = 1.44 ± 0.09 SE g AFDM m^{-2}, mid = 4.79 ± 0.81 SE g AFDM m^{-2}, and low = 2.07 ± 0.18 SE g AFDM m^{-2}, Fig. 2).

Chlorophyll *a* followed similar patterns as those described above (Table 5, Fig. 3). Significantly greater amounts were found in the absence of shrimps at both the high-altitude ($F_{1,4} = 11.45$, $P = 0.028$) and
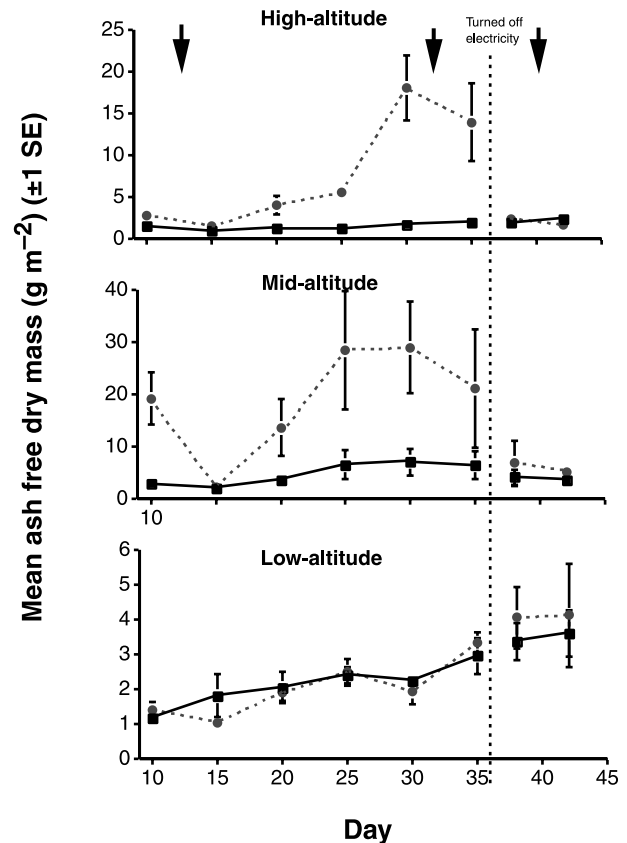
mid-altitude sites ($F_{1,3} = 28.77$, $P = 0.013$). Differences between treatments at these sites disappeared rapidly after electricity was turned off (Fig. 3). At the low-altitude site, there was no treatment difference ($F_{1,3} = 1.04$, $P = 0.38$). Chlorophyll *a* levels in controls were least at the low-altitude site (0.87 ± 0.05 SE mg m^{-2}), followed by the high-altitude site (1.17 ± 0.15 SE mg m^{-2}) and highest at the mid-altitude site (3.14 ± 0.31 SE mg m^{-2}).

Total algal biovolume and the biovolume of diatoms and filamentous algae were significantly greater in the absence of shrimps at both the high- and mid-altitude sites, but there were no treatment differences at the low-altitude site (Table 6). In controls at the high-altitude site, the algal assemblage was composed entirely of diatoms. Diatoms were mostly *Gomphonema* spp., followed by *Achnanthes* spp., *Nitzschia* spp., and a mix of other diatom genera (*Cymbella*, *Cocconeis*, *Navicula*, *Denticula* and *Eunotia*). In contrast, the algal community in the absence of shrimps was mostly filamentous green
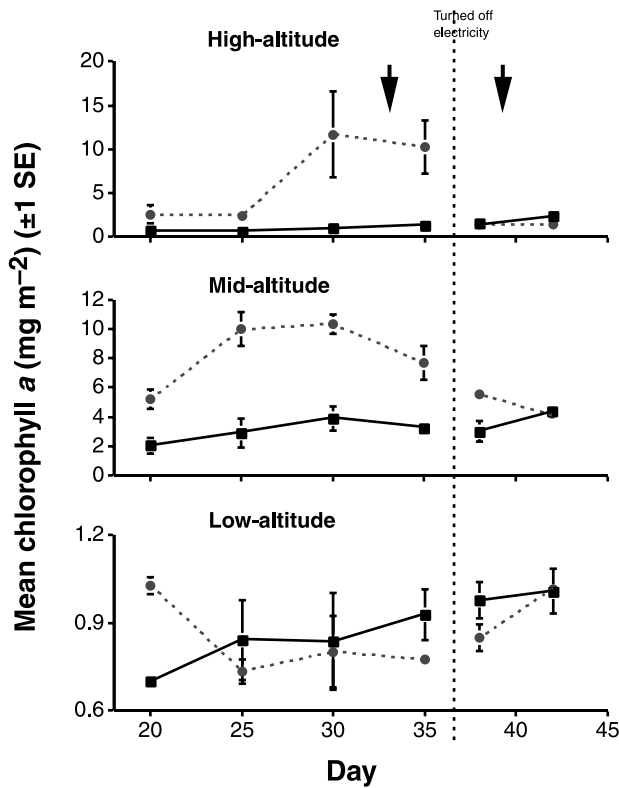
Fig. 3 Differences in chlorophyll *a* on tiles between treatments at each site (symbols described in Fig. 1).

Fig. 4 Differences in algal community composition between treatments at each site on day 35.

algae (*Oedogonium* and *Rhizoclonium*) and associated epiphytic diatoms (*Synedra* and *Fragilaria*) (Fig. 4). Accordingly, percent biovolume of diatoms significantly decreased and percent biovolume of filamentous algae significantly increased when shrimp were excluded (Table 6). Similar results were found at the mid-altitude site. Total algal biovolume, filamentous algal biovolume, and diatom biovolume were all significantly higher in the absence of shrimps
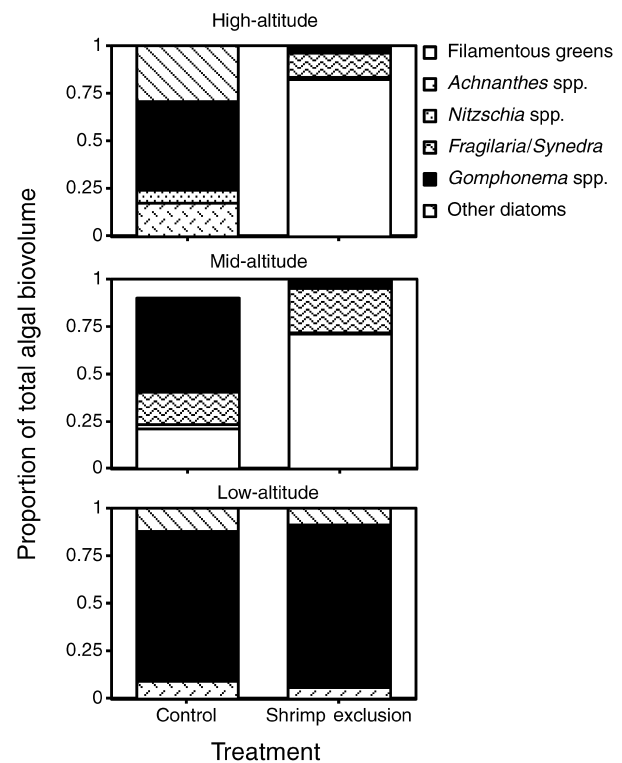
(Table 6). The algal assemblage in controls was dominated by diatoms, particularly *Gomphonema* spp.; however, some filamentous algae were present. Filamentous algae and some epiphytic diatoms (*Synedra* and *Fragilaria*) composed the majority of the algal assemblage in the shrimp exclusion treatment (Fig. 4). In contrast to the upper two sites, there were no differences in total algal biovolume between treatments at the low-altitude site (Table 6). Algal assem-

Table 6 Results of ANOVAS on total algal biovolume and absolute and percent biovolumes of filamentous algae and diatoms. *P*-values are presented with significant effects in bold

				Filamentous algae		Diatoms	
	Source	d.f	Total algal biovolume	Biovolume	Biovolume (%)	Biovolume	Biovolume (%)
Whole model	Treatment	1	**< 0.0001**	**< 0.0001**	**0.0004**	**0.0003**	**0.0004**
	Site	2	**< 0.0001**	**0.0002**	**0.0024**	**< 0.0001**	**0.0024**
	Treatment × site	2	**< 0.0001**	**0.0009**	**0.0086**	**0.0154**	**0.0086**
	Pair (site)	9	0.7351	0.5572	0.8087	0.8692	0.8087
	Error	9					
Each site separate	High-altitude	1,3	**0.0023**	**0.0001**	**0.0004**	**0.0341**	**0.0004**
	Mid-altitude	1,3	**0.0034**	**0.0308**	0.1266	**0.0087**	0.1266
	Low-altitude	1,3	0.5273			0.5273	

Table 7 Repeated measure ANOVAS on total insect biomass, Chironomidae and Ephemeroptera. *P*-values are presented and bold values indicate statistical significance

Source	d.f	Total biomass	Chironomidae	Ephemeroptera
Treatment	1	0.1064	**0.0001**	0.0644
Site	2	**0.0005**	**0.0001**	**0.0188**
Treatment × site	2	0.0833	**0.0038**	0.6332
Pair (site)	10	0.3025	**0.0738**	0.2394
Error	10			

blages in both treatments were similar to controls at higher altitude sites and were composed of diatoms, mostly *Gomphonema* spp. and *Achnanthes* spp. (Fig. 4).

Total insect biomass significantly varied among sites (Table 7). Insect biomass was highest at the mid-altitude site and least at the low-altitude site. There was no effect of treatment on total insect biomass (Table 7). However, chironomid biomass was significantly higher in the absence of shrimps at both the high-altitude ($F_{1,4} = 14.13$, $P = 0.02$) and mid-altitude sites ($F_{1,3} = 131.50$, $P = 0.0014$, Fig. 5). There was no difference in chironomid biomass between treatments at the low-altitude site ($F_{1,3} = 3.25$, $P = 0.17$). In contrast to sessile chironomids, mobile mayflies (Ephemeroptera; Baetidae and Leptophlebidae) were higher in controls, although this difference was marginally significant (Table 7). The biomass of mayflies was greatest at the high-altitude site and decreased with decreasing altitude.

There was no treatment effect on snail abundance. However, there was a significant site effect ($F_{2,10} = 302.25$, $P < 0.0001$). Snails were absent from the high-altitude site, at very low abundances at the mid-altitude site, and abundant at the low-altitude site (Tables 3 and 4).

Discussion

In this study, we found that shrimp effects on the benthos varied significantly along the altitude gradient. Specifically, shrimps had strong top-down effects at high- and mid-altitude sites and no effect at the low-altitude site. The lack of shrimp effects at the low-altitude site was probably because of very high densities of grazing snails which appeared to reduce organic and inorganic resources and obscure potential shrimp effects.
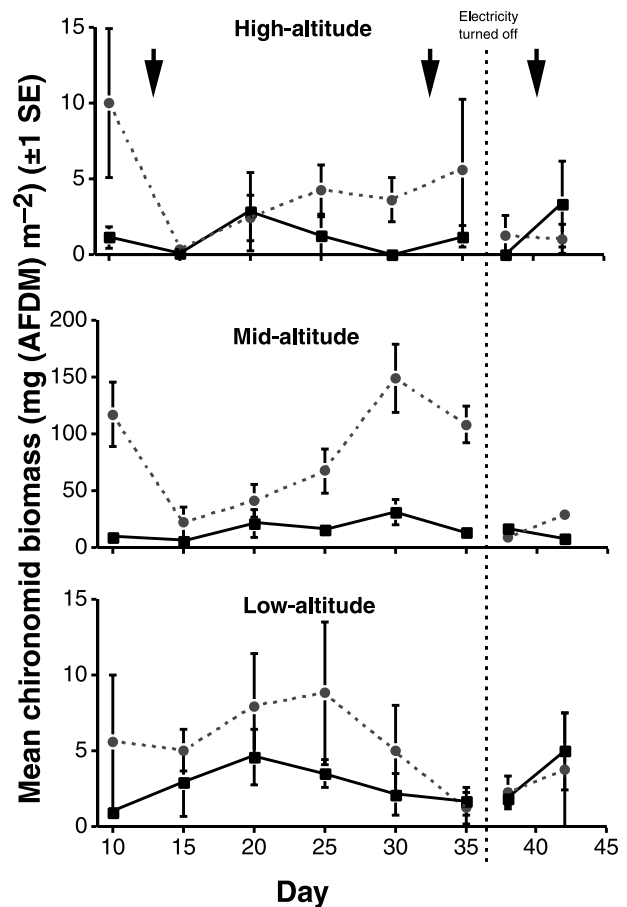

Fig. 5 A comparison of chironomid (Diptera: Chironomidae) biomass between treatments at each site (symbols described in Fig. 1).

Strong top-down effects of omnivorous shrimps at high- and mid-altitude sites

Results at both the high- and mid-altitude sites demonstrated that omnivorous freshwater shrimps can have a strong influence on the benthos. This was evident by significant treatment differences throughout the 35-day experiment as well as by the rapid disappearance of treatment differences when shrimps were allowed access to tiles (i.e. when electricity was turned off). We attribute treatment differences to shrimps rather than fishes because we observed high densities of shrimps feeding on the tiles while fishes were never observed on tiles during day or night. Electroshocking showed similar results; very high shrimp abundance and very low fish abundance. Fishes were mostly present in deeper areas near the centre of the channel and in deep pools.

Feeding and movement by *Atya* and *Xiphocaris* at the high-altitude site resulted in 'clean' tiles which accrued very little organic and inorganic matter. This supports previous studies in this stream and nearby tributaries that also found a strong negative effect of *Atya* and *Xiphocaris* on AFDM and inorganic cover (Pringle *et al.*, 1993, 1999; Pringle & Blake, 1994). The shrimp assemblage at the mid-altitude site, composed of *Macrobrachium* and *Xiphocaris* shrimps, also reduced the amount of organic and inorganic matter on tiles. In mid- and high-altitude reaches, shrimp effects on sediment and organic matter are similar to dominant consumers in other tropical streams such as the fish *Prochilodus mariae* in Venezuelan streams (Flecker, 1996).

The shrimp assemblage significantly reduced the biomass of chironomids at both the high- and mid-altitude sites. Chironomids are sessile and were probably consumed by shrimps directly or dislodged from tiles by shrimp feeding. In contrast to sessile chironomids, there were generally more mayflies in the presence of shrimps than in their absence. Mayflies are highly mobile and appear able to avoid predation by shrimps. Shrimps may facilitate mayflies by acting as ecosystem engineers (*sensu* Jones, Lawton & Shachak, 1994) by removing sediment, thus providing mayflies greater access to underlying algae (Pringle *et al.*, 1993). These results support earlier studies that observed similar effects of shrimps on mayflies and chironomids at nearby high-altitude sites (Pringle *et al.*, 1993; March *et al.*, 2001). This combination of a negative effect on chironomids with the positive effect on baetids probably resulted in the lack of shrimp effect on total insect biomass.

While previous studies in temperate streams have shown that omnivorous crayfishes can increase periphyton indirectly by reducing insect grazer abundance (Charlebois & Lamberti, 1996; Luttenton, Horgan, & Lodge 1998) we did not observe this effect. Shrimps had a strong negative effect on algal biomass (algal biovolume and chlorophyll *a*) at both the high- and mid-altitude sites. These results support previous studies conducted at high-altitude sites (Pringle & Blake, 1994; Pringle, 1996).

Grazing by shrimps at both the high- and mid-altitude sites removed filamentous algae (*Oedogonium* and *Rhizoclonium*) and resulted in a diatom-dominated algal assemblage (mostly *Gomphonema* spp.). The removal of upper-storey filamentous algae is a com-

mon effect of herbivory in streams and is because of their vulnerable position above the rest of the algal assemblage (see reviews in Feminella & Hawkins, 1995; Steinman, 1996). In the absence of grazers, filamentous forms are able to outcompete lower-storey diatoms and represent the majority of algal biomass. The natural distribution of filamentous algae at the high-altitude site supports our results. Filamentous algae are found in areas where shrimps do not graze (sections of vertical rock within 3 cm of the surface (Pringle, 1996) and corners of overhanging boulders in cascades [personal observation]).

Grazing snails and lack of shrimp effect at the low-altitude site

Our results suggest that the presence of snails in high abundance obscured potential shrimp effects at the low-altitude site. Snails may reduce resources available for shrimps, thus contributing to low shrimp abundances observed at this site.

Several lines of evidence support our hypothesis that snail grazing in both treatments at the low-altitude site overwhelmed shrimp effects. Higher densities of grazing snails were observed on tiles in both the control and shrimp exclusion treatments at the low-altitude site (mean = 2.7) compared with the mid- and high-altitude sites (mean = 0.03 and 0 snails tile^{-1}, respectively). While we did not directly quantify effects of freshwater snails on the benthic community, grazing snails in temperate streams have been shown to exert strong negative effects on standing stocks of organic matter and chlorophyll *a* (e.g. Steinman *et al.*, 1987; Rosemond *et al.*, 1993). Accordingly, standing stocks of inorganic and organic matter in both treatments at the low-altitude site were low and were similar to the grazed treatment (control) at the higher altitude sites. Furthermore, algal community composition in both treatments at the low-altitude site was typical of a grazed community and similar to the control treatment at the higher altitude sites. However, future studies manipulating both snails and shrimps at the low-elevation site are needed to fully understand the effects of snails.

While snails are probably responsible for the lack of shrimp effect at the low-altitude site, shrimp assemblage composition as well as water depth varied between low-altitude and higher altitude sites. The low-altitude shrimp assemblage contained primarily

Macrobrachium, thus differing from the other two sites. The only *Atya* and *Xiphocaris* individuals found at the low-altitude site were small juveniles that appeared to spend most of their time migrating upstream and little time feeding. However, this shift in shrimp assemblage composition probably did not contribute much to the lack of shrimp effect at the low-altitude site because *Macrobrachium* consume algae, insects and detritus and were observed to feed on tiles in a similar manner to *Xiphocaris*. Evidence supporting this contention is that *Macrobrachium* shrimps represented the majority of the biomass at the mid-altitude site where shrimps exerted strong effects. Water depth at base flow was shallowest at the low-altitude site. Differences in depth did not appear to be important factors contributing to the lack of shrimp effect at the low-altitude site. The flashy nature of discharge in the study stream resulted in dramatic changes in water depth at all three sites over the 35-day study period. However, despite these depth variations, inorganic matter, AFDM, and chlorophyll *a* remained relatively constant at the low-altitude site and at levels similar to those in controls at the mid- and high altitude sites, suggesting that the presence of grazing snails may be more important.

Importance of replicating the experiment along the altitude gradient

Most experimental studies examining the roles of species in benthic communities have been conducted at a limited spatial scale (but see Pringle *et al.*, 1999). While these studies have demonstrated that biota can have strong effects on many aspects of the benthic environment, we know very little about their effects beyond the context of a specific reach. By replicating our study at three sites along the altitude gradient we showed that results from previous studies at our high-altitude site were different than those obtained at lower altitude sites.

Understanding the role that shrimps play in determining community composition and how that role varies along an altitude gradient is especially important because shrimps inhabit many different reaches over their migratory life cycle. Recent anthropogenic disturbances such as damming and water withdrawal, as well as stream poisonings, have increased larval and adult shrimp mortality and resulted in removal of shrimps from entire reaches (Holmquist *et al.*, 1998;

Benstead *et al.*, 1999; C.M. Pringle, unpublished data). These anthropogenic disturbances may have dramatically different effects on the community, depending on location. For example, elimination of shrimps from a reach may not result in any significant changes in the benthic community at low-altitude sites. However, loss of shrimps from higher-altitude reaches will dramatically alter the entire community. Resource managers need to be aware of these issues when considering how and where to monitor the effects of anthropogenic disturbances on migratory biota.

Acknowledgments

References

Ahmad R., Scatena F.N. & Gupta A. (1993) Morphology and sedimentation in Caribbean montane streams: examples from Jamaica and Puerto Rico. *Sedimentary Geology*, **85**, 157–169.

Aiken K.A. (1998) Reproduction, diet, and population structure of the mountain mullet, *Agonostomus monticola*, in Jamaica, West Indies. *Environmental Biology of Fishes*, **53**, 347–352.

American Public Health Association (APHA) (1985) *Standard Methods for the Examination of Water and Wastewater*. 15th edn. APHA, Washington, D.C., USA.

Axler R.P. & Owen C.J. (1994) Measuring chlorophyll and phaeophyton: whom do you believe? *Lake and Reservoir Management*, **8**, 143–151.

Benke A.C., Huryn A.D., Smock L.A. & Wallace J.B. (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, **18**, 308–343.

Benstead J.P., March J.G. & Pringle C.M. (2000) Estuarine larval development and upstream postlarval migration of freshwater shrimps in two tropical rivers, Puerto Rico. *Biotropica*, **32**, 545–548.

Benstead J.P., March J.G., Pringle C.M. & Scatena F.N. (1999) Effects of a low-head dam and water abstraction on migratory tropical stream biota. *Ecological Applications*, **9**, 656–668.

Bhajan W.R., Canals M., Colon J.A., Block A.M. & Clements R.G. (1978) *A Limnological Survey of the Río Espíritu Santo Watershed, Puerto Rico (1976–77)*. Unpublished Report. Center for Energy and Environmental Research, Rio Piedras, Puerto Rico.

Buzby K.M. (1998) *The Effect of Disturbance on the Ecological Efficiency of a Small Tropical Stream*. PhD Dissertation. State University of New York, College of Environmental Science and Forestry, Syracuse, NY, 130 p.

Carpenter S.R., Kitchell J.F., Hodgson J.R., Cochran P.A., Elser J.J., Elser M.M., Lodge D.M., Kretchmer D., He X. & von Ende C.N. (1987) Regulation of lake primary productivity by food web structure. *Ecology*, **68**, 1863–1876.

Carr J.M., Hergenrader G.L. & Troelstrup N.H. (1986) A simple inexpensive method for cleaning diatoms. *Transactions of the American Microscopical Society*, **105**, 152–157.

Chace F.A. Jr & Hobbs H.H. Jr (1969) The freshwater and terrestrial crustaceans of the West Indies with special reference to Dominica. *U.S. National Museum Bulletin*, **292**, 1–258.

Charlebois P.M. & Lamberti G.A. (1996) Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society*, **15**, 551–563.

Covich A.P. (1988) Atyid shrimp in the headwaters of the Luquillo Mountains, Puerto Rico: filter feeding in natural and artificial streams. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **23**, 2108–2113.

Covich A.P. & McDowell W.H. (1996) The stream community. In: *The Food Web of a Tropical Rain Forest* (Eds D.P. Reagan & R.B. Waide), pp. 433–459. University of Chicago Press, Chicago, IL.

Crowl T.A., McDowell W.H., Covich A.P. & Johnson S.L. (2001) Freshwater shrimp effects on detrital processing and localized nutrient dynamics in a montane, tropical rain forest stream. *Ecology*, **82**, 775–783.

Feminella J.W. & Hawkins C.P. (1995) Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *Journal of the North American Benthological Society*, **14**, 465–509.

Fièvet E., Tito de Morais L. & Tito de Morais A. (1996) Quantitative sampling of freshwater shrimps: compar-

ison of two electrofishing procedures in a Caribbean stream. *Archiv für Hydrobiologie*, **138**, 273–287.

Flecker A.S. (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology*, **77**, 1845–1854.

Gruendling G.K. (1971) Ecology of the epipelic algal community in Marion Lake, British Columbia. *Journal of Phycology*, **7**, 239–249.

Holmquist J.G., Schmidt-Gengenbach J.M. & Yoshioka B.B. (1998) High dams and marine-freshwater linkages: effects on native and introduced fauna in the Caribbean. *Conservation Biology*, **12**, 621–630.

Hunte W. (1978) The distribution of freshwater shrimps (Atyidae and Palaemonidae) in Jamaica. *Zoological Journal of the Linnean Society*, **64**, 135–150.

Hunter M.D. & Price P. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724–732.

Jacoby J.M. (1985) Grazing effects on periphyton by Theodoxus fluviatilis (Gastropoda) in a lowland stream. *Journal of Freshwater Ecology*, **1**, 51–59.

Johnson S.L. & Covich A.P. (2000) The importance of night-time observations for determining habitat preferences of stream biota. *Regulated Rivers*, **16**, 91–99.

Johnson S.L., Covich A.P., Crowl T.A., Estrada-Pinto A., Bithorn J. & Wurtsbaugh W.A. (1998) Do seasonality and disturbance influence reproduction in freshwater atyid shrimp in headwater streams, Puerto Rico? *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **26**, 2076–2081.

Jones C.G., Lawton J.H. & Shachak M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Kitchell J.F. & Carpenter S.R. (1993) Synthesis and new directions. *The Trophic Cascade in Lakes* (Eds S.R. Carpenter & J.F. Kitchell), pp. 332–350. Cambridge University Press, Cambridge, U.K.

Luttenton M.R., Horgan M.J. & Lodge D.M. (1998) Effects of three Orconectes crayfishes on epilithic microalgae: a laboratory experiment. *Crustaceana*, **71**, 845–855.

March J.G. (2000) *The Role of Freshwater Shrimps: Patterns and Processes along a Tropical Island Stream Continuum, Puerto Rico.* PhD Dissertation. University of Georiga, Athens, GA, 207 p.

March J.G., Benstead J.P., Pringle C.M. & Ruebel M.R. (2001) Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 470–478.

March J.G., Benstead J.P., Pringle C.M. & Scatena F.N. (1998) Migratory drift of larval freshwater shrimps in

two tropical streams, Puerto Rico. *Freshwater Biology*, **40**, 261–273.

Marquet G. (1991) Freshwater crustaceans of French Polynesia: taxonomy, distribution, and biomass (Decapoda). *Crustaceana*, **61**, 125–140.

Menge B.A., Berlow E.L., Blanchette C.A., Navarrete S.A. & Yamada S.B. (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs*, **64**, 249–287.

Merritt R.W. & K.W.Cummins. (1984) *An Introduction to the Aquatic Insects of North America*, 2nd edn. Kendall/ Hunt, IA, U.S.A.

Paine R.T. (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93–120.

Polis G.A., Holt R.D., Menge B.A. & Winemiller K.O. (1996) Time, space, and life history: influences on food webs. In: *Food Webs* (Eds K.O. Winemiller & G.A. Polis), pp. 435–454. Chapman & Hall, New York, U.S.A.

Power M.E. (1990) Effects of fish in river food webs. *Science*, **250**, 811–814.

Power M.E. (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology*, **73**, 1675–1688.

Power M.E., Tilman D., Estes J.A., Menge B.A., Bond W.J., Mills L.S., Daily G., Castilla J.C., Lubchenco J. & Paine R.T. (1996) Challenges in the quest for keystones. *Bioscience*, **46**, 609–620.

Pringle C.M. (1996) Atyid shrimps influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. *Freshwater Biology*, **35**, 125–140.

Pringle C.M. & Blake G.A. (1994) Quantitative effects of atyid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: use of electricity for experimental exclusion. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1443–1450.

Pringle C.M., Blake G.A., Covich A.P., Buzby K.M. & Finley A. (1993) Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia*, **93**, 1–11.

Pringle C.M. & Hamazaki T. (1998) The role of omnivory in structuring a tropical stream: separating effects of diurnal fishes and nocturnal shrimps. *Ecology*, **79**, 269–280.

Pringle C.M., Hemphill N., McDowell W.H., Bednarek A. & March J.G. (1999) Linking species and ecosystems: effects of different macrobiotic assemblages on interstream differences in benthic organic matter. *Ecology*, **80**, 1860–1872.

Resh V.H. & De Szalay F.A. (1995) Streams and rivers of Oceania. In: *River and Stream Ecosystems* (Eds C.E. Cushing, K.W. Cummins & G.W. Minshall), pp. 717–737. Elsevier, Amsterdam.

Rosemond A.D., Mulholland P.J. & Elwood J.W. (1993) Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology*, **74**, 1264–1280.

SAS Institute Inc. (1994) *JMP Statistics and Graphics Guide.* SAS Inc., Cary, NC, U.S.A.

Steinman A.D. (1996) Effects of grazers on freshwater benthic algae. In: *Algal Ecology* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 341–374. Academic Press, San Diego, CA, U.S.A.

Steinman A.D., McIntire C.D., Gregory S.V., Lamberti G.A. & Ashkenas L.R. (1987) Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. *Journal of the North American Benthological Society*, **6**, 175–188.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Waide R.B. & Reagan D.R. (1996) The rain forest. In: *The Food Web of a Tropical Rain Forest* (Eds D.P. Reagan & R.B. Waide), pp. 2–16. University of Chicago Press, Chicago, IL.