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Stoneflies as ecological engineers – hungry predators reduce fine sediments in stream beds

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SUMMARY

1. We conducted experiments in a Colorado Rocky Mountain stream to measure the effect of foraging by predatory stoneflies (*Megarcys signata*) on fine sediment deposition and removal.
2. Cages containing one of four treatments were placed in the stream substratum and removed 3 days after fine sediment load to the stream was experimentally increased. Cages containing a stonefly but no prey accumulated less sediment than cages initially with no benthic invertebrates. Although cages with *Megarcys* plus prey also tended to have less sediment than controls, sediments were not reduced in cages with prey only.
3. Distance from sediment source, depth and current velocity at cages, final prey density and numbers of prey per predator gut at the end of the experiment had no effects on sediment accumulation in cages.
4. To determine the mechanisms underlying this effect, behavioural tests were conducted in a stream-side artificial stream system. To simulate the different hunger levels of stoneflies in cages, *Megarcys* were fed or starved for 3 days before behavioural trials that were repeated during high (night) and low (day) stonefly feeding periods. During night trials, foraging movements by starved *Megarcys* were more prolonged and active than those of fed stoneflies, regardless of the presence of prey. However, neither hunger level nor prey presence affected stonefly foraging behaviour during day trials.
5. Results of field experiments suggest that the presence of stoneflies enhances sediment removal from interstitial spaces. Behavioural observations indicate that nocturnal searching for prey by hungry *Megarcys* dislodges fine sediments from interstitial spaces.
6. Future studies should explore beyond the direct impacts of predators on stream invertebrate communities, and investigate the potential impact of predators on benthic microhabitat quality.

Introduction

Many human activities, such as timber cutting, cattle grazing, road construction and urban development, increase sediment loads in streams (Lynch, Corbett & Hoopes, 1977; Lenat, Penrose & Eagleson, 1981; Holopainen & Huttunen, 1992). Even streams that are protected from these anthropogenic disturbances by national forests and wilderness areas are often subjected to natural disturbances such as summer rainstorms and consequent sediment loading and deposition (e.g. Peckarsky, 1985; Pringle & Blake, 1994). As the current velocity declines, eroded particles are deposited on stream substrata and fill interstitial spaces (Culp, Wrona & Davies, 1986; Marsh, 1987), reducing habitat critical to many benthic invertebrates and often lowering benthic density (Lenat *et al.*, 1981; Peckarsky, 1985) and species diversity (Gray & Ward, 1982).

Although these studies illustrate the importance of physical factors in the erosion, deposition and resuspension dynamics of fine particles in streams, little is known about the effects of biota on these processes (Jones, Lawton & Shachak, 1994). After sediment deposition in a Black Forest stream (Germany), cages containing the predatory stonefly *Dinocras cephalotes* (Curt.) (Plecoptera, Perlidae) accumulated less fine sediment than cages without stoneflies at the same flow regimes (B.L. Peckarsky, S. Horn & B. Statzner, unpublished). These data suggested that the foraging activity of interstitial predators may affect sediment removal, and thereby modify the interstitial habitat for other species. Perlid and perlodid stoneflies are tactile predators that, during their active search for food (Peckarsky, 1982), could dislodge fine sediments from interstitial spaces, allowing them to be washed downstream. Such erosion potential has been demonstrated previously for large benthic invertebrates in Puerto Rican streams (Pringle *et al.*, 1993; Pringle & Blake, 1994) and in sediment-feeding fishes in Andean Piedmont streams (Flecker, 1992, 1996).

The objectives of this study were to determine whether *Megarcys signata* (Hagen) (Plecoptera, Perlodidae), a predatory stonefly species native to Rocky Mountain streams, affected fine sediment accumulation, and whether stonefly foraging was the mechanism responsible for dislodging sediments. To address these objectives a caging experiment measured the effect of *Megarcys* on sediment removal following experimental addition of fine sediments; and an experimental study of *Megarcys* foraging behaviour distinguished among alternative mechanisms to explain sediment removal by predators.

Materials and methods

Cage experiment

A cage experiment was conducted in Benthette Brook (described in Peckarsky & Penton, 1989), a first-order stream near the Rocky Mountain Biological Laboratory (RMBL) that is rarely subjected to natural sedimentation. Although cage mesh has been shown to affect rates of sedimentation (Peckarsky, 1985; Peckarsky & Penton, 1990), we excluded predators using cages rather than electric fences (Pringle *et al.*, 1993; Pringle & Blake, 1994), because predatory stoneflies may not be sufficiently larger than their prey to be affected differentially by an electric field (G.A. Blake, personal communication). Cages containing one of four treatments were placed in a single riffle:

1 control (no invertebrates);
2 predator treatment (one *Megarcys*);
3 prey treatment (other invertebrates but no *Megarcys*);
4 predator + prey treatment (one *Megarcys* plus prey).

All stoneflies were females of similar size (mean dry weight (DW) ± SE 37.7 ± 0.4 mg, length range 25–30 mm) to minimize differences in predator activity or behaviour based on predator sex or size. For treatments 3 and 4 we created homogeneous invertebrate prey communities that were representative of prey densities, sizes and species in Benthette Brook at the time of the experiment. Samples of the benthos were agitated and mixed in a 40-l container ('benthic blender'; see Peckarsky, 1991a) using a pump that aerated them while calibrated aliquots were removed and placed in cages. Eight samples of those initial prey communities were preserved in 70% ethyl alcohol and used to estimate initial prey densities.

Cage structure and use were designed to minimize differences between the caged environment and the stream environment and to reduce cage artefacts. The cages (described in Cooper, Walde & Peckarsky, 1990) were made of cylindrical Plexiglas, 10 cm diameter × 10 cm high, with clear Plexiglas bases (area 0.008 m^2) and removable plastic lids. Mesh windows on the sides and tops of the cages had openings 2 × 2 mm, which allowed water and sediments to flow through the cages, as well as departure and arrival of benthic invertebrate prey, but did not allow migration of *Megarcys*. To simulate a standardized natural substratum, we added eight 4-cm-diameter rocks and two 6-cm-diameter rocks (maximum dimension) with associated biofilms taken from the creek.

Along eight transects at ≈ 2 m apart we placed clusters of four cages adjacent to each other and flush with the surface of the substratum, their mesh openings being arranged to maximize flow through them. We chose locations for the cages that were in preferred flow microhabitats for stoneflies (Peckarsky, 1991b). We put rocks around the cages to enhance their integration into the natural habitat. During placement and removal of cages we slipped cylindrical sleeves of solid, open-ended plastic over the enclosures to prevent loss of invertebrates (Peckarsky & Penton, 1990). We placed one cage representing each treatment randomly in each cluster so that effects of treatments on sediment accumulation could be restricted to comparisons within transects. Different physical conditions among clusters of cages could alter rates of sedimentation on different transects, and so invalidate between-transect comparisons. At each cage we measured water depth, current velocity at cage surfaces (Marsh–McBirney model 201 flowmeter), and distance downstream from the sediment addition, and these were tested as possible covariates of sediment accumulation.

Fine inorganic sediment (silt) was suspended by people walking methodically through a beaver pond 10 m upstream of the study riffle. To determine how long the disturbance event should last to accumulate desired sediment loads in cages, the total interstitial space in each cage and the rate of sediment deposition were calculated in a pilot experiment using cages configured in the study riffle as described above. Determined by volume displacement, the mean ± 1 SE interstitial space per cage was 177.25 ± 14.27 ml. Disturbing the beaver pond substratum for 30 min deposited an average of 15 ml of sediment in cages spanning the length of the selected riffle. Thus, to fill approximately one-third of the available interstitial space in the cages, we disturbed the sediments of the beaver pond for 2 h after placement of the cages.

Cages were removed from the stream after 3 days, while their enclosed environments were still within the natural range of physical and resource conditions (Peckarsky & Penton, 1990). The volume (ml) of sediment that had accumulated in each cage was measured by washing all fine sediments into a jar and measuring their volume after 5 days of settling. The invertebrates in each cage were hand-picked and preserved in 70% ethyl alcohol. Recognizable prey parts found in the gut contents of each *Megarcys* were also identified and used to estimate whether predators had fed during the 72-h experiment. Since these stoneflies clear their guts in 24 h (Peckarsky, 1985), presence of prey in guts indicated that confined predators had fed in the latter part of the experiment.

We compared sediment accumulation between treatments only among cages within each cluster, by using multiple paired *t*-tests. These tests compared control cages with the three other treatments within each cluster, with alphas reduced to compensate for experiment-wise error (Bonferroni's $\alpha = 0.05n^{-1}$ where n = the number of pairwise comparisons per experiment). We did not use a blocked ANOVA because inclusion of a block variable reduced the power to detect the main effects of the treatments on sediment deposition. Instead, we used Spearman rank correlation coefficients to test associations between sediments in cages and distances from the sediment source. We also used Spearman rank correlation tests to determine associations between sediment accumulation and final prey density, predator gut contents, and current velocity, since these were possible covariates that could have affected sediment accumulation.

Behavioural experiments

To test the mechanism underlying sedimentation effects in cage experiments, we measured the effects of prey density and hunger levels on *Megarcys* movement during July–August 1993. As in the cage experiments, all stoneflies used in trials were similar sized females without wingpad development, because *Megarcys* typically become less active and stop feeding just before emergence (Peckarsky & Cowan, 1991). Prey used in these trials were *Baetis bicaudatus* Dodds (Ephemeroptera, Baetidae), which are the principal mayfly prey of *Megarcys* (Peckarsky, 1985; Peckarsky & Penton, 1989), and are abundant in montane and subalpine streams of the study area (Peckarsky, 1991b).

Female *Megarcys* were collected from Benthette Brook and held with or without unlimited *Baetis* for 3 days before behavioural trials. *Megarcys* can survive for at least 2–3 weeks without food (Peckarsky *et al.*, 1993), and are often found in nature with empty guts (Peckarsky, 1985). Since their gut clearance time is 24 h (Peckarsky, 1985), starved stoneflies should have been hungry after 3 days (Peckarsky & Penton, 1989), but not excessively so. The holding tanks (15-cm-diameter circular flow-through arenas) were part of a streamside system (described in Peckarsky & Cowan, 1991) receiving water from the East River, a third-order stream of which Benthette Brook is a tributary. Four treatments (starved or fed *Megarcys* with and without thirty *Baetis*) were replicated eight times each during the afternoon and night. *Megarcys* is primarily a nocturnal predator, spending the day under rocks and actively searching for prey on all substratum surfaces at night (Walde & Davies, 1985; Peckarsky & Cowan, 1995). Thus, trials were conducted during an inactive period and during a period of maximum feeding of *Megarcys* (Peckarsky & Penton, 1989). Containers used in behavioural trials (described in Peckarsky *et al.*, 1993) were larger versions of the holding tanks (25-cm-diameter flow-through arenas). The horizontal surface area of each was 0.049 m^2, with predator and prey densities corresponding to the mean densities in the East River (predators: 20 m^{-2}, prey: 600 m^{-2}; Peckarsky, 1991b).

We observed the foraging behaviour of *Megarcys* from above and below natural substrata in arenas raised on a 1-m^2 clear Plexiglas tray. Six East River rocks (10 cm diameter) with biofilm were placed in a non-overlapping arrangement, and spaces between them were filled with a thin layer of gravel so that test animals remained visible from either above or below (the site of most *Megarcys* activity; Allan, Flecker & McClintock, 1986; Peckarsky & Cowan, 1995). The foraging behaviour of each stonefly was observed once for 10 min after about a 10-min acclimation period, and recorded on audio cassette tape. Stressed stoneflies tend to hide under refuges rather than forage (Peckarsky & Penton, 1989). Therefore, we deemed stoneflies acclimated when they began to forage in arenas. To observe behaviour at night we used dim red light to which these species of stoneflies and mayflies are insensitive (Peckarsky & Cowan, 1995). *Baetis* that were captured and eaten during trials were replaced immediately to maintain a constant density of prey individuals.

The total time spent moving (% of total trial time minus time spent feeding) and the rate of movement (number of rocks visited per unit time spent moving) were recorded for each stonefly. Movement was defined as locomotion not including prey handling or stationary activities such as moving antennae or cerci. The effects of hunger level and presence of prey on these two interdependent response variables were analysed using a two-way multiple analysis of variance (MANOVA). Separate MANOVAs were conducted on the day and night trials. If MANOVAs were significant, subsequent two-way ANOVAs were conducted on each response variable separately to determine the specific effects producing the significant MANOVAs.

Results

Sediment experiment

The amount of sediment that accumulated in cages differed among treatments; cages containing stoneflies had less fine sediment than cages without predators, and cages with the predator-only treatment accumulated the least amount of sediment (Fig. 1). The only marginally significant difference among treatments was between the control and predator-only treatments (Table 1). Although there were differences in the rates of sediment accumulation among clusters of cages, accumulated sediments did not differ systematically with respect to distance downstream from the disturbance (Fig. 2). There were also no visible differences among cages in the particle size distribution of accumulated sediments, with all cages accumulating very fine silt. A Spearman rank correlation test indicated no association between sediment accumulation in cages and the distance downstream from the sediment source (Table 2). Therefore, we concluded that sediments did not dissipate or change qualitatively as they accumulated in downstream cages in the test riffle, and that variations among cage clusters were random. Further, the amount of sediment in each cage was not

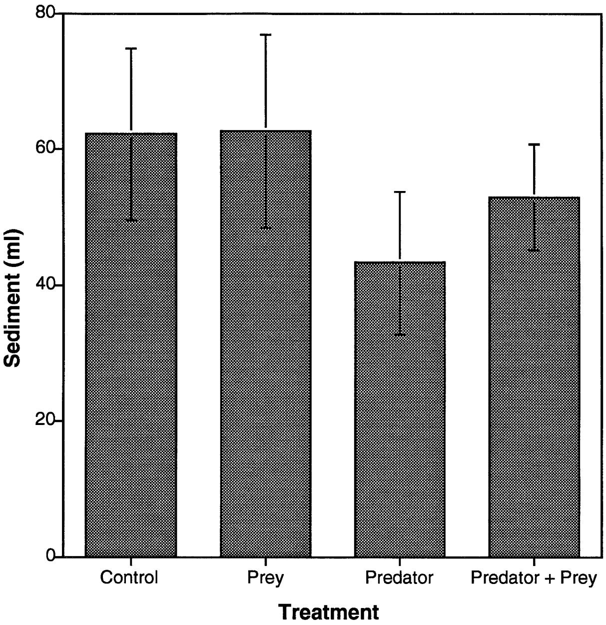

Fig. 1 Mean ± SE sediment (ml) remaining in cages after 3 days of exposure to each of four treatments (n = 8).

Table 1 Summary of paired t-tests comparing sediment accumulated (ml) in the control treatment with sediment accumulated (ml) in the prey, predator + prey, and predator treatments (n = 8; Bonferroni's α = 0.017)

Comparison	Mean difference	df	t	P
Control *v* prey	–0.38	7	–0.027	0.979
Control *v* predator + prey	9.4	7	0.526	0.615
Control *v* predator	19.0	7	3.09	0.018

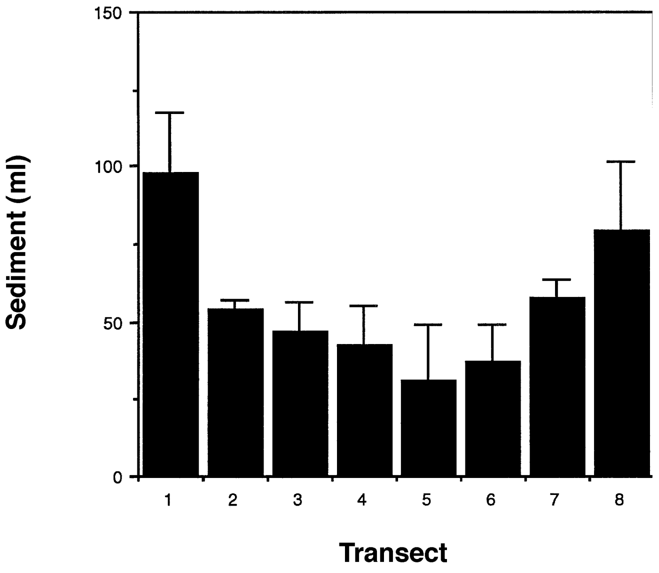

Fig. 2 Mean + SE sediment (ml) accumulating in each cluster of four cages arranged in order of increasing distance of transects downstream from the source of the disturbance.

Table 2 Spearman's rank correlation coeficients (R_s) and probabilities of significant association between sediment (ml) and distance from sediment source (m), water depth (cm), flow rate (cm s^{-1}), final prey density (no. m^{-2}) and predator gut contents (no. prey per predator gut) (n = 32)

	R_s	P
Distance from sediment source	–0.092	0.602
Water depth	0.056	0.760
Current velocity	–0.065	0.722
Prey density	–0.305	0.089
Predator gut contents	–0.072	0.694

associated with cage depth, current velocity, final prey density or predator gut contents (Table 2). Stonefly guts did not contain fine sediments, as shown in previous gut content analyses (Peckarsky, 1985). These data show that the presence of a *Megarcys* larva was the only measured variable causing differential sediment accumulation among cages.

Behavioural experiment

The behavioural trials were conducted to determine the specific mechanism responsible for increased sediment removal from cages with predators. During day trials, when *Megarcys* were relatively inactive, neither predator hunger levels nor prey density affected the time predators spent moving, or rate of predator movement (speed) (Fig. 3, Table 3). In contrast, during night trials, hungry predators spent significantly more time moving and moved at faster rates than well-fed stoneflies (Fig. 4, Table 3). As in the day trials, however, the presence or absence of prey in the observation arenas did not affect nocturnal foraging behaviour of *Megarcys* (Table 3). In both day and night trials, time stoneflies spent moving and rates of movement were independent of prey density. Therefore, the only variable that increased the potential for stoneflies to dislodge fine sediments was predator hunger level, and this effect was only significant at night, during the time of greatest stonefly activity.

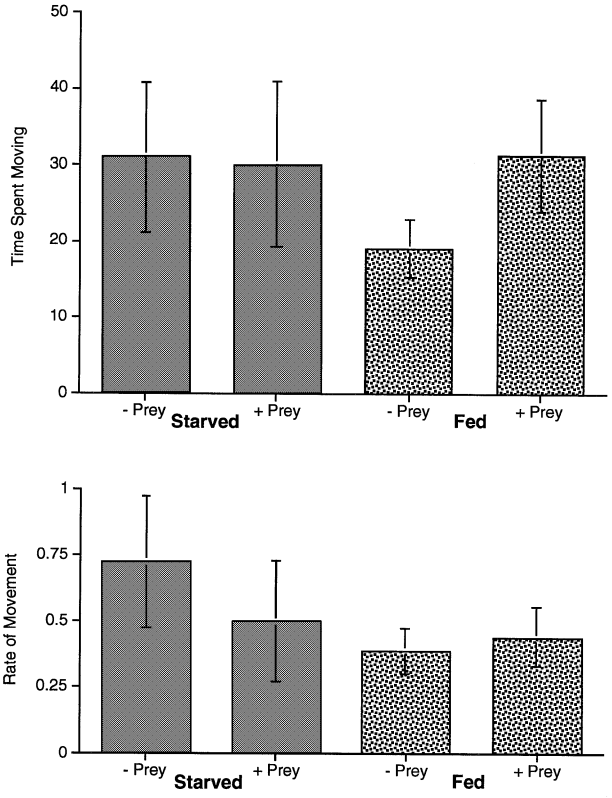

Fig. 3 Day trials: mean ± SE time spent moving (% = time moving divided by total time minus time feeding) and rate of movement (number of rocks visited per minute) by *Megarcys* for each treatment (n = 8).

Discussion

This study provides evidence that the predatory stonefly *Megarcys signata* increases the removal of fine sediments from the interstices of stream substrata, and that nocturnal foraging by hungry stoneflies is the mechanism underlying this effect. These data suggest

Table 3 Summary of multiple analysis of variance of hunger levels and prey presence on the time spent moving (% of total trial time minus time spent feeding) and rate of movement (no. rocks visited divided by total trial time minus time spent feeding) by *Megarcys signata* during the day and night behavioural trials. ANOVAs were conducted only when MANOVAs indicated significant effects

Source	Wilk's lambda	num df	den df	*F*	*P*
MANOVA: day					
Hunger level	0.951	2	27	0.698	0.506
Prey presence	0.842	2	27	2.54	0.098
Hunger level × prey presence	0.977	2	27	0.313	0.734
MANOVA: night					
Hunger level	0.776	2	27	3.89	0.033
Prey presence	0.956	2	27	0.625	0.543
Hunger level × prey presence	0.960	2	27	0.565	0.575
Source	Sum-of-squares	df	*F* ratio	*P*	
ANOVA: time spent moving, night					
Hunger level	5460	1	6.105	0.020	
Prey presence	179	1	0.200	0.658	
Hunger level × prey presence	155	1	0.174	0.680	
Error	250	28			
ANOVA: rate of movement, night					
Hunger level	3.58	1	8.04	0.008	
Prey presence	0.015	1	0.034	0.854	
Hunger level × prey presence	0.015	1	0.034	0.854	
Error	12.5	28			

that fine sediments in interstitial spaces are agitated, suspended and removed as a consequence of *Megarcys* movements as they patrol the substratum for benthic invertebrate prey. However, the effects of foraging behaviour were only significant in treatments with a stonefly and no prey, as in similar studies conducted on the European stonefly, *Dinocras cephalotes* (Statzner, Fuchs & Higler, 1996). If hunger levels of fed and starved stoneflies used in the behavioural trials were comparable with those of stoneflies in the predator + prey and predator-only treatments of the cage experiment, we can conclude that increased hunger levels accentuate the effects of *Megarcys* foraging behaviour on sediment removal by increasing the time spent moving and the rate of predator movement.

Behavioural trials also showed that *Megarcys* larvae maintained their natural foraging periodicity, including a daytime period of relative inactivity and a night-time period of maximum feeding despite altered hunger levels. Starved stoneflies spent significantly more time moving and at a faster rate than fed stoneflies, but they still concentrated their foraging during the night. This observation is consistent with other studies suggesting that during the day, avoidance of visual predaceous fish (Allan, 1978) pre-empted activity associated with increased hunger of *Megarcys* (B. L. Peckarsky & A. McIntosh, unpublished manuscript).

Numerous studies in a variety of aquatic systems have investigated the effects of fine sediments on benthos and vice versa, but few have analysed the complex and dynamic interactions among abiotic and biotic factors affecting sedimentation in streams. For example, much attention has been given to the large-scale adverse effects of human disturbances on North American streams. Increased sediment transport and deposition from disturbances such as periodic flushing of reservoir sediments (Gray & Ward, 1982) and eroded materials released into streams from road construction and timber harvesting (Lynch *et al.*, 1977; Lenat *et al.*, 1981; Holopainen & Huttunen, 1992) can result in lower densities and species diversity of fish, insect and plant communities. Benthic invertebrate populations have also been significantly reduced by the experimental addition of fine sediments to both natural (Bjorn *et al.*, 1977; Rosenberg & Wiens, 1978; Culp *et al.*, 1985) and laboratory streams (Luedtke & Brusven, 1976; McClelland & Brusven, 1980). Increased fine sediments may also create more favourable environments for some benthic invertebrate taxa, such as chironomids and oligochaetes (Gray & Ward, 1982).

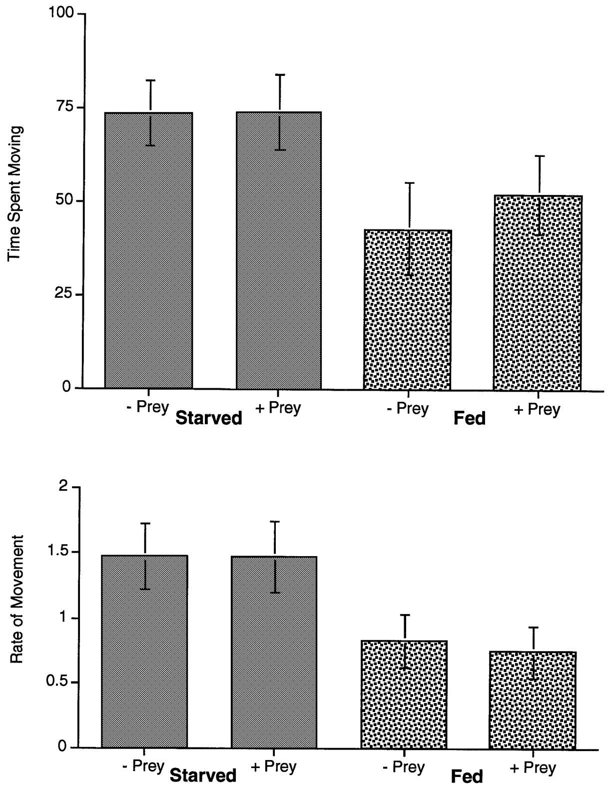

Fig. 4 Night trials: mean ± SE time spent moving (% = time moving divided by total time minus time feeding) and rate of movement (number of rocks visited per minute) by *Megarcys* for each treatment ($n = 8$).

More recently, however, investigators have measured biotic effects on stream sedimentation and their consequences for the rest of the benthic community. For example, in tropical streams detritivorous and algal feeding fish lower benthic invertebrate abundance by consuming or physically removing sediments that invertebrates use for food or retreat building (Power, 1984a,b, 1990; Flecker, 1992, 1996). Similarly, fish bioturbation and sediment consumption significantly reduced infaunal and meiofaunal abundances in marine soft-bottom systems (Brenchley, 1981; Palmer, 1988). Pit excavation by spawning fish has also been shown to affect the distribution and abundance of benthic invertebrates in streams and ponds (Hildebrand, 1971; Fuller & Cowell, 1985; Thorp, 1988). Others have assessed the effects of case-building benthic fauna on substratum creation, sediment stabilization and habitat modification in streams (Nilsen & Larimore, 1973; Pringle, 1985) and marine soft-bottom (Fager, 1964) systems. For example, increased surface area and habitat modification by chironomid and caddisfly case-building activities may enable other benthic invertebrate species to colonize the substratum (Nilsen & Larimore, 1973).

Few studies have addressed whether the interactive effects of biotic and abiotic factors on sediment resuspension and substratum stability create a mosaic of benthic habitats. For example, resuspension of sediments by deposit feeders can reduce the fitness and survival of suspension feeders, and thereby affect the structure of marine soft-sediment communities (Rhoads & Young, 1970). Increased sediment levels following rainstorms overrode the effects of predation in determining the structure of montane stream communities (Peckarsky, 1985). Ecosystem recovery following high sediment transport in tropical streams depended on sediment consumption and bioturbation by atyid shrimp (Pringle *et al.*, 1993; Pringle & Blake, 1994). These results indicate that atyid shrimp are not only dominant omnivores in tropical streams, but also organizers of stream community structure mediated by their effects on stream sediments.

In contrast to previous studies that have focused on stoneflies as dominant invertebrate predators in stream ecosystems (e.g. Peckarsky, 1985), this study suggests that *Megarcys* may also help restore invertebrate habitat altered during periods of increased sediment deposition. Since we used realistic stonefly densities and hunger levels, our data provide evidence that stonefly foraging behaviour may play an important role in maintaining the quality of interstitial spaces in their preferred microhabitats in the benthos. Corroborating evidence of this contention has been reported by Statzner *et al.* (1996), who measured a significant association between stonefly densities and sizes of interstitial spaces in a European stream. Many benthic invertebrates depend on interstitial spaces to provide habitat and protection, and some authors have suggested that prey species diversity (Gray & Ward, 1982) and density (Lenat *et al.*, 1981; Peckarsky, 1985) might be limited by the availability of interstitial spaces. Therefore, not only does *Megarcys* function as a predator on aquatic insects, but its presence in stream ecosystems may also affect the microdistribution and abundance of other benthic invertebrate species, mediated by its effect on the removal of accumulated fine sediments in streams. This dual role for large predatory invertebrates deserves further investigation.

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