

Quantitative Effects of Atyid Shrimp (Decapoda: Atyidae) on the Depositional Environment in a Tropical Stream: Use of Electricity for Experimental Exclusion

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Effects of biotic (shrimp) and abiotic (discharge) factors on the depositional environment were quantified in a montane stream in Puerto Rico. Electricity was used experimentally to exclude large (approximately >1 cm in length) biota without artificially increasing sedimentation as in cage enclosure/exclosure experiments in stream systems. Shrimp (>1 cm in length) were excluded from rock substrata by semicircular fences hooked up to battery-powered fence chargers which emitted continuous pulses of electricity. Unelectrified control substrata had natural high densities of atyid shrimp. Significantly greater masses of total sediment, fine and large organic particles, and algal biovolume occurred in shrimp exclusion treatments relative to controls. Shrimp exclusion treatments experienced slow and steady accumulation of sediments under base flow conditions and a large stepwise increase in sediment weight following a storm. No measurable sediment accrued in the presence of natural densities of shrimp under base flow conditions. Shrimp rapidly removed sediments that accrued during the storm ($440\text{--}620\text{ g}\cdot\text{m}^{-2}$ dry mass⁻¹), decreasing sediment mass in control treatments to near prestorm levels ($5\text{--}13\text{ g}\cdot\text{m}^{-2}$ dry mass⁻¹) within 30 h. Atyid shrimp can significantly affect the accumulation of organic and inorganic materials on rock substrata in stream pools between high-discharge events.

On a mesuré les effets de facteurs biotiques (crevette) et abiotiques (débit) sur les conditions de sédimentation d'un cours d'eau de montagne à Puerto Rico. On a utilisé, à titre expérimental, l'électricité pour tenir éloignés les gros organismes (>1 cm de longueur environ) sans accroître artificiellement la sédimentation comme on l'observe lors d'expériences avec confinement ou exclusion avec des cages dans les cours d'eau. Les crevettes (>1 cm de longueur) ont été tenues éloignées des substrats rocheux au moyen de clôtures semi-circulaires branchées à un régulateur alimenté par des batteries qui émet continuellement des impulsions électriques. Les substrats témoins, non électrifiés, étaient occupés par des crevettes atyidées en forte concentration naturelle. En mars, il y a eu beaucoup plus de sédiments totaux, de particules organiques fines et grosses et d'algues dans les secteurs d'où les crevettes étaient chassées que dans les secteurs témoins. Dans les secteurs d'exclusion de la crevette, il y a eu une lente et constante accumulation de sédiments dans des conditions d'écoulement de base et une hausse marquée et subite après une tempête. Il n'y a pas eu d'accumulation mesurable de sédiments là où il y avait des crevettes en densité naturelle et dans des conditions d'écoulement de base. Les crevettes ont rapidement enlevé les sédiments qui se sont accumulés durant la tempête ($440\text{--}620\text{ g}\cdot\text{m}^{-2}$ de masse sèche⁻¹), et ont ramené la masse des sédiments dans les parcelles témoins presque au niveau d'avant la tempête ($5\text{--}13\text{ g}\cdot\text{m}^{-2}$ de masse sèche⁻¹) en 30 h. Les atyidées peuvent avoir un effet considérable sur l'accumulation des matériaux organiques et inorganiques sur des substrats rocheux dans les trous d'eau entre des épisodes de fort débit.

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Effects of biological activity on rates of sediment transport, deposition, and accrual have long been recognized as an important phenomenon in soft bottom marine (Rhoads and Young 1970, 1971; Cullen 1973) and lentic (Tessenow 1964; Davis 1974; Krezoski et al. 1978; Nalepa et al. 1980) environments. This process has been termed "bioturbation" (Rhoads 1974; Brenchley 1981).

In lotic systems, it has generally been considered that sediment accrual and distribution patterns are controlled by the interplay of physical forces such as current velocity and the topography of the benthic landscape (e.g., Hynes 1972; Gordon et al. 1992), and investigations have historically

emphasized physical processes (Nielsen 1950; Einsele 1960; Schmitz 1961). Although little is known regarding the importance of bioturbation in streams, some studies have shown that biota can be important in both sediment removal and stabilization. Significant reductions in sediment cover have been observed as a result of fish feeding/foraging (Power 1990; Flecker 1992; W.S. Matthews and M.S. Stock, unpublished data) and spawning (Hildebrand 1971) activities. Retreat-building activities of benthic insects such as larval Chironomidae have been observed to both stabilize and increase sediment cover on benthic substrata (e.g., Nilsen and Larimore 1973; Wiley 1976; Pringle 1985; Pringle et al.

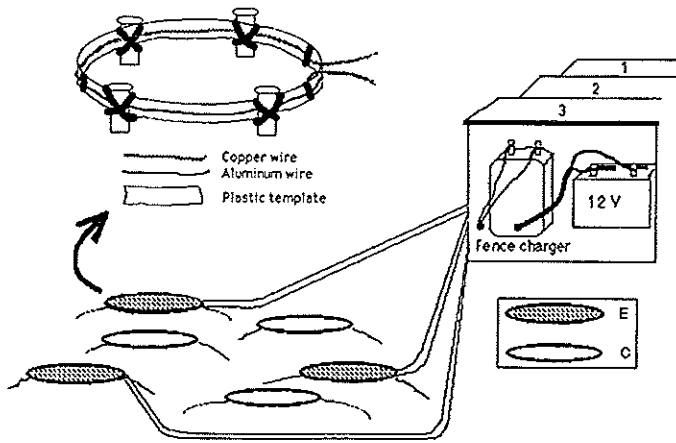


FIG. 1. Experimental setup illustrating placement of electrified (E) and control (C) hoops. Cutaway of plastic tub shows battery (12 V) and electric fence charger. Inset illustrates construction of electric hoop, where copper wire semicircles are charged, and aluminum wire provides support for circular plastic hoop (32 cm in diameter). This schematic diagram is not drawn to scale.

1988), and some reference has been made to effects of macrophytes in temporarily stabilizing the bedload in streams (Gessner 1950; Minckley 1963; Kopecky 1965).

Difficulties in quantitatively assessing effects of aquatic biota on sedimentation processes are numerous, particularly in running water systems because of artifacts introduced by experimental devices designed to exclude or enclose biota (see review in Cooper et al. 1990). This study is an outgrowth of previous studies in Puerto Rico (Pringle et al. 1993) that utilized cages to either exclude or enclose freshwater atyid shrimp which are the dominant faunal component in many tropical streams (Payne 1986). In these previous studies, enclosures were artificially stocked with atyid shrimp. While atyid shrimp clearly reduced sediment accrual on benthic substrata through their foraging activities (direct and indirect bioerosion and direct ingestion), both enclosures and exclosures experienced unnaturally high sedimentation (Pringle et al. 1993). We were therefore unable to quantify effects of natural densities of atyid shrimp on sediment cover or effects of discharge fluctuations on sediment accrual in the natural stream environment.

In the present study, we use electricity as a means of excluding shrimp to quantify the effect of natural densities of atyid shrimp on sedimentation in the absence of cage artifacts. An extensive literature review of aquatic, aquaculture, and fisheries databases has indicated that prior to this study, electricity has not been used as a mechanism to experimentally manipulate the presence and absence of organisms. Electricity has been used in aquatic management applications since the late 1800s (e.g., to exclude fish from water intake pipes and/or in attempts to prevent sea lamprey (*Petromyzon marinus*) from moving upstream). Electrofishing has been used widely for sampling fish, lamprey (Vibert 1967; Backiel and Welcome 1980; Reynolds 1983), and, more recently, freshwater shrimp in tropical streams (Penczak and Rodriguez 1990). In addition, fixed electrode devices, similar to those used in electrofishing, have been used to assess habitat use by stream fishes by collecting them from discrete habitats (e.g., in conditions of similar water velocity, depth, and bottom materials; Larimore and Garrels 1985; Weddle and Kessler 1993).

In this study, we tested the hypothesis that shrimp exclosures created by electricity on the natural stream bottom would experience significantly higher sedimentation than areas of the stream bottom accessible to natural densities of shrimp. Our objectives were to (1) quantify effects of natural shrimp densities on the weight accrual of organic and inorganic materials in the natural stream pool environment and (2) determine how a high-discharge event affects sediment cover in the presence and absence of natural densities of atyid shrimp.

Study Site and Methods

Research was carried out in the Quebrada Toronja, a first-order montane stream draining the Luquillo Experimental Forest of northeastern Puerto Rico (18°18'N, 65°47'W) that has a fauna dominated by atyid shrimp (up to 20 individuals·m⁻²; Pringle et al. 1993). The stream bottom of the Quebrada Toronja is characterized by large boulders, cobble, and finer sediments and silt between boulders. The Toronja (approximately 280 m above sea level) is a tributary of the Rio Sonodora within the Rio Espiritu Santo watershed.

Stream biota is largely dominated by two genera of shrimp, *Atya* (approximately three species) and *Xiphocaris* (one species), with lesser numbers of the genus *Macrobrachium* (four species). *Atya lanipes* and *Xiphocaris elongata* are the dominant taxa in pools of the Toronja and adjacent streams in the Espiritu Santo watershed, with populations reaching up to 25 individuals·m⁻² (Covich 1988). There are low numbers of benthic insects, low abundances of one species of predatory crab (*Epilobocera sinuatifrons*), and very low numbers of the algivorous fish *Sicydium plumieri* in the Toronja. For a more detailed description of watersheds of the Luquillo Forest and the study stream, see Lugo (1985) and Pringle et al. (1993), respectively.

Electric exclosure devices were constructed to exclude large (approximately >1 cm) invertebrates (e.g., shrimp) from foraging on rock substrata in a shaded pool (approximately 3.5 m length × 2.3 m width) of the Quebrada Toronja. The experiment was run from 5 to 14 September 1992, and treatments were designed to either exclude or allow access to shrimp and other relatively large organisms such as crabs and fish. These organisms were excluded from circular and relatively horizontal areas of rock on the stream bottom (approximately 32 cm in diameter) via an electric pulse. The pulse was created by an electric fence charger (Parmak® model STD-12 and Agway® model A-40-A (advertised to charge up to 15 miles of fence; approximately \$50 each)) powered by a 12-V battery (Fig. 1). The drawdown on the 12-V battery was less than 20% at the end of 1 wk. Fence chargers discharged continuously approximately 54–55 times per minute. The duration of the electric pulse was 2 ns.

Two pieces of insulated 12-gauge copper wire (between 4 and 5 m long) were attached to the two fence charger posts. The final 50 cm of each piece of wire was stripped and taped to the inside of a circular plastic hoop or template (32 cm in diameter, 2.5 cm high). Each of the two wires formed a semicircle, with the two wires from one fence charger opposite each other on the same hoop. To confer rigidity to the plastic hoop and copper wire, a stiff aluminum wire was attached to the outside of the template with electrical tape, and four supporting legs were constructed from 20-mL plastic scintillation vials weighted with

small stones. The legs were equally spaced around the wire to hold the hoop approximately 3 cm off the rock surface (see inset, Fig. 1). To keep the template from moving from its placement on the rocks, three or four lead fishing weights (100 g) were equally spaced around the circular template and tied to the aluminum wire with 30-lb. test fishing line.

Three replicates were installed for each of two treatments: electrified shrimp exclusion (E) and an unelectrified control (C). Each of three electric fence chargers was connected to a 12-V battery. Each fence charger and its associated battery were housed in a watertight tub that was placed on a large flat boulder at the upstream end of the pool, approximately 1 m above the stream water level. Small holes were drilled in the sides of tubs to allow passage of copper wires to electrified hoops in the stream below (Fig. 1). Control hoops were constructed in the same manner as electrified hoops; however, they lacked copper wire, were not hooked up to fence chargers and batteries, and were tethered to streamside vegetation with fishing line to prevent loss in the event of high stream discharge.

To characterize the current velocity affecting experimental treatments, velocities were measured with a Marsh McBirney® current meter at three locations inside the perimeter of each of the six hoops at the height of the wire hoop. Current velocity measurements were also taken in eight locations outside and adjacent to treatment hoops. The mean of the three measurements for each hoop was treated as the value for that hoop and was used in a nonparametric test of the null hypothesis that hoops have no effect on current velocity. Conductivity was measured at the study site with a meter.

Experimental treatments and control areas were sampled for sediments on 0, 1, 2, 4, 5, and 8 d. Normal safety precautions were followed when using electricity in water (e.g., Reynolds 1983), such as those used for electrofishing (e.g., rubber gloves used when current is on). Sediments were sampled from each replicate rock using a suction sampler (1.9 cm in diameter) modified from Loeb (1981). One sediment sample for each treatment replicate was placed into a Whirlpak® bag on days 1–4. On days 5 and 8, three replicate samples were pooled and taken to the laboratory for filtration. Samples were filtered onto glass fiber filters, placed in foil envelopes, and dried for 24 h at 50°C. Samples were then weighed, ashed at 500°C for 1 h, and reweighed to determine the sediment organic component or ash-free dry mass (American Public Health Association 1985).

Total dry mass of sediments and both inorganic and fine particulate organic components of sediments were compared between treatments over all observation dates using a repeated measures ANOVA. Data were $\ln(x + 1)$ transformed because of heteroscedasticity. The organic proportion of silt was compared using nonparametric statistics because the proportion data were also heteroscedastic and transformations were not sufficient to remedy the problem. Kruskal–Wallis, a one-way analysis by ranks test, was used to test the effect of time across treatments and the effect of day on each separate treatment. Mann–Whitney *U* was used to test the effect of treatment across time.

Gauge height (centimetres) was recorded on all sampling dates. Suspended sediments were also determined on each sampling date by filtering three 500-mL water samples collected from the study pool.

Algal periphyton was sampled on each observation date

using a smaller diameter (1.3 cm) suction sampler. One sample per each treatment replicate was preserved in a scintillation vial with 2% Formalin and transported to the laboratory. Algal samples collected on day 8 were analyzed for total biovolume and taxon composition. To determine the number of algal cells per square metre, each replicate sample was brought to a known volume, a 0.1-mL aliquot was pipetted into a Palmer cell and scanned at 400× until 500 “live” cells containing chloroplasts were identified, and the number of fields of view scanned to count 500 cells was recorded. Pennate diatoms that could not be identified to species at 400× were identified as naviculoids. To determine relative abundances of these pennate species, permanent mounts were made with Hyrax® from a cleaned (Carr et al. 1986) aliquot of each replicate sample and were scanned at 1000× until the same number of cells recorded as naviculoids in the Palmer Cell count were identified. The first 10 individuals of each taxon seen in each treatment were measured for length, width, and depth. The average of these measurements was used in an equation that best described the geometric shape of the cell to determine biovolumes. Total algal biovolume, diversity (Shannon’s information index as modified by Hill (1973)), and species richness were compared between the E and C treatments on day 8 using ANOVA.

Since shrimp rapidly seek cover in response to sudden movements on the stream bank and/or moving shadows cast on the water surface, we recorded numbers of individual shrimp (identified to genus) within each treatment replicate before sediment and algae were collected on each sampling date. After carefully approaching the stream, we made observations at distances of approximately 1.5 m from the stream bank in ≤ 1 min, so we would not disrupt natural shrimp foraging activities. To assess the behavioral response of benthic insects to the electric field, eight mayfly (*Cloeodes maculipes*) nymphs were removed from leaf litter collected in a riffle downstream of the study pool, introduced into the water column just upstream of an electrified hoop, and observed for approximately 8 min.

To confirm that fence chargers worked consistently, voltage measurements were taken in the center of each electric hoop on all sampling dates. The two probes of a voltmeter were taped at the end of a 2-m-long stick so that they were approximately 4 cm apart. The probes were then placed in the center of an electric hoop, the AC voltage was observed over 10 successive meter readings, and the highest reading was recorded. Measurements of AC voltage made within and outside the E hoops throughout the experiment ranged from 0.003 to 0.050 $V \cdot cm^{-1}$ and indicated that fence chargers were electrifying treatment hoops consistently throughout the experiment. Voltmeter readings indicated that the measurable electric field extended up to 20 cm from the outside perimeter of electrified hoops. These readings do not represent actual voltage due to the short duration of the electric pulse discharged by the fence charger and because our voltmeter did not measure instantaneous voltage but integrated voltage over a time interval. The peak circuit voltage was approximately 13 000 V and we estimate that discharge of the fence charger within the stream was approximately 6500–7000 V.

After final algae and sediment samples were collected on day 8, all large (approximately >1 cm diameter) particulate organic material (e.g., leaves and leaf parts) within each experimental hoop was placed in Whirlpak® bags. Leaf mate-

TABLE 1. Mean numbers of shrimp (± 1 SD) of *Atya* spp. (*Atya*), *X. elongata* (*Xipho*), and *Macrobrachium* spp. (*Macro*) within each experimental treatment ($n = 12$; averaged across four sampling dates and three replicates per treatment).

| Treatment | <i>Atya</i> | <i>Xipho</i> | <i>Macro</i> |
|--------------|---------------|---------------|---------------|
| Control (C) | 2.7 ± 1.5 | 2.0 ± 1.2 | 0.2 ± 0.4 |
| Electric (E) | 0.0 | 0.0 | 0.0 |

rial was rinsed with distilled water, washings were scanned with a dissecting scope, insects were enumerated, and dry weight of particulate organic material was determined.

A short experiment was conducted to ensure that observed differences in depositional patterns between E and C treatments within the Toronja were not a result of the charging of clay and sediment particles by electrified hoops. Two plastic wading pools (1.5 m in diameter) were filled with stream water (30 cm deep). One pool contained a control hoop and the second contained an electrified hoop. Sediments and detritus, collected from the study pool within the Quebrada Toronja, were added to each pool in equal amounts and mixed so that sediments were suspended within the water column. After approximately 24 h, the distribution of sediments within each pool was noted with respect to C and E hoops.

Results

On all sampling dates, we observed that shrimp attempting to enter electrified hoops reacted strongly to the electric pulse beginning at about 5–7 cm from the outside perimeter of the hoop. Individuals of *X. elongata*, which commonly swim in mid- to upper areas of the water column, occasionally strayed into this area and reacted to the electric pulse by jumping out of the water and skimming across the water surface. Large individuals of *Macrobrachium* spp. were observed to slowly approach electrified areas across the stream bottom with their foremost chelae extended. At approximately 5 cm from the electrified hoop, this foremost chela would begin to twitch with each electric pulse and the individual would then back away. This advance–retreat behavior was observed for both *Atya* and *Macrobrachium* spp. and was often repeated by the same individual.

Shrimp were observed in control hoops on all sampling dates; none were observed in electrified hoops. Observations over four dates indicated that control treatment hoops contained a mean of $5.5 (\pm 2.1 \text{ SD})$ shrimp ($n = 12$). While *Macrobrachium* spp. were rarely observed within controls, *Atya* spp. was most abundant, followed by *X. elongata* (Table 1), at approximate field densities. No fish (*S. plumieri*) or crabs (*E. sinuatifrons*) were observed in control hoops or in the study pool throughout the experiment.

Mean current velocities affecting both C and E treatments during base flow conditions were $2.2 (\pm 0.4 \text{ SD}) \text{ cm}\cdot\text{s}^{-1}$ ($n = 3$) and $2.1 (\pm 0.9 \text{ SD}) \text{ cm}\cdot\text{s}^{-1}$ ($n = 3$), respectively, and were not significantly different. Current velocities measured near but outside the experimental hoops were $2.8 (\pm 1.8 \text{ SD}) \text{ cm}\cdot\text{s}^{-1}$ ($n = 8$). Conductivity at the study site ranged from 90 to $102 \mu\text{S}\cdot\text{cm}^{-1}$.

Of the eight *C. maculipes* nymphs ($\leq 0.5 \text{ cm}$) that were introduced into the water column above electrified hoops,

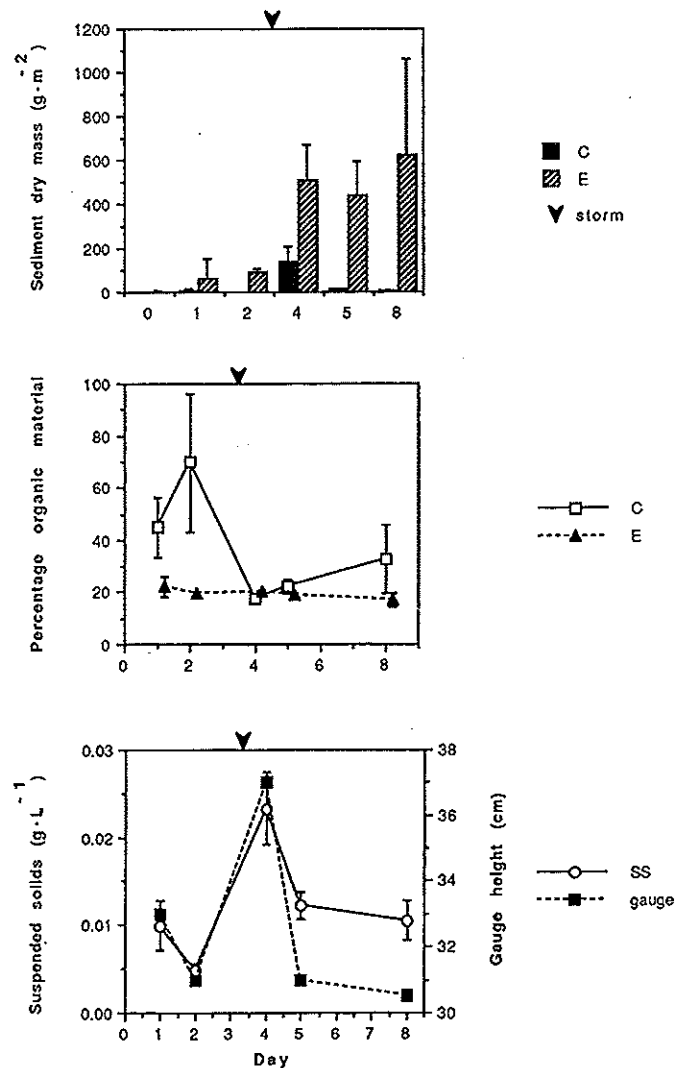


FIG. 2. Total dry mass of sediment and percentage organic material in control (C) and electrified shrimp exclusion (E) treatments after 0, 1, 2, 4, 5, and 8 d. Suspended solids (SS) and stream gauge (gauge) height throughout the experimental period are indicated in the lowermost graph. Data are means ± 1 SD. Note: arrowhead indicates the approximate timing of a storm event.

none appeared to be affected by the electric pulse. All individuals swam down and positioned themselves on the sediment covered rock within the electric hoop where they remained throughout the 8-min observation period. After 8 d, *C. maculipes* was found to inhabit large particulate leaf material in densities of $1.24 (\pm 1.24 \text{ SD}) \cdot \text{g}$ dry weight of leaves within E replicates. In contrast, C replicates were characterized by no visible large particulate organic material, and no *C. maculipes* were collected.

Electrified hoops rapidly filled with sediments and the sediment layer extended to approximately 5 cm outside the electrified hoop, corresponding to the observed range of shrimp response to the electric pulse. Total dry mass of sediment was significantly higher in the E treatment relative to the C treatment over the experimental period ($p = 0.0028$; Fig. 2). Significant interaction terms between treatments and time indicate that total sediment accrual differs through time between the two treatments ($p < 0.001$; Table 2). The fine particulate organic component of sediment was also

TABLE 2. Two-factor repeated measures ANOVA for total sediment dry mass.

| Source of variation | Degrees of freedom | Sum of squares | Mean square | F value | p value |
|---------------------------------------|--------------------|----------------|-------------|---------|---------|
| Treatment | 1 | 57.690 | 57.690 | 83.822 | 0.003* |
| Error A (replicates within treatment) | 3 | 2.065 | 0.688 | | |
| Day (repeated measure) | 4 | 18.519 | 4.630 | 32.693 | <0.001* |
| Treatment × day | 4 | 7.612 | 1.903 | 13.437 | <0.001* |
| Error B | 12 | 1.70 | 0.14 | | |

TABLE 3. Two-factor repeated measures ANOVA for fine particulate organic material.

| Source of variation | Degrees of freedom | Sum of squares | Mean square | F value | p value |
|---------------------------------------|--------------------|----------------|-------------|---------|---------|
| Treatment | 1 | 34.468 | 34.468 | 128.016 | 0.002* |
| Error A (replicates within treatment) | 3 | 0.808 | 0.269 | | |
| Day (repeated measure) | 4 | 10.579 | 2.645 | 31.246 | 0.001* |
| Treatment × day | 4 | 4.286 | 1.071 | 12.658 | 0.003* |
| Error B | 12 | 1.016 | 0.085 | | |

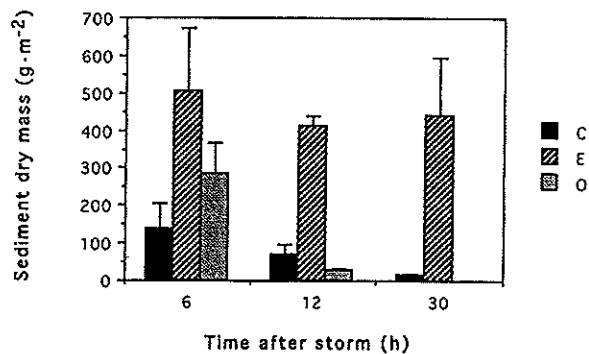


FIG. 3. Total dry mass of sediment in control (C) and electrified shrimp exclusion (E) treatments and on rocks located outside (O) the treatments at approximately 6, 12, and 30 h following a storm event. Data are means \pm 1 SD. Note: no measurement of sediment was made on rocks outside the treatments at 30 h.

significantly higher in the E versus C treatment over the experiment ($p = 0.001$; Table 3). Accrual of fine particulate organic material differs through time between the two treatments as indicated by the significant interaction term ($p = 0.003$; Table 3). Treatment had a significant effect on the percentage of fine particulate organic material across all observation dates, and times had a significant effect when assessed across both treatments (Table 4). Percentage of fine particulate organic material responded in different ways over time in the two treatments (Fig. 2): in the absence of shrimp, it remained consistently low throughout the experiment (18–21%) and did not change through time, while in the presence of shrimp, it changed significantly over time (Table 4), with the change corresponding to the 4-d storm (Fig. 2).

The storm on day 4 (Fig. 2) resulted in increases in sediment dry mass (both inorganic and organic components) in both treatments and on rocks sampled outside the treatments approximately 6 h after the storm (Fig. 3). Twelve hours

TABLE 4. Kruskal–Wallis analysis for effect of time on organic proportion of silt.

| Source of variation | Degrees of freedom | Test statistic | p level |
|-------------------------------|--------------------|----------------|---------|
| Treatment across all days | 4 | 5.573 | 0.233 |
| Day across C and E treatments | 1 | 157.000 | 0.006* |
| Day treatment E only | 4 | 8.233 | 0.083 |
| Day treatment C only | 4 | 10.527 | 0.032* |

poststorm, sediment cover in the C treatment had begun to decline, and after 30 h, it had returned to near prestorm levels, while sediment cover in the E treatment did not change significantly after the storm (Fig. 2 and 3). Sediment dry mass on rocks outside (O) treatments was not significantly different from that in the C treatment after the storm (Fig. 3).

After 8 d, no measurable large particulate organic material (e.g., macroscopic leaves and leaf parts) was present within the C treatment. However, the E treatment had accumulated 1.1 (± 0.5 SD) $\text{g}\cdot\text{m}^{-2}$ dry mass⁻¹ of leaves and leaf parts.

Total biovolume of algae after 8 d was significantly higher ($p = 0.002$) in the E treatment (Fig. 4). Both treatments were characterized by a diatom community dominated by the adnate taxon *Achnanthes lanceolata*. The E treatment had significantly higher algal diversity ($p = 0.0019$) and richness ($p = 0.0061$) than the C treatment.

Visual inspection of sediment distribution after approximately 24 h of settling time in the wading pools indicated a uniform sediment coating on the bottoms of pools containing both E and C hoops.

Discussion

In lentic and marine environments, bioturbation characteristically results in a highly depositional environment due

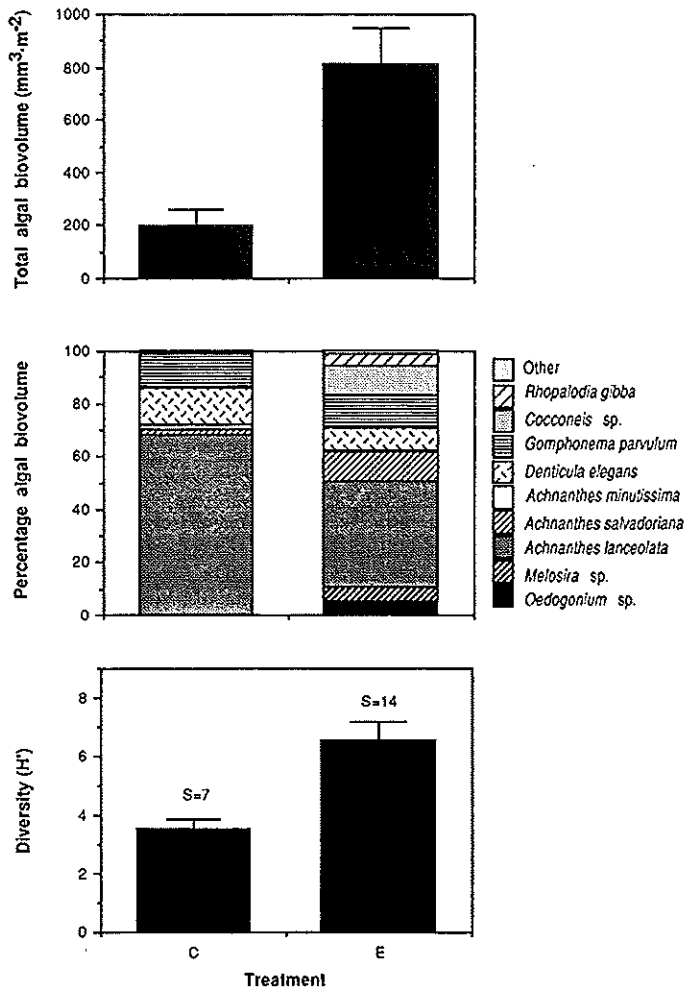


FIG. 4. Total algal biovolume, percentage biovolume of algal taxa, and diversity (H' where S = species richness) in control (C) and electrified shrimp exclusion (E) treatments after 8 d. Data are means \pm 1 SD.

to constant deposition and resuspension (e.g., Rhoads 1974; Brenchley 1981). By contrast, in lotic systems the presence of a unidirectional current interacts with the action of bioturbators to determine the depositional environment and patterns of sediment distribution. Once a particle is dislodged or put into suspension by the biota, the direction and magnitude of the current are important factors in determining where the particle will be redeposited.

Results presented here illustrate how biotic and abiotic forces interact to determine spatial and temporal patterns of sediment cover in a stream system (Fig. 2 and 3). Storms, accompanied by high current velocities and discharge, are important abiotic forces that redistribute inorganic and detrital material throughout the stream channel. Atyid shrimp are important biological agents affecting the depositional environment in stream pools during the interlude between storms: they have a significant impact on the distribution of inorganic sediments and both fine and coarse particulate organic materials.

Treatment differences change significantly through time because of the interaction between sediment removal activity of atyid shrimp and sediment accrual caused by a high-discharge event. Under base flow conditions, while sediments accumulate steadily within the E treatment, the C treatment does not experience sediment accumulation. Enhanced sed-

imentation during the storm on day 4 resulted in a stepwise divergence of C and E treatments. The storm provided a natural sedimentation event that affected both experimental treatments (Fig. 2 and 3). Many sediment and detrital particles were put into suspension as a result of the increased stream discharge during and after the storm, resulting in high water turbidity and suspended solids (Fig. 2). As stream discharge decreased after the storm, sediment and detrital particles were deposited on rock substrata in the study pool. While poststorm sediment cover in the C treatment was rapidly reduced, attaining prestorm conditions after only 30 h, sediment cover in the E treatment did not change significantly (Fig. 2). Thirty hours after the storm, sediment in the C treatment ($5\text{--}13 \text{ g} \cdot \text{m}^{-2}$ dry mass $^{-1}$) comprised only 1–3% of the sediment mass in the E treatment ($440\text{--}620 \text{ g} \cdot \text{m}^{-2}$ dry mass $^{-1}$).

The significant decrease in percent organic content of sediment in response to the storm event (Fig. 2) indicates that this variable is strongly affected by the interaction of biotic and abiotic events: atyid shrimp actively maintain a relatively high percent organic content (understory algae) on substrata between storms. Storms act to decrease percent organic material to the same low proportions found in the absence of shrimp through deposition of large amounts of inorganic material.

The use of electricity for experimental exclusion has enabled us to avoid confounding artifacts associated with cage enclosures/enclosures, such as reduction of current velocity, increased sedimentation, and shading effects (e.g. Miller 1986; Cooper and Dudley 1988; Cooper et al. 1990; Peckarsky and Penton 1990). Also, the densities at which experimental cage enclosures are stocked with a particular organism are often based on estimates of densities of that organism in the natural environment (e.g., Cooper et al. 1990). Not only are natural densities of many organisms (e.g., highly mobile taxa) difficult to estimate reliably, but the habitat conditions and carrying capacity of cages (and often cage controls) invariably differ from those of the natural environment because of factors mentioned above.

In contrast with cages, electrified hoops provide little resistance to the current and little dead space for sediment to settle out downstream. This is illustrated by the lack of significant difference in current velocity between experimental hoops and areas outside the hoops and the similarity of sediment dry mass in C hoops and outside rocks after the storm on day 4 (Fig. 3). Furthermore, the low resistance of experimental hoops to current and their placement close to the stream bottom is also an advantage over cages during high-discharge events, which can wash out experiments and carry cages downstream via increased current or battering by large floating woody debris. Provided that fence chargers and batteries are placed above maximum water levels and experimental templates (i.e., electrified and control hoops) are weighted sufficiently (or secured to the stream bottom), experimental setups can withstand moderately high discharge fluctuations.

Experimental artifacts were apparent in previous studies where we used cages to enclose or exclude atyid shrimp (Pringle et al. 1993). We visually estimated sediment cover on substrata in cages artificially stocked with shrimp and in cages excluding shrimp. In these studies, artificial substrata experienced higher sedimentation rates than natural substrata in both the absence and presence of shrimp. Such

artifacts made it impossible to quantify how biotic versus abiotic factors affect sedimentation. Many other studies have similarly demonstrated that cages act as sediment traps in streams (e.g., Peckarsky 1985; Peckarsky and Penton 1990), further illustrating the utility of electric exclosures.

Evidence supporting our contention that atyid shrimp (versus other organisms) are the biotic agents that are responsible for significant differences in sediment mass between treatments includes (1) observations of high atyid densities (*Atya* spp. and *X. elongata*) in control hoops (Table 1) and on rock surfaces outside the treatments in the study pool throughout this experiment, (2) relatively low numbers of the palaemonid shrimp *Macrobrachium* spp. (approximately 8.2% of the shrimp population, unpublished data) and the crab *E. sinuatifrons* within the study stream, and (3) the absence of the fish *S. plumieri* within the study pool. While the possibility exists that *Macrobrachium* and *E. sinuatifrons* may have some effect on sediment cover in control hoops, possibly during unobserved periods when they are nocturnally active (e.g., Covich 1988), their effect is probably insignificant relative to the intense foraging activity of large numbers of atyid shrimp which ingest substantial amounts of sediment and detritus, comprising between 40 and 50% of shrimp gut volume (Pringle et al. 1993).

Bioturbational processes by which *Atya* and *Xiphocaris* spp. reduce sediment accrual on benthic substrata in streams include both direct and indirect bioerosion and direct ingestion. Sediments and detritus are removed by atyid shrimp from rock substrata in pools (1) indirectly, via body movements as shrimp move over substratum surfaces causing sediments to be swept into the water column and displaced downstream by the current, and/or (2) directly, via brushing activity of cheliped fans (*Atya* spp.) and/or picking with cheliped pincers (*X. elongata*), whereby sediment particles are either ingested and redistributed in the form of fecal material or rejected and carried downstream by the current (Pringle et al. 1993).

Assuming that there is no difference in algal immigration rate in shrimp presence versus shrimp absence treatments, significant treatment differences in algal biovolume over 1 wk may be attributed to increased success in the settling or deposition of algal colonists in the absence of shrimp foraging (i.e., versus actual productivity). Differences between the results of this experiment and those of previous cage experiments (Pringle et al. 1993), which found that shrimp presence enhanced algal biovolume, can be attributed to different experimental design(s) and experimental duration. In previous experiments (Pringle et al. 1993), we only sampled understory algae *directly attached* to the substratum (as a consequence of a manual sediment removal treatment which was a main component of the experimental design), while in the current study, we sampled algal communities associated with both the sediment and underlying substratum. Previous experiments addressed a different question, evaluating effects of shrimp on the biovolume accrual of a *developing understory* algal community on artificial substrata over 21–30 d.

Higher algal diversity and species richness in the absence (E) than in the presence (C) of shrimp (Fig. 4) can be attributed to the removal of upperstory algal forms by shrimp foraging activities. The algal community in the shrimp absence treatment is characterized by significant numbers of upperstory filamentous forms (e.g., *Melosira* sp. and

Oedogonium sp.), while the algal community in the shrimp presence treatment lacks these upperstory taxa.

This electric exclusion technique can be modified to accommodate different sets of biotic and abiotic conditions in aquatic systems, and results should be interpreted according to the behavioral responses of organisms within a particular set of environmental conditions. The size of the area affected by the electric pulse and the strength of the pulse itself are dependent on the conductivity of the water, habitat conditions (e.g., substratum surface topography), the type of fence charger utilized, and the construction and dimensions of electrified templates. For instance, in surface waters with high conductivity (e.g., tropical streams in Costa Rica that are enriched with geothermally derived solutes), the electric pulse is not effective in excluding biota (C.M. Pringle, personal observation). Use of a fence charger designed to electrify a greater length of fence (e.g., 25 versus 15 miles) will affect the strength of the pulse and/or the size of the area affected. In our study, benthic insects were not excluded by the electric pulse, as demonstrated by the presence of *C. maculipes* nymphs and retreats of larval Chironomidae. Different environmental conditions (e.g., relative conductivity of the water) will alter the effect of the electric pulse on insects, and different taxa or sizes of insects may be affected.

In conclusion, the electric exclosure technique enabled us to examine the interaction of biotic and abiotic forces in determining spatial and temporal patterns of sediment cover in the absence of the cage artifact of high sedimentation. Electric exclosures were effective in excluding shrimp and had significantly higher mass of total sediment, fine and large particulate organic materials, and algal biovolume than areas of the stream bottom accessible to natural densities of shrimp. Substrata in control treatments accessible to natural densities of shrimp experienced no sediment accumulation under base flow conditions. A storm resulted in high sediment cover on rocks in stream pools (400–600 g·m⁻²), and natural densities of atyid shrimp rapidly removed this accumulated sediment in control treatments, reducing sediment mass by over two orders of magnitude, resulting in prestorm levels (5–13 g·m⁻²) in less than 30 h.

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