Freshwater Biology (1996) **35,** 125–140

Atyid shrimps (Decapoda: Atyidae) influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico

CATHERINE M. PRINGLE
Institute of Ecology, University of Georgia, Athens, GA 30602, U.S.A.

SUMMARY

1. Atyid (Decapoda: Atyidae) shrimps influence the distribution of algal communities over different scales in tropical montane streams of Puerto Rico. Within pools of an atyid-dominated stream, atyid shrimps enhanced patchiness in algal communities along the depth gradient. Algal bands occurred in shallow pool margins where atyids did not forage ($<$ 3 cm below water surface), with significantly greater standing crop, taxon richness, and structural complexity than deeper areas. In deeper water, atyids reduced small-scale patchiness in algal community composition and maintained a low-growing understorey turf dominated by sessile diatoms (Bacillariophyta) and, sometimes, closely cropped, filamentous blue-greens (Cyanophyta).
2. Among pools of the atyid-dominated stream, atyids interacted with light to determine algal patchiness between stream margins and deeper areas. In sunny pools, algal standing crop was 140-fold greater in pool margins than in deeper areas where atyids foraged. In shaded pools, however, standing crop in pool margins was only 5-fold greater than in deeper areas. Effects of light on algal standing crop were greater outside atyid foraging areas than within, indicating that shrimp grazing overrides the positive effects of light.
3. In contrast to the atyid-dominated stream, algal communities in an atyid-poor stream were characterized by a high biomass of loosely attached epipelic diatoms and no depth zonation. Interstream rock and shrimp transplant experiments indicated that atyids significantly reduced algal standing crop and altered community composition on rocks from atyid-poor streams within 24 h. Results support the hypothesis that atyid shrimps play a major role in determining observed interstream differences in algal communities.

Introduction

Over the last decade considerable attention has focused on ecological heterogeneity and patch dynamics over different scales (e.g. Pickett & White, 1985; Goigel-Turner, 1987; Kolasa & Pickett, 1991; Naeem & Colwell, 1991). For example, increased patchiness has been found to enhance: (i) the persistence of predator and prey populations by providing prey with spatial refugia; and (ii) the co-existence of competitors by permitting spatial differentiation of resource use (e.g. Murdoch, 1977; Hastings, 1978; Hanski, 1981, 1983; Tilman, 1982).

In stream systems, scientists are faced with the problem of recognizing and explaining patterns in community organization in an extremely dynamic environment (Pringle *et al.*, 1988; Townsend, 1989). Studies have greatly enhanced our understanding of how fine-grained resource patchiness affects the behaviour of insect grazers (e.g. Kohler, 1984, 1985; Hart, 1981, 1985), and how grazers themselves (e.g. insects and snails) affect algal resource abundance, species composition and primary production (e.g. Gregory, 1983; Lamberti & Resh, 1983; Ward, Dahm &

Cummins, 1985; Steinman *et al.*, 1987; Hill & Harvey, 1990; Rosemond, Mulholland & Elwood, 1993; Rosemond, 1993).

Less is known regarding how stream fauna affect the spatial heterogeneity of algal vegetation over widely different spatial scales in lotic systems. Also, while the effects of grazing fish on algae in streams have been documented (e.g. Power & Matthews, 1983; Power, Matthews & Stewart, 1985; Power, 1987), we know very little about how other types of macrobiota affect the spatial heterogeneity of lotic algae.

This study examined the effects of shrimps on the spatial heterogeneity of algal communities in tropical montane streams of Puerto Rico. Omnivorous atyid (Decapoda: Atyidae) taxa (*Atya* spp. and *Xiphocaris elongata* Guerin-Meneville) dominate the faunal biomass of some high elevation streams in Puerto Rico's Luquillo Mountains (Lugo, 1985; Covich, 1988; Pringle *et al.*, 1993; Pringle & Blake, 1994), reaching densities of up to 25 ind. m^{-2}. In streams where predaceous fish are present, atyid shrimp are scarce (and often absent from stream pools; personal observation).

Individual shrimps are much bigger than insects and most gastropods. These highly mobile and relatively long-lived omnivores have the potential, through bioturbation and feeding, to affect lotic community structure on spatial and temporal scales quite different from smaller and less mobile invertebrates (Pringle *et al.*, 1993). Previous studies indicate that atyid shrimps act as key organizers of lotic community structure in streams where they are abundant, by reducing sediment cover, and affecting both primary producers and benthic insects (Pringle *et al.*, 1993; Pringle & Blake, 1994).

While previous cage enclosure/exclosure experiments found that the presence of shrimps enhanced the biovolume of understorey algae developing on 'bare' clay tiles (Pringle *et al.*, 1993), we know nothing about the potential impact of atyids on algal communities that have developed in streams where shrimps are absent or scarce. This is of interest because dams and water abstraction (for municipal water supplies) within catchments of the Luquillo experimental forest (Naumann, 1994) could alter the distributional patterns of predatory fish, which in turn can affect the distribution of their atyid prey (Garcia, 1994; Garcia & Hemphill, 1995). As a result, streams currently lacking atyid shrimps may be dominated by them in the future.

The objectives of this study were:

1 to examine variation in the abundance and composition of algae within and among pools of an atyid-dominated and atyid-poor stream;

2 to determine effects of atyid shrimps on algal communities (i.e. standing crop, community structure, physiognomy) that developed in the absence of atyids, through within- and inter-stream rock and shrimp transplant experiments.

Study site

This study was carried out in the Luquillo Experimental Forest located in the north-eastern corner of the island of Puerto Rico. Experiments were run in two second-order perennial streams, the Quebradas Toronja and Bisley-3.

The Toronja and Bisley are located in the separate adjacent catchments of the Rio Espiritu Santo and Mameyes, respectively. Both the Espiritu Santo and Mameyes have similar mean discharges of 1.702 $m^3 s^{-1}$ (24-year mean) and 1.660 $m^3 s^{-1}$ (13-year mean), respectively (U.S. Geological Survey, 1990).

Highland tributaries within the Espiritu Santo and Mameyes drainage basins have distinctively different macrobiotic assemblages. The Toronja (Espiritu Santo) is dominated by atyid shrimps, including three species of *Atya* and one species of *Xiphocaris*, though it has lesser numbers of the palaeomonid shrimp, *Macrobrachium* (four species) (Pringle *et al.*, 1993; Pringle & Blake, 1994). In addition to shrimps, the algivorous fish, *Sicydium plumieri* (Bloch), and the predaceous crab, *Epilobocera sinuatifrons* (A. Milne-Edwards), occur. In contrast, Bisley (Mameyes) is dominated by *Macrobrachium* spp., while atyids are very scarce and often absent from many pools (personal observation and E. Garcia, U.S. Forest Service, personal communication). Three additional fish taxa occur in Bisley: the predaceous mountain mullet, *Agonostomus monticola* (Bancroft), *Awaous tajasica* (Lichtenstein), and the eel, *Anguilla rostrata* (LeSueur) (L. Nieves, unpublished data).

A major difference between the two catchments is the presence of a low dam (1.2 m high and 20.7 m wide) and upstream impoundment (≈ 250 m^3) on the lower Espiritu Santo (< 50 m.a.s.l.), while the Rio Mameyes is the last free-flowing river within the Luquillo Experimental Forest.

Both the Toronja and Bisley drain the tabonuco vegetative zone, which is dominated by the tree *Dacryodes excelsa* Vahl. (Burseraceae). Both streams drain similar volcanoclastic geological formations of andesitic to basaltic sandstones, mudstone and breccia (Seiders, 1971), and have steep gradients and boulder-lined channels. Soils of the area are primarily acidic clays (Roberts, 1942). Stream bottom substrata are comprised of bedrock, large boulders and cobbles. While both streams are characterized by moderate hardness and a circumneutral pH, Bisley has generally higher nutrient concentrations ($NO_2 + NO_3$-N $248.3 \pm 210.5\ \mu g\ l^{-1}$; NH_4-N $16.0 \pm 22.9\ \mu g\ l^{-1}$; SRP $5.2 \pm 5.6\ \mu g\ l^{-1}$) than the Toronja ($NO_2 + NO_3$-N $115.4 \pm 69.0\ \mu g\ l^{-1}$; NH_4-N $18.3 \pm 22.6\ \mu g\ l^{-1}$; SRP $1.2 \pm 1.5\ \mu g\ l^{-1}$) ($n = 41$ and 58, respectively, for N and P; W. McDowell unpublished data).

When this study began in January 1991, terrestrial vegetation in both catchments still showed the effects of Hurricane Hugo, which passed through the Luquillo Forest on 18 September 1989. The hurricane caused extensive tree defoliation and crown loss and some trees were uprooted (Scatena & Larsen, 1991; Frangi & Lugo, 1991). Crown loss via trunk snapping was particularly pronounced in the upper Mameyes catchment (Walker, 1991), and resulted in minimal shading of the Bisley streambed. Tree damage in the Espiritu Santo catchment was not as pronounced. At the time of this study refoliation of riparian vegetation along the Toronja had progressed to the extent that only a few infrequent light gaps remained.

Materials and methods

Shrimp foraging behaviour

In both the Bisley and Toronja, three emergent rocks with steep rock faces were selected in each of three pools for observation of shrimp and fish foraging. A $900\ cm^2$ quadrat was established on each rock face that extended down from the stream surface to greater depths. Within each quadrat, shrimp type (taxon) and number were recorded in two zones along a depth gradient (< 3 cm depth and > 3 cm depth) for 10 min observation periods per quadrat during both the day ($n = 5$) and night ($n = 5$) on five different dates for each stream. Night observations were made with a flashlight.

Algal distribution patterns within and among pools

The taxonomic composition and biovolume of epilithic periphyton communities were determined by sampling rocks in both shallow pool margins, where atyid shrimp had not been observed to forage (< 3 cm below water surface), and within a standardized depth range within the area of atyid foraging activity ($\approx$ 8–15 cm below water surface). Algal communities were sampled in January 1991 during a period of stable base flow, following a 12-day dry period. In Bisley, where there was minimal post-hurricane closure of the riparian canopy, only sunny pools ($n = 3$) were sampled. In the Toronja, where refoliation of riparian vegetation was almost complete, pools in only two light gaps were available for sampling ($n = 2$), in addition to shaded pools ($n = 3$). The criterion for selection of sunny pools was a relatively open canopy ($\leqslant 60\%$) permitting direct insolation for $> 3\ h\ day^{-1}$. Shaded pools ($\geqslant 95\%$ canopy cover) received no direct sunlight other than sunflecks. Canopy cover was measured with a spherical densitometer.

Three emergent rocks were randomly selected per pool and algae were quantitatively sampled on rock faces in each of the two depth zones (< 3 cm and $\approx$ 8–15 cm below the water surface) using a suction sampling device modified from Loeb (1981). Samples were preserved with $\approx 2\%$ formalin for later algal identification and enumeration. More detailed methods for diatom and soft algae identification, enumeration and biovolume determination are given by Pringle *et al.* (1993).

Based on microscopic observations of intact algal communities, algae were further classified by growth forms into the following categories: upperstorey filamentous, upperstorey epiphytic, upperstorey loosely attached, middlestorey stalked and erect, understorey loosely attached, or understorey adnate. A split-plot ANOVA (whole plot sun/shade; within plot depth) on log-transformed data was used to examine effects of light and microhabitat location on algal biovolumes in the Toronja. A two-way ANOVA was also used to compare algal species richness. For Bisley, a one-way ANOVA on log-transformed data tested whether depth zone significantly affected algal biovolume and species richness. Species diversity was determined using Shannon's Information Measure (H') as modified by Hill (1973). Similarity of algal community composition among natural epilithic microhabitats was calculated with Stander's Similarity Index (SIMI; Stander, 1970; Johnson & Millie, 1982), using the relative abundance of each taxon based on biovolume. A Mann–Whitney *U*-test evaluated the effect of microhabitat location on algal diversity ($P < 0.05$) and whether diversity differed between Bisley and microhabitats above the area of atyid foraging in light gaps of the Toronja.

Rock and shrimp transplant experiments

Rock and shrimp transplant experiments were designed to assess the immediate effects of atyids on three different algal communities that developed in the absence of atyid foraging. By examining the short-term (i.e. 16–40 h) effects of atyids on algal communities in cage enclosures, the confounding effects of cage artefacts encountered in previous experiments were avoided [e.g. heavy sediment deposition through time (Pringle *et al.*, 1993)]. Three different experiments were conducted.

1 A *within-stream rock transplant experiment* was designed: (i) to evaluate the grazing response of atyid shrimps in an atyid-dominated stream (characterized by low algal standing crops within atyid foraging areas) to introduced rocks with high algal standing crops (dominated by upperstorey, loosely attached algae) from the same stream; and (ii) to relate the effects of shrimps on algae to observed patterns of algal flora within this stream. Rocks collected in shallow areas of the Rio Toronja (where atyids were not observed to forage) were transplanted into cage enclosures with atyids, cage exclosures without atyids, and outside areas within a pool of the Toronja that was characterized by high densities of atyids (20–35 m^2) and no fishes.

2 An *inter-stream rock transplant experiment* was designed: (i) to evaluate the grazing response of atyids, in an atyid-dominated stream, to introduced rocks with high algal standing crops (dominated by middlestorey stalked and erect algae) from a stream characterized by low densities of atyids; and (ii) to examine effects of atyids on these algal communities. This experiment was designed to test the hypothesis that atyid shrimps have the potential to reduce algal standing crop and alter community composition in streams currently lacking atyids. Rocks collected from a pool in the Rio Mameyes [characterized by very low numbers of atyids (< 1 m^2)] were transplanted into cage enclosures, exclosures, and outside areas of the Toronja study pool.

3 An *inter-stream shrimp transplant experiment* tested the hypothesis that the grazing pressure of atyids is low in a stream pool characterized by low numbers (< 1 m^2) of atyid shrimp (Bisley-3) relative to an atyid-dominated stream (Toronja). Atyids from the Toronja were transplanted into cage enclosures incubated in a pool within Bisley-3 and exposed to algae-covered rocks (dominated by an understorey of loosely attached, biraphid, epipelic diatoms) collected in shallow areas of that stream. Algae-covered control rocks were also placed in cage exclosures and outside treatments to examine the potential effects of natural densities of grazing fishes and shrimps within Bisley-3. Unlike experiments 1 and 2, where it was predicted that there would be significantly less algal standing crop in the outside and shrimp enclosure treatments relative to the exclosure treatment, in this experiment it was predicted that outside treatments would have high algal standing crops, similar to those found in the exclosure treatment.

In all three experiments, algae-covered rocks were exposed to three different treatments with five replicates per treatment: (i) shrimp enclosures (S); (ii) shrimp exclosures—no shrimp (NS); and (iii) outside (O) of cages exposed to natural biota. All experiments were terminated after algal mats on rocks were no longer visible to the unaided eye (between 16 and 40 h). Detailed observations of visits by fishes and shrimps to the outside treatments were made over a 1 h observation period at the beginning of each experiment.

In both experiments 1 and 2, eight rocks (3–6 cm diameter) were placed into individual cages that either enclosed ($n = 5$) or excluded ($n = 5$) shrimp. In addition, five clusters of eight rocks, placed on stream bedrock outside of cages (in current velocities between 3 and 5 cm s^{-1}), served as outside treatments exposed to natural biota (i.e. a total of 120 rocks). The inter-stream shrimp transplant experiment followed the same experimental design except that two larger rocks (12–14 cm diameter) were used in each treatment replicate (total = 30 rocks), since smaller rock sizes were not common in Bisley-3.

Each cage enclosure/exclosure consisted of a plastic basket (25 cm wide, 75 cm long, 24 cm deep) with 1 × 10 cm slot openings on all four sides which allowed current to pass through. Cages were modified after those described by Lamberti, Feminella & Resh

(1987). A styrofoam collar was placed around the top of each cage and cages were installed in a pool within the stream channel where they floated partially submerged (≈ 18 cm water depth). Cages were placed in areas of low current velocity (3–5 cm s^{-1}) in the upstream section of study pools and tethered to bankside vegetation. Shrimp enclosures in each experiment were stocked with two mature *Atya lanipes* Holthuis (8–10 cm long), the most abundant species of *Atya* in the Toronja (Pringle & Blake, 1994). Shrimp densities within cage enclosures were based on field observations of approximate distances between shrimps on the pool bottom and were within the range of densities estimated for *Atya* spp. within pools of the Toronja (10–15 m^{-2}). A 12-cm segment of opaque polyvinyl tubing (3-cm diameter) was placed in each cage to provide cover for shrimps. *Atya lanipes* were collected in the Rio Toronja 1–2 days before each experiment using unbaited, funnel-shaped minnow traps with enlarged access holes. In the inter-stream shrimp transplant experiment, animals were placed in a cooler with stream water and ice and transported by car to Bisley-3, where they were placed in cages.

Algae were quantitatively sampled on exposed rock faces (one rock randomly selected per replicate) using the syringe sampling device modified from Loeb (1981) and samples were analysed as described previously. The mean length of *Phormidium* was estimated for the inter-stream rock transplant experiment by measuring ten filaments in each replicate of each treatment.

In experiment 1, a one-way ANOVA on log-transformed data tested the effects of treatment on biovolume and richness. Multiple comparisons were made with a Tukey–Kramer HSD test. In experiments 2 and 3, a one-way ANOVA on log-transformed data tested the null hypothesis that there was no significant difference in the total biovolume of periphyton among treatments. If the hypothesis was rejected, multiple comparisons were made with Tukey's test. Richness was compared with a one-way ANOVA on untransformed data and diversity was compared with a Kruskal–Wallis test. The criterion for significance for all statistical tests was $P < 0.05$.

Results

Shrimp foraging behaviour

In the Toronja and Bisley-3, no fishes or shrimps (> 1 cm in length) were observed to forage on rock faces within shallow pool margins < 3 cm in depth (Table 1). In Bisley-3, which contains predaceous mountain mullet (*Agonostomus monticola*), very few atyids were observed, while in the Toronja, *Atya* spp. and *Xiphocaris elongata* were frequently observed (Table 1). The grazing scars of *Atya* were particularly apparent at depths greater than 3 cm in the Toronja. *Atya* individuals foraged both horizontally and vertically on the rock surface using their cheliped fans as brushes and leaving a sediment-free trail.

Algal distribution patterns in pools

In the Quebrada Toronja, depth zone and light had significant effects on total algal biovolume (Fig. 1a). Algal biovolume was significantly higher in light gaps than in shade and the effect of light on algal biovolume was greater in pool margins outside than within atyid foraging areas.

In the Toronja, a significant difference in algal biovolume was found between depth zones in both the sun and shade. The dramatic difference in algal biovolume between depth zones in the sun was due to the high biovolume of filamentous *Phormidium* spp., which comprised > 99% of algal biovolume in pool margins (Table 2). Within atyid foraging areas in sunny pools, the community was dominated by short filaments of *Phormidium* and understorey adnate forms (e.g. *Achnanthes lanceolata*, *Cocconeis placentula*; Table 2, Fig. 1b). In shaded pool margins, *Phormidium* comprised only 37% of algal biovolume abundance, whereas understorey adnate diatoms (e.g. *Achnanthes lanceolata*) comprised over half. Within atyid foraging areas in shaded pools, *Phormidium* was absent and *A. lanceolata* comprised over 86% of algal biovolume (Table 2, Fig. 1b). Species richness was significantly greater above than within atyid foraging areas for both sunny and shaded pools of the Toronja (Fig. 1c). Depth zone had no significant effect on algal diversity, although there was a significant effect of light.

In Bisley-3, no vertical zonation of algal biovolume or species composition occurred with depth (Fig. 2). High algal biovolumes along the depth gradient in Bisley-3 were within the same order of magnitude as algal biovolumes measured in ungrazed sunny pool margins of the Toronja. The community was dominated by understorey, loosely attached, motile diatom taxa (50–60%), e.g. *Surirella* spp., including *Surirella linearis*, *Nitzschia vermicularis*, *Gyrosigma acuminatum*

Table 1 Mean numbers (± 1 SE) of macrobiota observed in 30 × 30 cm quadrats established along depth gradients on rock faces in pools of the Toronja and Bisley–3. Observations were made in each quadrat for 10-min periods during the day and night and are recorded as means over all dates ($n = 5$ dates). XIPHO = *Xiphocaris elongata*; ATYA = *Atya* spp.; MACRO = *Macrobrachium* spp.; GOBI = Gobiidae (*Awaous tajasica* or *Sicydium plumieri*); MUG = Mugilidae (*Agonostomus monticola*)

		Shrimp			Fish	
	Depth (cm)	XIPHO	ATYA	MACRO	GOBI	MUG
Toronja						
Day	< 3	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	> 3	7.63 ± 5.36	5.23 ± 4.45	0.40 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Night	< 3	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	> 3	5.72 ± 6.35	7.20 ± 3.45	0.62 ± 0.50	1.00 ± 0.00	0.00 ± 0.00
Bisley						
Day	< 3	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	> 3	0.14 ± 0.22	0.20 ± 0.20	0.40 ± 0.20	0.51 ± 0.65	0.52 ± 0.63
Night	< 3	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	> 3	0.20 ± 0.20	0.30 ± 0.15	0.20 ± 0.15	0.00 ± 0.00	0.40 ± 0.20

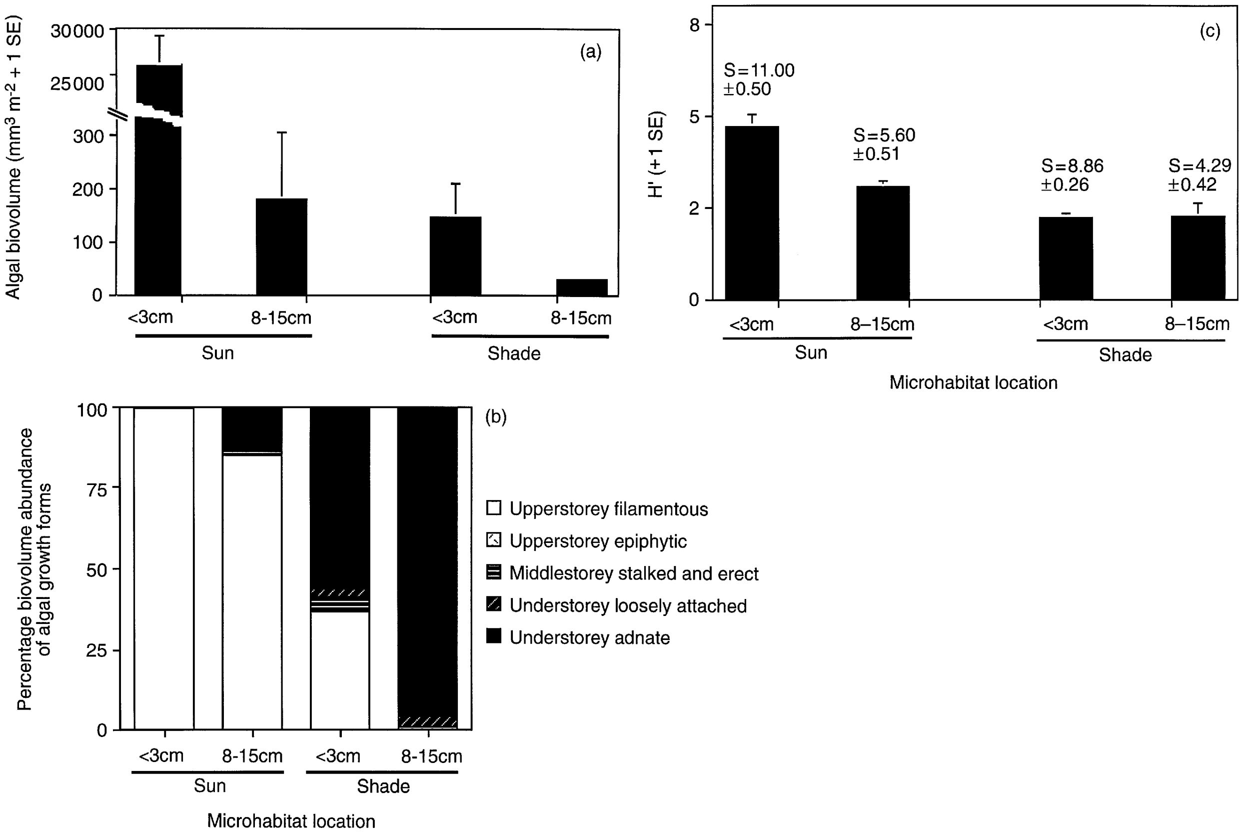

Fig. 1 Algal distribution patterns in sunny and shaded pools of the Toronja in microhabitats outside of (< 3 cm) and within (8–35 cm) the zone of atyid foraging activity. (a) Algal biovolume (x + 1 SE); (b) percentage biovolume abundance of algal growth forms (where specific algal taxa included in each growth form category are indicated in Table 2); and (c) algal diversity (H' + 1 SE), with richness (S + 1 SE) indicated above each bar.

and *Frustulia rhomboides*, middlestorey stalked and erect forms, e.g. *Gomphonema* spp. and *Synedra ulna*, and upperstorey filamentous taxa, e.g. *Phormidium* and an unidentified genus of Chlorophyta (Table 3, Fig. 2b).

Depth zone had no significant effect on algal diversity or taxon richness in Bisley-3. Algal diversity and richness were significantly greater in Bisley-3 than in atyid foraging areas of the Toronja, although they

Table 2 Algal biovolume (mm^3 ± 1 SE) in sunny and shaded areas of the Toronja in pool margins (<3 cm) and deeper areas (8–15 cm). Algal taxa are grouped according to growth form. *Category contains some *Lyngbya* spp. (<10%)

	Microhabitat location							
	Sun				Shade			
Algal growth form taxa	<3 cm		8–15 cm		<3 cm		8–15 cm	
Upperstorey filamentous								
Phormidium spp.*	26373.02	(3372.02)	27.06	(25.30)	53.77	(53.77)	0.00	(0.00)
Unidentified Chlorophyta	0.00	(0.00)	125.28	(125.28)	0.00	(0.00)	0.00	(0.00)
Tabellaria spp.	0.00	(0.00)	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)
Upperstorey epiphytic								
Achnanthes minutissima Kutz.	0.57	(0.09)	0.66	(0.12)	0.50	(0.10)	0.26	(0.09)
Middlestorey stalked and erect								
Gomphonema parvulum Kutz.	0.84	(0.41)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
G.olivaceum Lyng.	9.12	(1.21)	2.43	(1.09)	4.18	(1.08)	0.07	(0.05)
Synedra spp.	0.00	(0.00)	0.00	(0.00)	0.67	(0.67)	0.00	(0.00)
Opephora martyi Herib.	3.27	(0.97)	0.00	(0.00)	1.20	(0.43)	0.00	(0.00)
Understorey loosely attached								
Denticula spp.	0.02	(0.02)	0.00	(0.00)	0.05	(0.04)	0.00	(0.00)
Frustulia rhomboides Ehr.	13.96	(6.32)	0.23	(0.23)	2.00	(1.00)	0.93	(0.28)
Navicula contenta A. Grunow.	0.32	(0.11)	0.02	(0.02)	0.18	(0.08)	0.01	(0.00)
N.minima Grun.	0.02	(0.02)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
Nitzschia spp.	0.96	(0.31)	1.10	(0.07)	0.64	(0.24)	0.00	(0.00)
Surirella spp.	0.04	(0.04)	0.00	(0.00)	0.54	(0.27)	0.00	(0.00)
Understorey adnate								
Achnanthes exigua Grun.	0.27	(0.23)	0.06	(0.06)	0.85	(0.35)	0.05	(0.05)
A.lanceolata Breb. ex Kutz.	31.81	(7.39)	19.29	(5.62)	78.23	(14.99)	24.78	(3.99)
Cocconeis placentula Ehr.	2.53	(0.46)	4.41	(0.92)	2.64	(0.82)	2.73	(0.96)
Coccoid Chlorophyta	56.45	(56.45)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
Total biovolumes	26493.20	(3403.06)	179.53	(123.62)	145.45	(63.55)	28.83	(4.23)

were not significantly different from values for pool margins outside atyid foraging areas in the Toronja.

Rock and shrimp transplant experiments

During the 1–2 day duration of experiments 1, 2 and 3, there was no rain and stream discharge was relatively stable. As a result, sedimentation was not a problem as it had been in previous experiments conducted over 20–30-day periods (Pringle *et al.*, 1993).

In experiment 1 (within-stream rock transplant), a significant difference in total algal biovolume was found among treatments; significantly greater biovolumes occurred in shrimp exclosure (no shrimps, NS) relative to the shrimp enclosure (S) and the outside (O) treatments after 16 h (Fig. 3a). Rocks in outside treatments in the Toronja study pool immediately (within 5 min) attracted high densities (three–six individuals per rock) of atyid shrimps, primarily *Atya* spp. After 1 h, similar high shrimp densities were still apparent on rocks in outside treatments.

Shrimp enclosure and outside treatments had very different algal community compositions than shrimp exclosures (mean SIMI = 0.0153). Shrimp enclosures and outside treatments were dominated by understorey adnate (e.g. *Achnanthes lanceolata*, *Cocconeis placentula*) and middlestorey stalked and erect (*Cymbella affinis* and *C. tumida*) taxa (Fig. 3b). In the shrimp exclosure treatment, algal community biovolume was dominated by the loosely attached, upperstorey diatom *Terpsinoe musica*, and upperstorey filamentous blue-green algae (primarily *Phormidium* spp.). Similarity in algal species composition among replicates within a treatment was higher in the shrimp presence

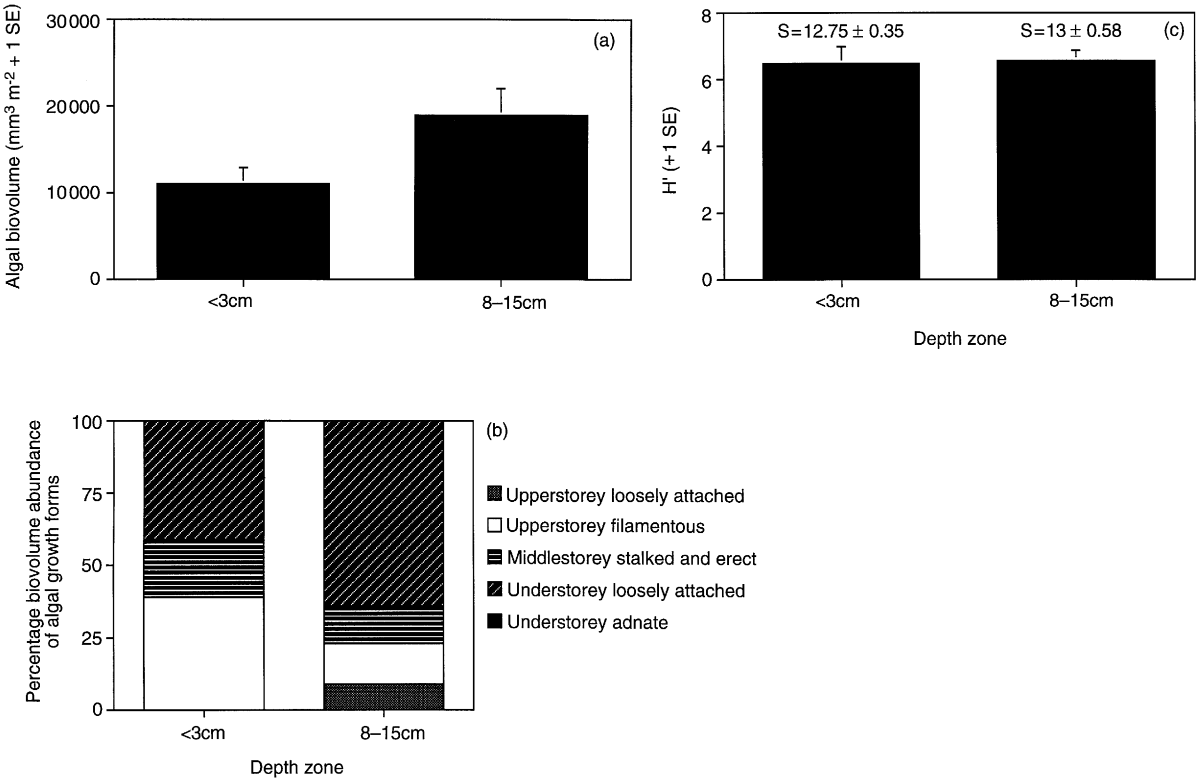

Fig. 2 Algal distribution patterns in shaded pools of Bisley-3 in depth zones outside (< 3 cm) and within (8–15 cm) the zone of atyid foraging activity. (a) Algal biovolume ($x + 1$ SE); (b) percentage biovolume abundance of algal growth forms (where specific algal taxa included in each growth form category are indicated in Table 3); and (c) algal diversity ($H' + 1$ SE), with richness ($S + 1$ SE) indicated above each bar.

treatment [mean SIMI (S) = 0.7195; mean SIMI (O) = 0.7644] than in the shrimp absence treatment [mean SIMI (NS) = 0.3527]. The mean SIMI value for algal species composition among replicates of the initial community (before exposure to shrimp) was 0.4675. While no significant difference in diversity was found between treatments, species richness was significantly greater in the shrimp exclosure (Table 4a).

In experiment 2 (inter-stream rock transplant: Mameyes→Toronja), total algal biovolume was significantly greater in the shrimp exclosure (NS) treatment than the shrimp enclosure (S) and outside (O) treatments after 16 and 40 h (Fig. 4a). As in experiment 1, rocks in the outside treatment immediately attracted high densities of atyids (three–six individuals per rock).

Similarity in algal species composition among replicates was high within the shrimp enclosure and outside treatments [mean SIMI (S) = 0.7232; mean SIMI (O) = 0.8660] and also among replicates in the shrimp exclosure treatment and the initial Mameyes pool community [mean SIMI (NS) = 0.6349; mean SIMI (initial community) = 0.6291].

All three treatments (S, NS and O) were dominated by upperstorey filamentous algae (primarily *Phormidium* spp.), and middlestorey stalked and erect algal forms (e.g. *Cymbella affinis*, *C. tumida* and *Gomphonema parvulum*; Fig. 4b). Significantly greater biovolumes of upperstorey filamentous algae (*Phormidium* and *Lyngbya* spp.), middlestorey stalked and erect forms (*Cymbella affinis*, *C. tumida*, *Gomphonema cleveii*, *G. gracile*, *G. parvulum* and *Synedra* spp.), and understorey loosely attached forms (*Navicula minuta*, *N. decussis* and *Denticula elegans*) were found in shrimp exclosures than shrimp enclosures and outside treatments. No significant difference in the biovolumes of understorey adnate taxa [e.g. *Achnanthes lanceolata*, *Cocconeis placentula* and an unidentified coccoid green (Chlorophyta) alga] were seen between shrimp presence and absence treatments. These understorey taxa represented a greater percentage

Table 3 Algal biovolume ($mm^3 \pm 1$ SE) in sunny areas of the Bisley-3 in pool margins (<3 cm) and deeper areas (8–15 cm). Algal taxa are grouped according to growth form. *Category contains some *Lyngbya* spp. (<10%)

	Depth zone			
Algal growth form taxa	<3 cm		8–15 cm	
Upperstorey loosely attached				
Terpsinoe musica Ehr.	0.0	(0.0)	1649.38	(1649.38)
Upperstorey filamentous				
Phormidium spp.*	2220.66	(1075.63)	1152.81	(331.37)
unidentified Chlorophyta	2042.17	(1319.62)	1454.90	(1135.88)
Characium spp.	5.61	(5.62)	27.07	(11.82)
Middlestorey stalked and erect				
Gomphonema parvulum Kutz.	25.96	(8.84)	16.12	(8.62)
G.olivaceum Lyng.	15.05	(7.25)	19.44	(14.56)
Synedra ulna (Nitz.) Ehr.	2140.59	(356.69)	2462.32	(395.24)
Opephora martyi Herib.	36.33	(17.60)	9.26	(2.65)
Understorey loosely attached				
Frustulia rhomboides Ehr.	673.72	(190.35)	776.01	(189.93)
Gyrosigma accuminatum (Kutz.) Rabh.	374.72	(88.95)	547.36	(97.85)
Navicula contenta A. Grunow.	0.0	(0.0)	0.28	(0.14)
Nitzschia palea (Kutz.) W.Sm.	76.06	(15.06)	181.95	(56.90)
N.vermicularis (Kutz.) Grunow	2509.81	(471.45)	3376.35	(912.48)
Nitzschia spp.	1.45	(1.45)	0.0	(0.0)
Surirella linearis Ehr.	466.05	(196.98)	4485.71	(2485.80)
Surirella spp.	354.63	(150.37)	2683.21	(1015.13)
Understorey adnate				
Achnanthes exigua Grun.	3.65	(3.65)	2.02	(2.02)
A.lanceolata Breb. ex Kutz.	14.64	(4.93)	16.14	(7.06)
Cocconeis placentula Ehr.	40.02	(9.02)	48.26	(7.71)
Total biovolumes	11001.13	(1900.21)	18908.58	(3100.40)

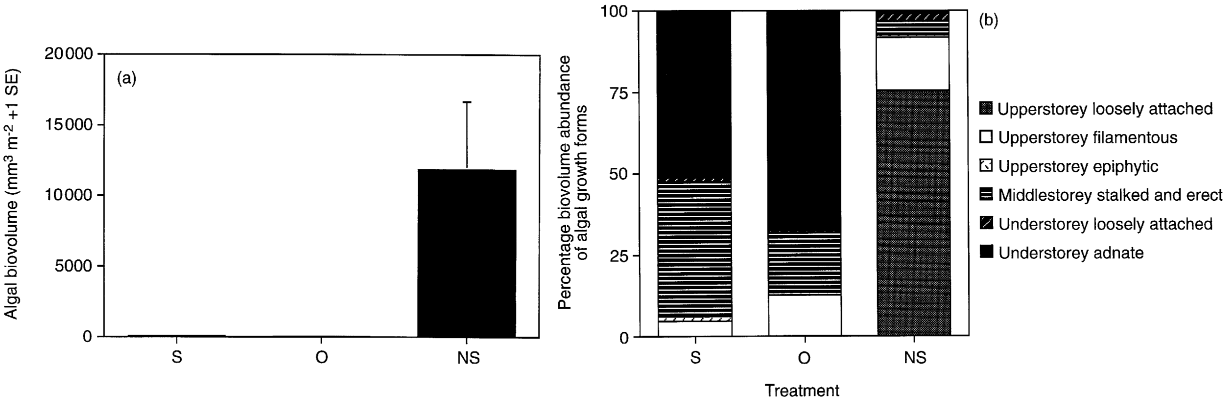

Fig. 3 Results of experiment 1 (within-stream rock transplant: Toronja). (a) Algal biovolume ($x + 1$ SE) and (b) percentage biovolume abundance of algal growth forms after 16 h of treatment exposure. S = shrimp enclosure, O = outside cage (exposure to natural biota in stream pools), and NS = shrimp exclosure (no shrimp).

Table 4 Mean algal species diversity (H' ± 1 SE) and richness (S ± 1 SE) in treatments of rock and shrimp transplant experiments. Experiment 1, within-stream rock transplant in Toronja; experiment 2, inter-stream rock transplant: Mameyes→Toronja; experiment 3, inter-stream shrimp transplant: Toronja→Bisley-3. S = shrimp enclosure, O = outside cage (exposure to natural biotic assemblages in stream pools), and NS = shrimp exclosure (no shrimp)

		Treatment (16 h)		
	Initial community	NS	S	O
Experiment 1				
H'				
0 h	5.41 ± 0.75			
16 h		6.20 ± 0.39	5.80 ± 1.01	2.93 ± 0.57
S				
0 h	15.20 ± 0.84			
16 h		15.80 ± 0.50	9.40 ± 8.90	8.60 ± 0.75
Experiment 2				
H'				
0 h	3.86 ± 0.71			
16 h		2.57 ± 0.68	3.89 ± 0.70	3.05 ± 0.70
40 h		4.46 ± 2.13	5.11 ± 0.38	3.36 ± 0.40
S				
0 h	10.80 ± 2.95			
16 h		9.80 ± 1.50	7.80 ± 1.10	9.00 ± 1.87
40 h		13.80 ± 0.96	14.50 ± 1.73	14.80 ± 1.92
Experiment 3				
H'				
0 h	9.05 ± 0.63			
24 h		8.55 ± 1.20	10.00 ± 0.90	9.52 ± 0.57
S				
0 h	18.20 ± 0.84			
24 h		17.35 ± 0.50	18.23 ± 1.50	17.50 ± 0.75

of the total biovolume in the atyid enclosure than in the exclosure treatment. Mean filament length of *Phormidium* was significantly greater in the atyid exclosure than enclosure and outside treatments at 16 and 40 h (Fig. 4c). No significant difference existed in algal diversity or richness between treatments in the inter-stream rock transplant experiment after either 16 or 40 h (Table 4b).

In experiment 3 (inter-stream shrimp transplant experiment: Toronja→Bisley) a significant difference in total algal biovolume occurred among treatments, with significantly greater biovolume in the shrimp exclosure and the outside treatments relative to the shrimp enclosure treatment after 24 h (Fig. 5a). In contrast to rock transplant experiments in the Toronja, rocks in outside treatments in the Bisley study pool attracted no shrimps within a 1 h observation period at the start of the experiment, although one individual fish, *Sicydium plumieri*, was seen grazing near one of the outside treatments. Macrobiota that were observed in the pool during the experiment include: (i) twelve atyids which confined their foraging activities to the top of a large algae and sediment-covered boulder (≈ 35 cm depth) located upstream of cages and control rocks; (ii) three predaceous mountain mullet (*Agonostomus monticola*) which confined their feeding activities to deeper areas of the pool and remained hidden most of the time; (iii) six gobids (*S. plumieri*) which appeared to forage freely at all depths throughout the pool; and (iv) two large *Macrobrachium* spp. which hid under rocks and were visible only occasionally.

Shrimp exclosures (NS) and outside (O) treatments were dominated by understorey loosely attached diatoms, whereas the shrimp enclosure (S) was dominated by upperstorey filamentous algae (Fig. 5b). Both NS and O treatments had significantly greater biovolumes of upperstorey filamentous algae (*Phormidium* and *Lyngbya* spp.), understorey loosely attached diatoms (*Frustulia rhomboides*, *Gyrosigma acuminatum*, *Navicula* spp., *Nitzschia* spp. and *Surirella* spp.) than did the S treatment. No significant difference existed in algal diversity or richness between treatments after 24 h (Table 4c).

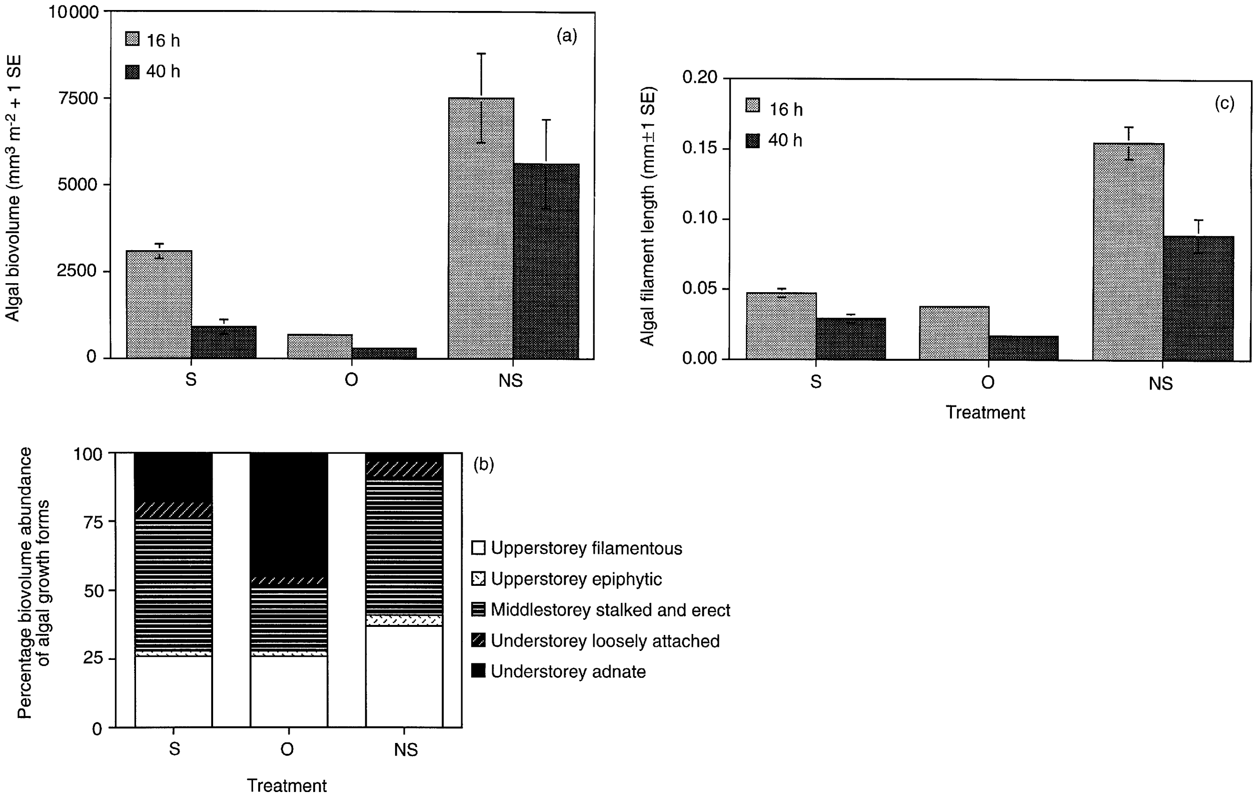

Fig. 4 Results of experiment 2 (inter-stream rock transplant: Mameyes→Toronja). (a) Algal biovolume (x + 1 SE) after 16 and 40 h of treatment exposure; (b) percentage biovolume abundance of algal growth forms after 40 h of treatment exposure; and (c) algal filament length (x + 1 SE) of *Phormidium* spp. after 16 and 40 h of treatment exposure. S = shrimp enclosure, O = outside cage (exposure to natural biota in stream pools), and NS = shrimp exclosure (no shrimp).

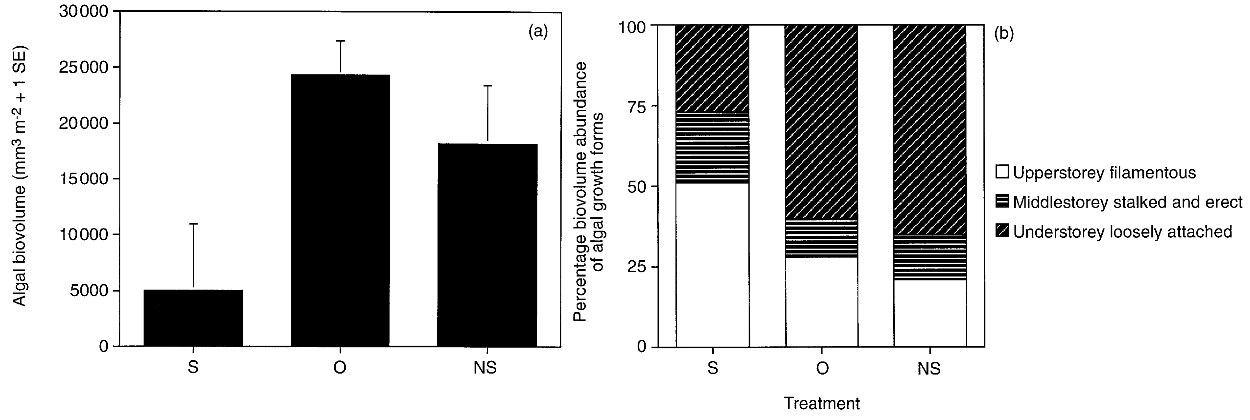

Fig. 5 Results of experiment 3 (inter-stream shrimp transplant: Toronja→Bisley). (a) Algal biovolume (x + 1 SE) and (b) percentage biovolume abundance of algal growth forms after 24 h of treatment exposure. S = shrimp enclosure, O = outside cage (exposure to natural biota in stream pools), and NS = shrimp exclosure (no shrimp).

Discussion

Spatial scale is a critical element in definitions of landscape heterogeneity and diversity: a landscape may appear to be heterogeneous at one scale yet homogeneous at another (Meentemeyer & Box, 1987). Atyid shrimps affected distributional patterns of algal communities differently over different scales. Within stream pools in an atyid-dominated stream, they enhanced patchiness in standing crop, taxon richness, and structural complexity between areas in which they foraged and shallow marginal areas (< 3 cm depth) that they avoided. Within deeper foraging areas, they reduced local, small-scale patchiness in algal community composition by simplifying the structural complexity of the community and maintaining a low-growing understorey algal turf. Among pools, the interaction of shrimp foraging and light determined algal patchiness between stream margins and deeper areas, with differences most pronounced in sunny pools. Inter-stream rock and shrimp transplant experiments, between atyid-dominated and atyid-poor streams, indicate that algal communities in streams lacking atyid shrimps would be strikingly different if atyid shrimp were present at high densities.

In atyid-dominated streams of Puerto Rico, shrimp appear to play a role analogous to that reported for some taxa of grazing fish in other tropical and temperate streams. Previous studies have found that herbivorous fish regulate algal distribution patterns within pools along depth gradients, and among pools (Power & Matthews, 1983; Power *et al.*, 1985; Power, 1987; Power, Dudley & Cooper, 1989). Results presented here suggest that atyid shrimp can affect algal distribution, standing crop, physiognomy, and community composition on not only small scales (within and among stream pools on a scale of micrometres to metres) but also on larger scales (i.e. among streams separated by many kilometres).

Reduction of algal standing crop and local, small-scale patchiness in algal communities within atyid foraging area

The foraging activities of atyid shrimp represent a relatively constant biotic disturbance within the benthic landscape that acts to decrease local, small-scale patchiness *within* atyid foraging areas. By constantly sweeping and picking rocks with their chelae, atyids reduce spatial variability in algal standing crop and species composition within their foraging areas that might result from physical factors, such as microscale differences in current velocity.

Atya lanipes uses its cheliped fans as filters where there is sufficient current, and as brushes in habitats with little current (e.g. within pools outside of the plunge zone and experimental cages). It scrapes substratum surfaces with its pereiopods and collects loosened periphyton, sediment and detritus with its cheliped fans which are expanded against the substratum and then closed rapidly. Sclerotized denticles on each fan also act to loosen periphyton from the substratum (e.g. Felgenhauer & Abele, 1983). In contrast, *X. elongata* feeds on particulate material, both on the substratum and within the water column, with its cheliped pincers. This taxon is a primitive member of the Atyidae and it is the only extant atyid that has chelipeds terminating in pincers (Bouvier, 1925).

These modes of feeding have the net result of mowing algal turfs, significantly reducing algal standing crop by reducing filament length of upperstorey algae, such as *Phormidium*, and removing associated upperstorey epiphytic taxa (*Achnanthes minutissima*) and large diatoms that are either upperstorey and loosely attached (e.g. *Terpsinoe musica*) or middlestorey stalked and erect growth forms (*Cymbella tumida*). Other studies have noted that herbivory by insects and snails in freshwater benthic habitats also removes overstorey algae resulting in dominance by sessile understorey forms (e.g. Pringle, 1979; Kesler, 1981; Jacoby, 1985; Steinman *et al.*, 1987; Hill & Harvey, 1990; Tuchman & Stevenson, 1991).

In experiment 1 (within-stream rock transplant), the similarity in algal community composition among replicates of shrimp presence treatments was consistently higher than among replicates in the shrimp absence treatment and the initial algal community, indicating that atyid foraging activities result in lower patchiness in community composition. Also, in experiment 2 (inter-stream rock transplant), similarity in algal community composition was comparably high among replicates within shrimp presence treatments. While it was also fairly high in the shrimp absence treatment, this probably reflected the lack of extreme patchiness within the initial algal community that was transplanted from atyid-free pools of the Mameyes catchment.

Atyids can also reduce fine-grained patchiness of algae within their foraging areas by altering the nature of the substratum through constant sediment removal (Pringle & Blake, 1994) and by removing sessile benthic insects (Pringle *et al.*, 1993). Previous studies (Pringle *et al.*, 1993) indicated that *Atya lanipes* and *Xiphocaris elongata* interfere with the establishment of retreat-building chironomid (Chironomidae: Diptera) larvae, through direct removal of larvae and/or indirectly through depression of sediment resources available to larvae for the construction of retreats. In these previous experiments, retreat-building chironomid larvae covered large portions of the surface of benthic substrata in shrimp exclusion treatments, creating fine-grained patchiness in substratum type (Pringle *et al.*, 1993). Studies in a north temperate stream indicated that the small-scale patchiness produced by retreat-building Chironomidae creates heterogeneity in not only substratum type, but also nutrient resources, and can be a major factor influencing algal community composition (Pringle, 1985; Pringle *et al.* 1988). Removal of chironomid retreats and their associated algal coatings by atyid shrimps thus acts further to reduce patchiness within foraging areas.

Maintenance of large-scale algal patchiness within and among stream pools: interactions between biotic and abiotic factors

As a consequence of not foraging within certain areas of the stream (i.e. shallow pool margins < 3 cm below water surface), atyid shrimp maintain large-scale algal patchiness in the system. In the Toronja, this patchiness takes the form of depth zonation in algal standing crop, community composition, structural complexity, and taxon richness (Fig. 1). While potentially higher nutrient availability and light in shallow water may result in depth gradients in algal standing crop, this explanation does not account for the lack of algal zonation with depth in Bisley-3 (Table 3, Fig. 2) where atyid shrimp are scarce, nor does it account for the sharp visual boundary in algal abundance in the Toronja that corresponds to the 3 cm depth zone.

Stream discharge fluctuations may also affect algal zonation patterns along depth gradients. The observation that patch intensity (i.e. the magnitude of the difference between visible algal standing crops in epilithic microhabitats above and within shrimp foraging areas on vertical rock faces) is diminished after periods of high flow (personal observation), may be due to algal scouring during high discharge, or possibly to expansion of the feeding range of atyid shrimps in conditions of elevated base flow.

My results support the hypothesis that greater patch intensity (between areas within and outside of atyid foraging) in light gaps of the Toronja, relative to shaded areas (Fig. 1a), is due to greater algal growth rates in light gaps. There appears to be an interaction between the effects of atyid foraging (depth zone) and of light (sun *v* shade). The effect of light on algal standing crop is greater outside the area of atyid foraging than within (Fig. 1a). This supports the contention that shrimps graze algae within their foraging areas and reduce its standing crop, overriding effects of light. Higher algal growth rates in light gaps may result in higher algal biovolumes in shallow pool margins between scouring events. Results suggest that higher algal growth rates in light gaps, in combination with shrimp foraging activity, enhance patch intensity between epilithic microhabitats, whereas in shaded areas, patch intensity is reduced because of light limitation of algal standing crop accrual. My findings also support the hypothesis that defoliation caused by Hurricane Hugo enhanced depth zonation of algae in the atyid-dominated Toronja by creating light gaps along the stream channel which allowed filamentous algae to reach high standing crops outside atyid foraging areas.

Algal bands in pool margins not only exhibit greater species richness, structural complexity and standing crop, but they are also a potential source of algal colonists. They provide important habitat for benthic insects that are scarce in areas of atyid foraging, including the grazing caddisfly *Cariboptila orophila* Flint (Glossosomatidae: Trichoptera), and retreat-building Chironomidae (Pringle *et al.*, 1993).

'Structural' taxa (e.g. Huston, 1994) that increase the structural complexity of the algal community include filamentous algae such as *Phormidium*. This taxon provides the spatial structure upon which other algal species depend. Mowing of upperstorey *Phormidium* by atyids resulted in reductions in epiphytic taxa such as *Achnanthes minutissima*, which concentrated in high numbers on tips of *Phormidium* filaments.

Bands of algae in shallow pool margins have been observed in both temperate and tropical streams (Power, 1987), and have been attributed to lack of grazing by fish, which feed in deeper waters to avoid predation by terrestrial predators. Predators can change the effects of grazers on algal communities, often releasing algae from grazing pressure and allowing it to attain high standing crops in areas that are dangerous for grazers (Power, 1987).

There seem to be few potential terrestrial predators of shrimps in the Luquillo Mountains, so it is not clear if *direct* predation is responsible for the observed zonation patterns of algae. Green-backed herons (*Buto-*

rides striatus (Linnaeus)) and belted kingfishers (*Ceryle alcyon* (Linnaeus)) occasionally migrate up from lowland areas and have been observed to feed on shrimps (E. Garcia, personal communication), but they are at most infrequent predators (B. Waide, personal communication). Apart from feral cats, which apparently feed on rats, birds and roadside garbage (E. Garcia, personal communication), large mammals do not occur in the forest. None the less, atyid shrimp exhibit behavioural responses that suggest they are vulnerable to terrestrial predators. In response to movement on the streambank, shrimps cease filter feeding and rapidly seek cover within rock crevices on the stream bottom. Shrimps seek cover most rapidly in response to sudden movements which cast shadows on the water surface (personal observation).

Potential effects of high atyid densities on the algal flora of atyid-poor streams

Experiments 2 and 3 (inter-stream rock and shrimp transplants) indicated that there is relatively high grazing pressure in the atyid-rich Toronja compared with the atyid-poor Bisley-3. Algae-covered rocks from the Mameyes drainage immediately attracted high densities of atyid shrimp (three–six individuals per rock) when placed in the Toronja. Algal standing crop was significantly reduced on these outside rocks relative to rocks in cages that excluded shrimp (Fig. 4). In Bisley-3, no shrimps were observed on rocks in outside treatments and there was no significant difference in algal standing crop between outside treatments and shrimp exclosures (Fig. 5).

My results support the hypothesis that algal communities in the Mameyes would be quite different if atyid shrimp were present in high densities. This is of interest given evidence that dams and water abstraction activities in catchments of the Luquillo Experimental Forest can potentially affect distribution patterns of atyid shrimp both directly and indirectly by affecting the distribution of fish predators (e.g. *Agonostomus monticola*; Garcia, 1994; Garcia & Hemphill, 1995). Increasing water diversions (for municipal water supplies) from reservoirs created by dams in the lower reaches of rivers draining the Luquillo Experimental Forest often result in significant stream dewatering (Naumann, 1994) below dams, which interferes with fish and shrimp migrations (Garcia, 1994; Garcia & Hemphill, 1995). On an average day, 53% of the water leaving the forest via stream flow is diverted before it reaches the ocean (Naumann, 1994). A recently proposed dam/water abstraction project on the Mameyes River, the last free-flowing stream within the Luquillo Experimental Forest, has thus been a major cause for concern within the U.S. Forest Service (Garcia, 1994).

In conclusion, atyid shrimps can influence the distribution of algal communities over widely different spatial scales in montane streams of Puerto Rico. High densities of atyid shrimps, like those occurring in the Toronja and other tributaries of the Espiritu Santo, can significantly affect the spatial heterogeneity of algal communities by reducing standing crop, simplifying structural complexity, and altering community composition. The evidence is that algal communities in streams lacking atyid shrimp would be dramatically different if atyid shrimp were present in high densities.

Acknowledgements

This work was supported by National Science Foundation grants BSR-87-17746 to C.M. Pringle and by BSR-91-07772 to C.M. Pringle and F.J. Triska. The study was designed to complement ongoing studies of the long-term Ecological Research Program in the Luquillo Experimental Forest funded by grant BSR-88–11902 from the National Science Foundation to the Centre for Energy and Environmental Research (University of Puerto Rico) and the Institute of Tropical Forestry (Southern Forest Experimental Station). Additional support was provided by Cornell University. Special thanks are extended to G. Blake for her assistance in the laboratory and with statistical analyses, and to J. March for creating figures. I am grateful to K. Buzby and G. Lewis for their help in the field in transferring rocks from the Rio Mameyes to the Toronja, and to J. Affolter, R. Beymer, G. Blake, K. Buzby, A. Covich, B. Harvey, N. Hemphill, J. March, A. Rosemond, F. Scatena, B. Waide, two anonymous reviewers, and A. Hildrew for their valuable comments on the manuscript. I also gratefully acknowledge the hospitality of the staff at the El Verde Field Station, particularly A. Estrada-Pinto and H. Lugo.

References

Bouvier E.L. (1925) Récherches sur la morphologie, les variations, la distribution géographique des crevettes de la famille des Atyides. *Encyclopedie Entomologique, Series A*, **4**, 1–370.

Covich A.P. (l988) Atyid shrimp in the headwaters of the Luquillo Mountains, Puerto Rico: filter feeding in natural and artificial streams. *Verhandlungen der Internationale Vereinigung fur Theoretische und Angewendte Limnologie*, **23**, 2108–2113.

Felgenhauer B.E. & Abele L.G. (1983) Ultrastructure and functional morphology of feeding and associated appendages in the tropical fresh-water shrimp *Atya innocous* (Herbst) with notes on its ecology. *Journal of Crustacean Biology*, **3**, 336–363.

Frangi J.L. & Lugo A.E. (1991) Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica*, **23**, 324–335.

Garcia E. (1994) *Proposed Mameyes dam/water withdrawal project: potential biological effects.* Internal report available from the U.S. Fish and Wildlife Service, Caribbean National Forest, Palmer, PR.

Garcia E.R. & Hemphill N. (1995) Do low elevation dams influence shrimp and fish species in Puerto Rican montane streams [Abstract]? *Bulletin of the North American Benthological Society*, **12**, 110.

Goigel-Turner M. (1987) *Landscape Heterogeneity and Disturbance*. Springer Verlag, New York.

Gregory S.V. (1983) Plant–herbivore interactions in stream systems. *Stream Ecology: Application and Testing of General Ecological Theory* (eds J.R. Barnes and G.W Minshall), pp. 157–189. Plenum Press, New York.

Hanski I. (1981) Coexistence of competitors in patchy environment with and without predation. *Oikos*, **37**, 306–312.

Hanski I. (1983) Coexistence of competitors in patchy environment. *Ecology*, **64**, 493–500.

Hart D.D. (1981) Foraging and resource patchiness: food experiments with a grazing stream insect. *Oikos*, **37**, 46–52.

Hart D.D. (1985) Causes and consequences of territoriality in a grazing stream insect. *Ecology*, **66**, 404–414.

Hastings A. (1978) Spatial heterogeneity and the stability of predator–prey systems: predator-mediated coexistence. *Theoretical Population Biology*, **14**, 380–395.

Hill M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427–432.

Hill W.R. & Harvey B. (1990) Periphyton responses to higher trophic levels and light in a shaded stream. *Canadian Journal of Fisheries and Aquatic Science*, **47**, 2307–2314.

Huston M.H. (1994) *The Ecological Regulation of Biodiversity.* Cambridge University Press, Cambridge.

Jacoby J.M. (1985) Grazing effects on periphyton by *Theodoxus fluviatilis* (Gastropoda) in a lowland stream. *Journal of Freshwater Ecology*, **3**, 265–274.

Johnson B.E. & Millie D.F. (l982) The estimation and applicability of confidence intervals for Stander's similarity index (SIMI) in algal assemblage comparisons. *Hydrobiologia*, **89**, 3–8.

Kesler D.H. (1981) Periphyton grazing by *Amnicola limosa*: an enclosure–exclosure experiment. *Journal of Freshwater Ecology*, **1**, 51–59.

Kohler S.L. (1984) Search mechanisms of a stream grazer in patchy environments: the role of food abundance. *Oecologia*, **62**, 209–218.

Kohler S.L. (1985) Identification of stream drift mechanisms: An experimental and observational approach. *Ecology*, **66**, 1749–1761.

Kolasa J. & Pickett S.T.A (eds) (1991) *Ecological Heterogeneity.* Springer-Verlag, New York.

Lamberti G.A. & Resh V.H. (1983) Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. *Ecology*, **64**, 1124–1135.

Lamberti G.A., Feminella J.W. & Resh V.H. (1987) Herbivory and intraspecific competition in a stream caddisfly population. *Oecologia*, **73**, 75–81.

Loeb S.L. (1981) An *in situ* method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. *Limnology and Oceanography*, **26**, 394–399.

Lugo A.E. (1985) *Water and the ecosystem of the Luquillo Experimental Forest*. Tech. Rep. 50–63, U.S.D.A. Forest Service, Southern Forest Experimental Station, New Orleans, LA 70118.

Meentemeyer V. & Box E.O. (1987) Scale effects in landscape studies. *Landscape Heterogeneity and Disturbance* (ed. M. Goigel-Turner), pp. 15–34. Springler-Verlag, New York,

Murdoch W.W. (1977) Stabilizing effects of spatial heterogeneity in predator–prey systems. *Theoretical Population Biology*, **11**, 252–273.

Naeem S. & Colwell R.K. (1991) Ecological consequences of heterogeneity of consumable resources. *Ecological Heterogeneity* (eds J. Kolasa and S.T.A. Pickett), pp. 224–255. Springer-Verlag, New York.

Naumann M. (1994) *A water use budget for the Caribbean National Forest of Puerto Rico*. Masters thesis, Universitat Trier, available through the International Institute of Tropical Forestry, Call Box 25000, Rio Piedras, Puerto Rico.

Pickett S.T.A. & White P.S (eds) (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.

Power M.E. (1987) Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. *Predation: Direct and Indirect Impacts on Aquatic Communities* (eds W.C. Kerfoot and A. Sih), pp. 333–351. University Press of New England, Hanover, NH.

Power M.E. & Matthews W.J. (1983) Algae-grazing minnows (*Campostoma anomalum*), piscivorous bass (*Micropterus* spp.) and the distribution of attached algae in a small prairie-margin stream. *Oecologia*, **60**, 328–332.

Power M.E., Matthews W.J. & Stewart A.J. (1985) Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. *Ecology*, **66**, 1448–1556.

Power M.E., Dudley T.L. & Cooper S.D. (1989) Grazing catfish, fishing birds, and attached algae in a Panamanian stream. *Environmental Biology of Fishes*, **26**, 285–294.

Pringle C.M. (1979) *The feeding behavior of Baetis with special reference to the effects of chironomid (Insecta: Diptera) tube-building activities on the diatom flora*. Masters thesis, University of Michigan, Ann Arbor, MI.

Pringle C.M (1985) Effects of chironomid (Insecta: Diptera) tube-building activities on stream diatom communities. *Journal of Phycology*, **21**, 185–194.

Pringle C.M., Naiman R.J., Bretschko G., Karr J.R., Oswood M.W., Webster J.R., Welcomme R.L. & Winterbourn M.J. (1988) Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society*, **7**, 503–524.

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 understorey algal biomass. *Oecologia*, **93**, 1–11.

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.

Roberts R.C. (1942) *Soil survey of Puerto Rico*. U.S. Department of Agriculture, Series 1936, no. 8. U.S. Government Printing Office, Washington DC.

Rosemond A.D. (1993) Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. *Oecologia*, **94**, 585–594.

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.

Scatena F.N. & Larsen M.C. (1991) Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, **23**, 317–323.

Seiders V.M. (1971) *Geologic map of the El Yunque quadrangle, Puerto Rico*. U.S. Geological Survey, Miscellaneous Geological Invest Map I-658. U.S. Department of the Interior, Washington, DC.

Stander J.M. (1970) *Diversity and similarity of benthic fauna of Oregon*. Masters thesis, Oregon State University, Corvallis, OR.

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.

Tilman D. (1982) *Resource competition and community structure*. Monographs in Population Biology no. 17. Princeton University Press, Princeton.

Townsend C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, **8**, 36–50.

Tuchman N.C. & Stevenson R.J. (1991) Effects of selective grazing by snails on benthic algal succession. *Journal of the North American Benthological Society*, **10**, 430–443.

U.S. Geological Survey (1990) *Water resources data Puerto Rico and the U.S. Virgin Islands, Water year 1990*. Prepared in cooperation with the Commonwealth of Puerto Rico and the Government of the U.S. Virgin Islands and other agencies.

Walker L.R. (1991) Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **23**, 379–385.

Ward A.K., Dahm C.N. & Cummins K.W. (1985) *Nostoc* (Cyanophyta) productivity in Oregon stream ecosystems: invertebrate influences and differences between morphological types. *Journal of Phycology*, **21**, 223–227.

(*Manuscript accepted 27 September 1995*)