Net spinning caddisflies as stream ecosystem engineers: the influence of *Hydropsyche* on benthic substrate stability

B. J. CARDINALE,*†‡ E. R. GELMANN* and M. A. PALMER*§

Department of Biology, University of Maryland, College Park, Maryland 20742, USA, ‡Department of Zoology, University of Wisconsin-Madison, Madison, WI 53706, USA, and §Department of Entomology, University of Maryland, College Park, Maryland 20742, USA

Summary

1. Organisms that physically modify or create habitat (*ecosystem engineers*) can have a profound influence on community and ecosystem dynamics.

2. Here evidence is presented that one of the most abundant and widely distributed lotic insects could act as an ecosystem engineer in streams by increasing the stability of benthic substrates during flooding.

3. Natural densities of larval net spinning caddisflies (Hydropsychidae) were established in stream channels that had standardized physical properties. The mobility of three particle sizes were measured during simulated flooding and the fraction of particles eroded compared with that of control streams.

4. Larvae increased the initial velocity required to erode sediments by 10–30%. At velocities sufficient to scour 87% of particles from control channels, 57–100% remained stable in channels colonized by larvae.

5. Assuming larvae have similar effects in natural streams, caddisflies could be expected to increase the recurrence interval of a substrate scouring flood from 1·67 year to 2·41 year, corresponding to a 17% decrease in the probability of bed scour per year.

6. Our study suggests these insects could play an important role in generating the spatial 'refuges' that moderate the resistance of lotic communities to flooding. It is argued that, as has occurred in marine systems, a better understanding of how freshwater organisms engineer their physical environment has much potential to complement our historical focus on the abiotic forces that constrain populations and communities.

Key-words: Benthic particle erosion, Hydropsychidae, lotic ecosystems, Trichoptera

Functional Ecology (2004) **18**, 381–387

Introduction

Over the past decade ecologists have increasingly come to recognize the ecological importance of organisms that physically modify, maintain or create new habitat (Jones, Lawton & Shachak 1994). Such *ecosystem engineers* are now thought to be pervasive in nature, and understanding the community and ecosystem level consequences of their impact has become the subject of much research (Jones, Lawton & Shachak 1997). Studies to date have focused primarily on how the structures formed by engineers increase physical habitat heterogeneity and, in turn, influence the diversity of communities (e.g. Ceballos, Pacheco & List 1999; Gallagher, Jumars & Trueblood 1983; Wright, Jones & Flecker 2002). Less appreciated, but perhaps equally important, is the effect engineers can have on habitat stability (Jones *et al*. 1997). Disturbance is a primary

determinant of the spatial and temporal dynamics of species (Petraitis, Latham & Niesenbaum 1989); therefore, taxa that make habitats more resistant to physical disturbances are likely to play a key role in generating the landscape mosaics that influence the abundance and diversity of organisms.

In stream ecosystems, high discharge events such as floods are a dominant source of physical disturbance known to influence the spatial and temporal patterns of diversity for nearly all major groups of lotic organisms (Allan 1995; Poff *et al*. 1997). While floods can have a direct effect on benthic flora and fauna by scouring individuals from substrates, the greatest reduction in population sizes during floods occurs when discharge becomes great enough to mobilize streambed sediments (e.g. Bond & Downes 2000; Cobb, Galloway & Flannagan 1992). As a consequence, spatial 'refuges' – areas of a streambed that remain stable during flooding – are thought to be a key factor that moderates the ecological impact of disturbance in streams (Lancaster 2000; Townsend, Scarsboro & Doledec 1997).

†Author to whom correspondence should be addressed. E-mail: bjcardinale@wisc.edu

Here we present experimental evidence suggesting that a widespread species of arthropod could act as an ecosystem engineer in streams by increasing the stability of the benthic habitat. Hydropsychid caddisflies are one of the most diverse and abundant families of lotic insects worldwide, and can account for as much as 80% of macroinvertebrate biomass in some streams (Wallace & Merritt 1980). Many Hydropsychidae construct filtration nets in the pore spaces of streambeds, which they use to filter particulate organic matter from the water. Caddisfly larvae are often associated with areas of a streambed that exhibit high stability during floods (Cobb *et al*. 1992; Death 1995; O'Connor 1993). It is generally assumed that, like other invertebrates, caddisflies preferentially colonize areas that are stable to avoid disturbance (Death 1996), or that they have higher rates of survival in stable habitats during flooding (Matthaei, Arbuckle & Townsend 2000). An alternative, though not mutually exclusive view, is that the caddisflies themselves confer resistance to a benthic habitat as their filtration net binds particles together into a more stable matrix.

To test the hypothesis that net spinning caddisfly larvae increase the stability of benthic substrates, we performed an experiment in standardized stream channels using a species of Hydropsychidae that is widely distributed throughout the eastern United States (*Hydropsyche depravata*). Four densities of *H. depravata* comparable to the range of naturally occurring densities were established in the experimental channels, and then the magnitude of discharge was increased to simulate flooding. The mobility of three size classes of particles was measured and compared with control channels in order to assess the *engineering effect* of the caddisfly larvae on substrate stability.

Materials and methods

EXPERIMENTAL DESIGN

Tests of the biological factors influencing bed stability are rare in natural settings because of the difficulty in manipulating benthic organisms without also disrupting sediments. As a consequence, studies examining the influence of biota on particle transport have generally been performed in experimental channels (flow tanks and flumes) where the physical forces that influence bed stability can be controlled (Muschenheim, Grant & Mills 1986; Nowell & Jumars 1987; Vogel & LaBarbera 1978). Following in this tradition, we performed our work in recirculating stream channels (modelled after the design of Vogel & LaBarbera 1978) where hydrodynamic and substrate properties were standardized, and the effect of caddisflies on benthic particle stability could be interpreted unambiguously (descriptions of the channels are given in Cardinale & Palmer 2002; Cardinale, Palmer & Collins 2002).

Each of the experimental stream channels (0·1 m wide × 0·1 m deep × 1·0 m long) had a 'false bottom'

that bounded a 59 cm^2 working section located 8× the channel width from the flow entrance (as recommended by Nowell & Jumars 1987). Forty millilitres of each of three particle classes (2, 4 and 8 mm) were homogenized and added to the working section of the channels prior to the experiment. We focused on these size classes because they are characteristic of many of the low-gradient Piedmont streams that we study (see Palmer *et al*. 2000). After sediments were added, the channels were filled to a depth of 8 cm, velocity was gradually raised to 21·5 cm s^{-1} (measured above the working section at 0·4 × water depth with a 1 cm diameter Nixon instruments (Cheltenham, UK) propeller flow meter), and sediments were allowed to settle for 24 h prior to the start of the experiment. At ambient conditions, the mean motion Reynolds number, *Re*, was estimated to be $1·7 \times 10^4$, the Froude number, *Fr*, was ~0·24, and the roughness Reynolds number, *Re**, was ~80. These dimensionless values, which collectively describe the properties of water motion, indicate that bulk flow in the channels was subcritical-turbulent with flow near the bed being hydraulically rough (see Jumars & Nowell 1984; Nowell & Jumars 1984; Vogel 1994 for review of these parameters). These properties are typical of the hydrodynamic conditions of many streams under non-flood conditions (summarized by Davis & Barmuta 1989).

Three levels of caddisfly density (1527, 3054 and 4582 larvae m^{-2}) were initially established in each of three replicate channels per treatment, with additional channels maintained as controls with no larvae. Larval densities at the end of the experiment were lower than initial values owing to intraspecific competition, drift and pupation (mean = 904, 1977 and 2542 larvae m^{-2} for the three treatment levels). Densities did, however, remain distinct throughout the study period with initial and final densities closely related (final = 0·58 × initial, $r^2 = 0·94$). Final densities were also comparable to those reported for caddisfly larvae in natural stream ecosystems (Benke & Wallace 1997; Georgian & Thorp 1992), and were within the range of densities that we have documented in our field sites (Table 1).

Individuals added to the experimental channels were selected from similarly sized, 4th instar larvae collected from the Patuxent River, MD, and maintained in a holding tank. Measurements of head capsule width (a correlate of larval body size) at the end of the experiment confirmed that individuals were equally sized between density levels (ANOVA $F_{2,6} = 0·23$, $P = 0·80$). While a uniform size distribution does not necessarily mimic natural populations, it was unclear to us whether inclusion of variable age classes would increase particle stability (perhaps because of complementary use of pore sizes) or decrease particle stability (perhaps by reducing the mean impact of an individual). Given this uncertainty, we felt it was appropriate to homogenize size structure for this experimental setting.

After reducing velocity in the channels to <5 cm s^{-1}, larvae were released uniformly over the working sections.

Table 1. Densities of *Hydropsyche* in 12 streams in the mid-Atlantic United States determined from three replicate Surber samples collected on single dates in the summer of 2000. All streams were characterized by gravel beds having 2–10 mm particles (2nd axis diameter) similar to that used in this study. These streams are used in the analyses presented in Fig. 3, with discharge data collected from the U.S. Geological Survey gauge shown

USGS gauge	Site	*Hydropsyche* (no. m^{-2})
03023100	French Creek at Meadville, Pennsylvania	2550
01622000	North River near Burketown, Virginia	1650
01470500	Schuylkill River at Berne, Pennsylvania	1500
01626000	South River near Waynesboro, Virginia	1100
01467048	Pennypack Creek at Philadelphia, Pennsylvania	250
01572025	Swatara Creek near Pine Grove, Pennsylvania	250
03074500	Redstone Creek at Waltersburg, Pennsylvania	200
01471510	Schuylkill River at Reading, Pennsylvania	100
01559000	Juaniata River at Huntingdon, Pennsylvania	100
01571500	Yellow Breeches Creek near Camp Hill, Pennsylvania	100
01470779	Tulpehocken Creek near Bernville, Pennsylvania	50
02053800	SF Roanoke River near Shawsville, Virgiania	50

Table 2. Effects of larval hydropsychid density, particle size and stream velocity on the *engineering effect* of caddis larvae. The engineering effect is the increase in streambed stability relative to control channels. A repeated measures ANOVA was used to model the engineering effect with the subject being channels in which repeated measures of stability were taken over five increasing levels of velocity. Non-significant, higher-order terms (two- and three-way interactions) were excluded from the model via backwards elimination. The most parsimonious model fit to the data is given below

Effect	Numerator d.f.	Denominator d.f.	*F*-value	*P*-value
Density	2	6	5·10	0·05
Velocity	4	108	49·41	<0·01
Particle size	2	108	3·03	0·05
Density × velocity	8	108	3·88	<0·01
Density × particle size	4	108	2·31	0·06

Following a brief period of acclimation (10 min), mid-channel velocity was raised back to 21·5 cm s^{-1} (over a period of 30 min), corresponding to a discharge of 1720 cm^3 s^{-1}. Larvae were allowed to colonize the substrates and build catchnets for a period of 10 days, which is sufficient for the construction of fully functioning structures (Cardinale *et al*. 2001). During this period we maintained a constant water depth (8 cm), water temperature (16 °C) and food supply (see Cardinale & Palmer 2002).

PARTICLE STABILITY

At the end of 10 days, we measured the stability of benthic particles in each stream channel. Larvae were not removed from substrates before measurements as this would have probably disrupted the benthos and, in turn, influenced particle stability. Experimental channels were selected in random order and velocity was increased in five equidistant increments ranging from 60·5 to 84·5 cm s^{-1} ($Re \approx 5·3 - 6·8 \times 10^4$, $Fr \approx 0·75 - 0·95$). These levels spanned the minimum velocity required to

scour particles in the control channels to the maximum that could be manipulated. Each velocity level was maintained for a period of 2 min during which all mobilized particles were captured in a downstream net. Pilot studies indicated that 2 min was a sufficient period for all particles to be transported. Particles captured at each flow level, and those remaining in the working section at the end of all measurements, were sieved into 2, 4 and 8 mm size fractions and counted. As the fastest velocity treatments were always exposed to 10 min of elevated flow while the slowest were exposed for only 2 min, one limitation of our study is that we cannot decouple the magnitude and duration of flow events.

The mean proportion of stable particles in the control channels was subtracted from the proportion of stable particles in channels colonized by caddisflies to determine the *engineering effect* of caddisflies – that is, the altered stability of particles specifically because of the presence of larvae. A repeated measures ANOVA was then used to model the *engineering effect* as function of caddisfly density, flow velocity, benthic particle size and the two- and three-way interactions. In the analysis, channels were treated as the subject on which repeated measures of particle stability were taken over the five levels of velocity. Non–significant interactions were removed through backwards elimination to obtain the most parsimonious model fitting the observations (Littell *et al*. 1996). All statistical assumptions were verified.

Results

Caddisfly larvae had a significant and substantial impact on the stability of benthic particles. In control channels, particle movement was first observed at a mid-channel velocity of 66·5 cm s^{-1} (Fig. 1a). In contrast, particle movement first occurred at 72·5 cm s^{-1} for channels colonized with the lowest density of caddisflies, corresponding to an increased erosion velocity of 10%. At the highest larval densities, all benthic particles remained stable until velocity reached 84·5 cm s^{-1}, corresponding to an increase of 30%. The *engineering effect*, which reflects the change in bed stability specifically imposed by the presence of caddisfly larvae, depended on both larval density and flow velocity ($F_{8,108} = 3·88$, $P < 0·01$ for the density–velocity interaction, Table 2). The engineering effect was maximal for all larval densities at a mid-channel velocity of 78·5 cm s^{-1}, ranging from an increased stability of 37% at the lowest density to 86% at the highest (Fig. 1b). At velocities greater than 78·5 cm s^{-1}, most particles were scoured from the channels irrespective of caddisfly density (Fig. 1a). However, it is worth noting that 16–42% more of the benthos remained intact beyond this threshold in channels colonized by larvae (Fig. 1b).

The engineering effect of the caddisfly larvae also depended on an interaction between larval density and particle size ($F_{4,108} = 2·31$, $P = 0·06$, Table 2). At the
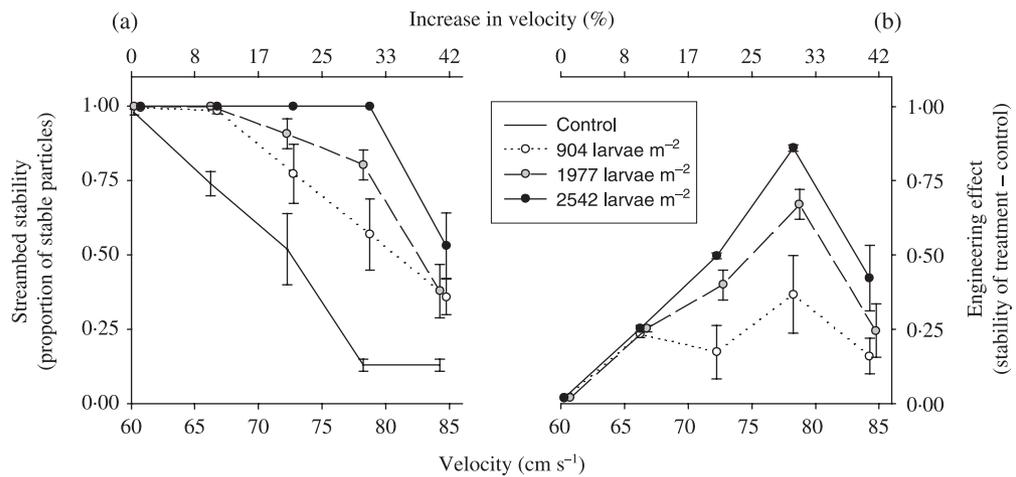
Fig. 1. The influence of hydropsychid caddisfly larvae on the stability of benthic particles. (a) The proportion of particles that remained stable (*y*-axis) with increasing levels of velocity displayed as an absolute scale on the bottom *x*-axis, and a relative scale on the upper *x*-axis. (b) The engineering effect, which is the increased stability of particles due to the presence of caddisfly larvae, as a function of larval density and velocity. Data points are the mean ± 1 SE.
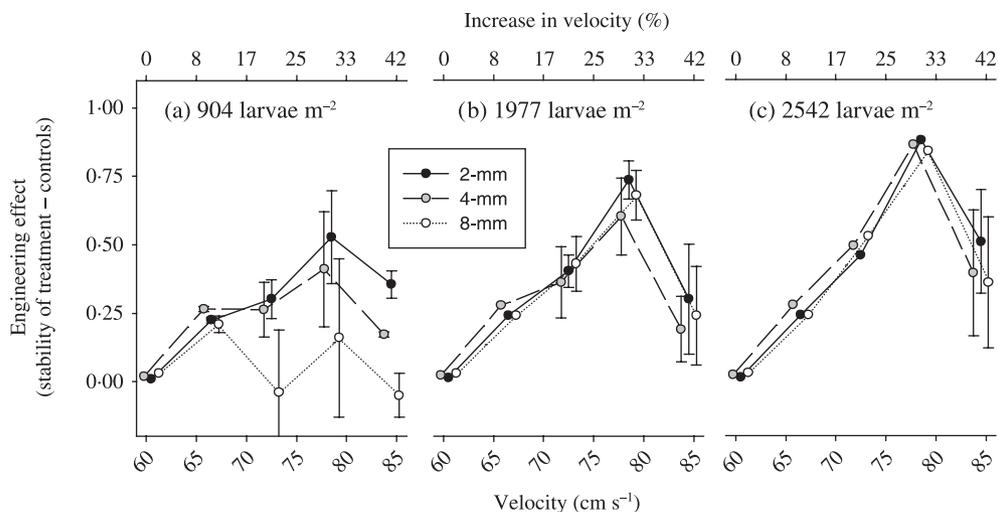

Fig. 2. The engineering effect of caddisfly larvae on three size classes of benthic particles. Results are displayed separately for the three levels of larval density to emphasize changes in the engineering effect (also see Table 2). Data points are the mean ± 1 SE.

lowest caddisfly density, there were significant differences in the stability of the three particle size classes with larvae stabilizing the smaller particles to a greater extent than larger particles (Fig. 2a). At a velocity of 78·5 cm s^{-1}, where the engineering effect of caddis larvae was greatest (Fig. 1b), larvae increased the stability of 2 and 4 mm particles by 53% and 41%, respectively, compared to an increase in the stability of 8 mm particles of just 17% (Fig. 2a). As caddisfly density increased, the engineering effect on the three particle size classes converged across all velocities (Fig. 2b,c).

Discussion

Hydropsychid caddisflies are among the most abundant and widely distributed groups of insects inhabiting streams throughout the world (Wallace & Merritt 1980). Our study suggests that these insects could act as ecosystem engineers in streams by increasing the stability of benthic habitats during high-discharge events. We found that the presence of net spinning caddis larvae increased the velocity required to initialize sediment erosion in experimental stream channels by 10–30%, depending on larval density. At velocities sufficient to scour 87% of all benthic particles in control channels, 57–100% of the streambed remained stable in channels colonized by caddis larvae. Such results suggest that caddisflies play an important role in creating the spatial 'refuges' – areas of streambed that remain stable during flooding that are known to moderate the resistance of lotic communities to physical disturbance (Lancaster 2000; Townsend *et al.* 1997).

Experimental channels such as those used in this study have been widely utilized as model systems to study the effects of biota on the physical properties of benthic habitats (Muschenheim *et al.* 1986; Nowell &
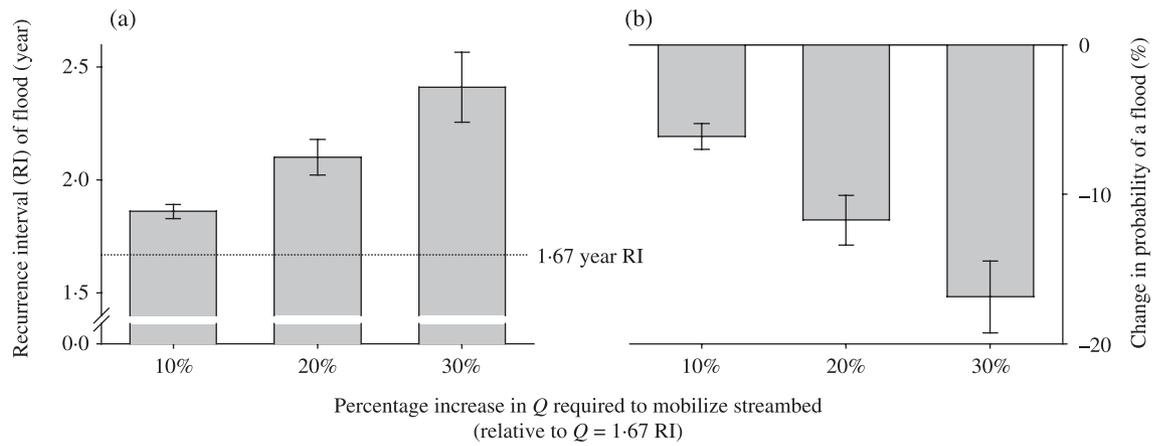
Fig. 3. The potential influence of net spinning caddisfly larvae on the frequency and probability of bed-scouring floods in natural streams. Twelve streams in Pennsylvania and Virginia, inhabited by *Hydropsyche* and characterized by gravel substrates (see Table 1), were chosen for analysis of their flood/frequency curves (see text for details). Assuming that the 1·67-year recurrence interval, RI, is a 'bankful' flood with discharge great enough to mobilize streambed sediments (a widely used definition of disturbance, Leopold *et al.* 1964; Poff & Ward 1989), we calculated how caddisflies would change (a) the recurrence interval of a flood, and (b) the probability of a flood occurring in a given year. For these calculations we assumed that caddisflies increase the discharge required to mobilize sediments by 10, 20 or 30% (*x*-axis) – a range equivalent to caddisfly effects shown in Fig. 1.

Jumars 1987; Vogel & LaBarbera 1978). While such experimental units are an obvious over-simplification of natural habitats, they allow one to unambiguously determine whether an organism affects the stability of surficial sediments. This is often not possible in natural settings owing to the inability to manipulate organisms and their biogenic structures without disrupting sediments, and the difficulty in controlling the physical factors that regulate particle transport. Nonetheless, extrapolating results from any model to a real system is problematic for a number of reasons, and the results of this study should be interpreted conservatively until a practical means to manipulate the densities and net-structures of these animals *in situ* can be found.

Nevertheless, it is worth noting that in standardizing conditions among the experimental channels, several parameters thought to influence bed stability were held within the range of naturally occurring values. For example, several hydrodynamic properties that moderate bed mobility were within the range of conditions documented for natural stream systems, animal densities were comparable to those in natural streams, and the particles sizes used were similar to those of streams we study. This does not necessarily ensure that particle behaviour under the experimental conditions was comparable to that in natural systems. It does, however, suggest to us that it is worth considering how hydropsychid caddisflies might alter the frequency and probability of bed scouring floods if their effect on particle stability under field conditions were comparable to that documented in this study. During a survey of the distribution of *Hydropsyche* in the mid-Atlantic United States, we sampled caddis larvae in 12 streams that had gravel substrates similar in size to those used in the current study (Table 1). For each of these 12 streams we used data available from the US Geological

Survey (the NWISWeb system) to calculate flood frequency curves from each stream's maximum annual discharge series (Black 1991). We assumed a 'bed-mobilizing flood' represented a discharge exceeding the 1·67-year recurrence interval. This magnitude of event is thought to represent a bankful flow at which physical forces alone are sufficient to mobilize streambed particles (Emmett & Wolman 2001; Leopold, Wolman & Miller 1964; Poff & Ward 1989).

Assuming that caddisflies increase the discharge required to scour particles by 10–30% above purely physical transport (like that documented in this study), the presence of caddis larvae might be expected to increase the recurrence interval of a bed-scouring flood from 1·67 year to between 1·86 and 2·41 year (Fig. 3a). If larvae increased the discharge required to move particles by just 10%, the probability of bed scour in any given year would decline by a mean 6% (range = 2·7–10·7% for the 12 streams examined). If caddisflies increased the discharge required to move particles by 30%, such as occurred at the highest densities in this study (Fig. 1a), then the probability of bed scour in a given year would drop by a mean 17% (range 7·4–29·8%, Fig. 3b). These scenarios focus only on initial bed movement; larval impacts are also likely to reduce the proportion of benthic habitat scoured even after particle mobility has been initiated (as in Fig. 1b). Obviously, these calculations require several simplifying assumptions, and they are only useful in outlining some of the possible effects of caddisflies in natural environments. They do, however, suggest these effects could be substantial when larval densities are high.

While there is a rich literature detailing the physical forces that moderate bed mobility in streams (see Emmett & Wolman 2001), relatively little attention has been paid to the potential for benthic organisms to

engineer their habitats in ways that modify physical forces. This contrasts with other aquatic systems where the engineering effects of biota on surficial sediments have been investigated to a much greater extent. In marine environments, for example, there is a long history of work documenting biological activity in sediments as being either stabilizing or destabilizing (Frey 1973; Nowell, Jumars & Eckman 1981; Rhoads 1974). The destabilizing effects of organisms are often mediated by changes in flow that result in localized scour of particles (Eckman, Nowell & Jumars 1981). However, these destabilizing effects are frequently offset by (a) faunal secretions that cement particles together, (b) bioturbation that alters the vertical distribution of particles, (c) the incorporation of fine particles into larger pellets and pseudofaeces, (d) microbial exudates that generate mucous coatings, and (e) the development of dense infaunal structures that deflect kinetic energy from the bed (Eckman 1985; Wright, Schaffner & Maa 1997).

In our study, a probable mechanism for the engineering effect of caddisflies is that the silk secretions of the larvae used in the construction of filtration nets bound particles together, resulting in a more stable particle matrix. We did not document this mechanism directly because of the difficulty in separating animals from their benthic habitat without also disrupting sediments. Nonetheless, it seems the most plausible explanation given that net spinning caddis larvae are well known to construct catchnets across multiple particles for structural support (Merritt & Cummins 1984; Wallace & Merritt 1980). A matrix of substrates connected by filtration nets would almost certainly confer stability by increasing the force required to erode particles. Our data suggest that the engineering effect of caddisfly larvae potentially differs between particle size classes. Smaller particles were stabilized to a greater extent than large particles at low caddisfly density, but this engineering effect converged among particle size classes at intermediate to high densities. It could be that as density increases, larvae build different sizes, shapes or types of nets that differentially alter the stability of particle size classes. Alternatively, larval preference for small substrates could differentially stabilize particles at low densities, but these preferences might be eliminated as density increases and space becomes limited. Further work is needed to distinguish these possibilities.

Acknowledgements

References

Allan, J.D. (1995) Stream ecology: *Structure and Function of Running Waters*. Chapman & Hall, London.

Benke, A.C. & Wallace, J.B. (1997) Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology* **78**, 1132–1145.

Black, P.E. (1991) *Watershed Hydrology*. Prentice Hall, Inc, Englewood Cliffs, NJ.

Bond, N.R. & Downes, B.J. (2000) Flow-related disturbance in streams: an experimental test of the role of rock movement in reducing macroinvertebrate population densities. *Marine and Freshwater Research* **51**, 333–337.

Cardinale, B.J. & Palmer, M.A. (2002) Disturbance moderates biodiversity–ecosystem function relationships: experimental evidence from caddisflies in stream mesocosms. *Ecology* **83**, 1915–1927.

Cardinale, B.J., Palmer, M.A., Swan, C.M., Brooks, S. & Poff, N.L. (2001) The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* **83**, 412–422.

Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002) Species diversity increases ecosystem functioning through interspecific facilitation. *Nature* **415**, 426–429.

Ceballos, G., Pacheco, J. & List, R. (1999) Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* **41**, 161–172.

Cobb, D.G., Galloway, T.D. & Flannagan, J.F. (1992) Effects of discharge and substrate stability on density and species composition of stream insects. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1788–1795.

Davis, J.A. & Barmuta, L.A. (1989) An ecologically useful classification of mean and nearbed flows in streams and rivers. *Freshwater Biology* **21**, 271–282.

Death, R.G. (1995) Spatial patterns in benthic invertebrate community structure: products of habitat stability or are they habitat specific. *Freshwater Biology* **33**, 455–467.

Death, R.G. (1996) The effect of patch disturbance on stream invertebrate community structure: the influence of disturbance history. *Oecologia* **108**, 567–576.

Eckman, J.E. (1985) Flow disruption by an animal-tube mimic affects sediment bacterial colonization. *Journal of Marine Research* **43**, 419–435.

Eckman, J.E., Nowell, A.R.M. & Jumars, P.J. (1981) Sediment destabilization by animal tubes. *Journal of Marine Research* **39**, 361–374.

Emmett, W.W. & Wolman, M.G. (2001) Effective discharge and gravel-bed rivers. *Earth Surface Processes and Landforms* **26**, 1369–1380.

Frey, R.W. (1973) Concepts in the study of biogenic sedimentary structures. *Journal of Sedimentary Petrology* **43**, 6–19.

Gallagher, E.D., Jumars, P.A. & Trueblood, D.D. (1983) Facilitation of soft bottom benthic succession by tube builders. *Ecology* **64**, 1200–1216.

Georgian, T. & Thorp, J.H. (1992) Effects of microhabitat selection on feeding rates of net spinning caddisfly larvae. *Ecology* **73**, 229–240.

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

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–1957.

Jumars, P. & Nowell, A. (1984) Fluid and sediment dynamic effects on marine benthic community structure. *American Zoologist* **24**, 45–55.

Lancaster, J. (2000) Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance. *Journal of Animal Ecology* **69**, 442–457.

Leopold, L.B., Wolman, M.G. & Miller, J.P. (1964) *Fluvial Processes in Geomorphology*. W.H. Freeman, San Francisco.

Littell, R.C., Miliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute, Inc, Cary, NC.

Matthaei, C.D., Arbuckle, C.J. & Townsend, C.R. (2000) Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. *Journal of the North American Benthological Society* **19**, 82–93.

Merritt, R.W. & Cummins, K.W. (1984) *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Publishing Co., Dubuque.

Muschenheim, D., Grant, J. & Mills, E. (1986) Flumes for benthic ecologists: theory, construction, and practice. *Marine Ecology Progress Series* **28**, 185–196.

Nowell, A.R.M. & Jumars, P. (1984) Flow environments of aquatic benthos. *Annual Review Ecology and Systematics* **15**, 303–328.

Nowell, A. & Jumars, P. (1987) Flumes: theoretical and experimental consideration for simulation of benthic environments. *Oceanography and Marine Biology Annual Review* **25**, 91–112.

Nowell, A.R., Jumars, P.A. & Eckman, J.E. (1981) Effects of biological activity on the entrainment of marine sediments. *Marine Geology* **42**, 133–153.

O'Connor, N.A. (1993) Resource enhancement of grazing mayfly nymphs by retreat-building caddisfly larvae in a sandbed stream. *Australian Journal of Marine and Freshwater Research* **44**, 353–362.

Palmer, M.A., Swan, C.M., Nelson, K., Silver, P. & Alvestad, R. (2000) Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landscape Ecology* **15**, 563–576.

Petraitis, P., Latham, R. & Niesenbaum, R. (1989) The maintenance of species diversity by disturbance. *Quarterly Review of Biology* **64**, 393–418.

Poff, N. & Ward, J. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Science* **46**, 1805–1818.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E. & Stromberg, J.C. (1997) The natural flow regime: a paradigm for river conservation and restoration. *Bioscience* **47**, 769–784.

Rhoads, D.C. (1974) Organism–sediment relationship on the muddy sea-floor. *Oceanography and Marine Biology Annual Review* **12**, 263–300.

Townsend, C.R., Scarsboro, M.R. & Doledec, S. (1997) The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* **42**, 938–949.

Vogel, S. (1994) *Life in Moving Fluids*. Princeton University Press, Princeton, NJ.

Vogel, S. & LaBarbera, M. (1978) Simple flow tanks for research and teaching. *Bioscience* **28**, 638–645.

Wallace, J. & Merritt, R. (1980) Filter-feeding ecology of aquatic insects. *Annual Review of Entomology* **25**, 103–133.

Wright, J.P., Jones, C.G. & Flecker, A.S. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**, 96–101.

Wright, L.D., Schaffner, L.C. & Maa, J.P.-Y. (1997) Biological mediation of bottom boundary layer processes and sediment suspension in the lower Chesapeake Bay. *Marine Geology* **141**, 27–50.