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Distributional responses to flow disturbance by a stream-dwelling snail

Joseph R. Holomuzki and Barry J. F. Biggs

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This study examines how flow disturbance influences distributions of the snail Potamopyrgus antipodarum, a common grazer in New Zealand streams, at the drainage basin, substratum, and rock face scales. We analyzed survey data from 48 streams across New Zealand to relate snail densities to hydrological patterns and conducted experiments in a laboratory flow tank and in artificial streams in field conditions to evaluate refugium effects of different substrate types in high flows. The survey showed that local densities were significantly inversely related to flood frequency, suggesting flow disturbance influenced regional distributions of P. antipodarum. The survey also revealed that lake-fed streams and low-gradient streams in foothill regions tended to have fewer, less severe floods and higher snail densities than high-gradient (>1%) streams in mountain and foothill regions. Results from both the flow tank and artificial stream experiments showed that finer-grained substrates provided better refugium from dislodgment conditions than larger substrates (i.e., cobbles) when bed sediments were artificially stabilized. In the flow tank where velocities were incrementally increased, dislodgment rates of snails were significantly lower on artificial gravels than on artificial cobbles or bedrock. Snails moved to low-velocity patches (i.e., crevices) on all substrates as current velocities increased. However, more snails accumulated in crevices between gravels and pebbles than between cobbles; the relatively high turbulence between cobbles, in part, contributed to high dislodgment rates from this substrate. Similar differences in dislodgment vulnerability and flow refugium effects were observed in experiments using real substrates in artificial streams in field conditions. A substrate size-flood duration experiment showed that significantly more snails were dislodged from cobbles and pebbles than from gravels and that more were dislodged in longer-lasting high discharge events (30 min) than in brief ones (1 min). Another experiment in which snails were transported downstream (1, 3, 6 or 9 m) from non-stabilized substrate patches similarly showed that snail dislodgment and mortality rates were generally higher from cobbles than from gravels and pebbles. Like other studies, we found that larger substrate particles were less likely to move than smaller ones (gravels) under similar hydraulic conditions. However, we discovered that the best refugium conditions for resisting dislodgment are not necessarily linked to larger substrate size. Our findings also suggest that flooding may alter local densities of snails by moving and relocating snails rather than by killing them. The observed patterns of distributions of these snails appear to result from complex interactions between hydrological/hydraulic features and substrate architecture.

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Copyright © OIKOS 1999 ISSN 0030-1299 Printed in Ireland – all rights reserved Ecological communities are commonly affected by physical disturbance (e.g., fire, waves, floods). Often, however, the impact of the disturbance is not uniform across the physical, and hence, biotic environment. Spatial heterogeneity in environments creates physical patches that are differentially affected by the disturbance so that some may act as refugia to mitigate the effects of the disturbance event. Movements by organisms to refugia may be active or passive. In either case, higher survivorship in refugia relative to other patches, and subsequent movements from refugia after the disturbance to more heavily impacted patches, are often critical in resetting demographies of populations and community structure (Grime 1979, Sousa 1984, Pickett and White 1985, Huston 1994).

In many ways streams may provide a model system for studying refugia-disturbance interactions. Floods are an obvious source of disturbance in these systems. These disturbances elevate current velocities, which in turn, can mobilize bed sediments, wash away individual organisms, and cause death (e.g., Resh et al. 1988, Yount and Niemi 1990, Giller et al. 1991, Biggs 1995, Dodds et al. 1996). Sources responsible for population or community recovery include drift from lesser disturbed headwaters or tributaries, recolonization from lateral areas along stream banks or the hyporheos (deep sediments), hatching from eggs, and resumption of an aquatic existence (e.g., amphibious bugs or beetles) (reviewed by Sedell et al. 1990, Mackay 1992). In addition, the recent realization that hydraulic forces associated with high flows can vary significantly over rather small spatial scales has led to the suggestion that patches of flow refugia within disturbed areas of the stream channel also may contribute to recolonization of impacted areas (Lancaster and Hildrew 1993a, b, Lancaster 1996, Lancaster and Belyea 1997).

Habitat features such as substrate size, type, and stability within stream channels can create physical patches that are differentially affected by flow disturbance. For example, large stable boulders or debris dams of wood can sometimes provide shelter from high flow forces during disturbance events (Suren 1991, Uehlinger 1991, Borchardt 1993, Palmer et al. 1995, 1996, Biggs et al. 1997). Hydraulic forces in high flows vary not only between different substrate types but can vary also within types and even over surfaces of a single stone (Statzner and Higler 1986, Statzner et al. 1988, Hart et al. 1996). Such observations have led researchers to ask whether mobile organisms exhibit very short-term reactions to resist disturbance forces. While evidence suggests that some fishes (e.g., Meffe 1984) and benthic invertebrates (Lancaster and Hildrew 1993b, Winterbottom et al. 1997) survive flooding events by occupying low-flow areas, the mechanisms involved in avoiding high flow forces are not well understood.

The extent to which spatial refugia mitigate high-flow effects on stream organisms may vary, in part, with the intensity and frequency of the disturbance. For example, smaller, less stable bed sediments may provide adequate flow refugia in streams with relatively mild, infrequent floods, but not in streams with severe, frequent floods that cause considerable bed movement (Scarsbrook and Townsend 1993). Interplay between bed sediment refugia and disturbance intensity/frequency are believed by some to be key determinants of biotic structure in streams (e.g., Poff and Ward 1990, Townsend and Hildrew 1994, Townsend et al. 1997). Thus, the potential implications of how bed sediments mitigate disturbance effects in streams seem far reaching, which should serve to drive inquiries into the dynamics between increasing flows, bed architecture, and loss or movements of organisms in these ecosystems.

Many studies have revealed that high discharge events can sometimes cause severe population losses and changes in community structure (e.g., Resh et al. 1988, Niemi et al. 1990, Giller et al. 1991, Flecker and Feifarek 1994, Townsend et al. 1997). Further, the extent to which flooding can dislodge organisms from substrates appears to be directly related to the degree to which substrates are tumbled or shifted (Reice 1985, Power and Stewart 1987). However, we have a poor understanding of how changes in near-bed flows (≤ 2 cm from the bottom), the hydraulic environment experienced by most benthic organisms, affect risk of dislodgment and of how susceptibility of dislodgment is mitigated by substrate type. Further, though downstream transport distance increases with current velocity (Ciborowski 1983, Allan and Feifarek 1989), little is known about the fate of organisms once transported or how downstream transport distance affects mortality. Considering that discharge-driven disturbances are a dominant organizing factor in many streams (Hildrew and Townsend 1987, Resh et al. 1988, Hildrew and Giller 1994, Wootton et al. 1996), such information is needed to make confident predictions about population and community recovery to flow disturbance.

The purpose of this study was to examine how high flows in disturbance events affect distributions of the small amnicolid snail, *Potamopyrgus antipodarum*, on three spatial scales: on rock faces, between substrate types, and between streams in different drainage basins. These snails are endemic to many New Zealand streams and lakes and may potentially affect structure and function of these systems. When at very high densities $(>3000 \text{ m}^{-2})$, these grazers can significantly reduce algal biomass, modify algal assemblage (Winterbourn and Fegley 1989, Biggs and Lowe 1994), and displace other macroinvertebrates (Death 1991) in streams. These snails are seldom eaten by predaceous native and non-native fishes (Bonnett et al. 1989, Kusabs and Swales 1991, Sagar and Glova 1995), and thus represent a 'trophic dead-end' in many systems (but see Levri 1998). *Potamopyrgus* are now also found as an exotic species in southeastern Australia (Schreiber et al. 1998), Europe (Statzner 1981), the Laurentian Great Lakes in North America (Zaranko et al. 1997), and the northwestern United States (Montana and Idaho) (B. Kerans unpubl.), where they are beginning to alter biotic structure and function in some habitats. Information on how flood disturbance affects their local densities and distributions may help us predict how different aquatic ecosystems will respond to their invasion.

We examined field survey data and conducted experiments in a laboratory flow tank and in artificial streams in field conditions to address the following questions: 1) How does flood frequency and magnitude affect densities of *Potamopyrgus antipodarum* in New Zealand streams? 2) Do snails make microspatial adjustments on rock faces to resist dislodgment as nearbed current velocity incrementally increases? 3) How does duration of the flow disturbance affect dislodgment and mortality rates in different substrates? 4) How does transport distance affect flood-induced mortality?

Methods

Field survey

Data on P. antipodarum densities were obtained from 48 streams from 1989 to 1994 from the New Zealand National Water Quality Monitoring Network (Smith and McBride 1990) to address whether regional distributions were related to flood frequency. Each stream was sampled at the same location on 1-3 occasions over the six-year sampling period for a total of 62 collections. Seven replicate samples were taken each collection with a Surber sampler (area: 0.1 m², net: 250 µm-mesh) in late summer to early autumn when streams were at base-flows. Bed sediments at all sites but one were a mixture of moderately sorted gravels (8-64 mm) and cobbles (64-256 mm). All samples were collected from relatively shallow areas ($\sim 15-30$ cm depths) where water velocities, as measured by an Ott current meter (at 0.6 of the depth from surface to bottom), ranged from 30 to 60 cm s⁻¹. Snails were preserved in 70% ethanol upon collection and separated from substrates in the laboratory.

Hydrological data at each sampling site were obtained from the National Water Resources Archive administered by the National Institute of Water and Atmospheric Research. Sites covered a wide range of flood regimes, from lake- and spring-fed streams with few floods to high-gradient (>1% slope) mountain streams with >20 floods per year. The frequency of floods at each site was quantified by using the hydrological descriptor FRE₃, the frequency of high flow events per year that exceed $3 \times$ the median daily discharge (Clausen and Biggs 1997). A different FRE₃ was computed for the 12 streams sampled more than once over the six-year sampling period. Because these streams were sampled in different years and because sampling reach topography changed considerably in some streams between years due to sediment movements, these different FRE₃ values for the same stream in different years were treated independently in statistical procedures (i.e., n = 62). For these reasons, and because *Potamopyrgus* has a relatively short life span $(\sim 12 \text{ mo})$ (Winterbourn 1970), average snail densities from these streams in different years were also treated independently. We first pooled all stream types and used regression analysis (SYSTAT 7.0) to test whether log (x+1) transformed densities were a function of FRE_3 In doing this, we wished to see whether FRE_3 was a predictor of regional distributions of Potamopyrgus. We then ran separate regression analyses for each stream type (i.e., lake-fed, mountain, foothill $\leq 1\%$ gradient], foothill [>1% gradient]) to evaluate how general patterns between snail density and FRE₃ may be influenced by stream physiognomy.

Laboratory flow tank experiment

The relationship between dislodgment and current velocity, and changes in snail movements over rock faces with incremental increases in flow, were examined in four different size classes of artificial substrates in a laboratory flow tank, as used in Biggs and Thomsen (1995). The tank (1.5 m long, 0.4 m wide) was constructed of 16-mm thick Plexiglas and recirculated 197 L of water in a closed loop (Fig. 1A). Untreated, high-quality aquifer water (19°C) was circulated over substrates by twin, three-bladed motorboat propellers (each 17 cm in diameter) connected by a pulley-notch belt and powered by a 3 hp (2.2 kW) motor. Substrates were placed on the top, horizontal portion of the loop behind two sets of plastic screens that acted as collimators. Water first flowed through a wider screen (4.0 cm wide, 8×8 mm mesh), then through a second thinner screen (2.0 cm wide, 8 mm mesh), situated 12 cm behind the first, to produce a steady flow. A 0.7-m-long section behind the second screen contained a removable Plexiglas plate $(0.61 \times 0.41 \text{ m})$ on which one of four artificial substrate types was attached by silicon caulk. The plate with attached substrate was kept stable during increased flows by a third screen (2.0 cm thick, 8) mm mesh) immediately behind the plate and by four removable plastic fasteners $(30 \times 30 \times 10 \text{ mm})$; two per side) screwed into the sides of the tank above the plate's edges. Substrates were made of sheets of molded plastic (sheet dimensions: 0.6×0.4 m) that mimicked four different sizes of coarse particles: "gravels", "pebbles", "cobbles" or "bedrock". "Gravel" substrates were represented by 366 evenly-spaced, 2-cm-diameter hemispheres (roughness height = 1 cm) per sheet. "Pebble" substrates were represented by 119 evenly-spaced, 4-cmdiameter hemispheres (roughness height = 2 cm) per sheet, while "cobbles" had 28 evenly-spaced, 8-cm-diameter hemispheres (roughness height = 4 cm) per sheet. Center-to-center distances between hemispheres for "gravels", "pebbles" and "cobbles" were 4.5, 8.0, and 9.0 cm, respectively. "Bedrock" was represented by a flat sheet without bed elements (= hemispheres). Surfaces of all substrates were coated by a very short (~0.1 mm) uniform layer of pulverized fiber to somewhat represent the coarse surface texture of natural stones.

Current velocity was measured 2 cm from the tops of bed elements at 15 different motor settings at increments of ~100 revolutions (i.e., 15 different velocities) with an Ott current meter. Current readings were taken for 60 s at each setting over 1-2 centrally located elements for each substrate type through a small, elliptical port (3×8 cm) in the flow tank lid. Near-bed velocities on flat sheets ("bedrock") were also taken at one central locality. We realized that this lack of spatial replication limited our ability to assess flow heterogeneity over upstream and downstream bed elements. However, the advantage of a small-sized port was that it limited the amount of entrained air bubbles entering the tank, hence increasing the accuracy of current readings, particularly at higher velocities.

Adult snails were collected every 2-3 d in early February 1997 from the upper branch of the Kaiapoi River, located 26 km N of Christchurch, New Zealand and kept in aerated aquifer water at 19°C in the labora-



Fig. 1. Schematics of A) the laboratory flow tank, and B) the artificial stream channels at the Silverstream Field Station. Arrows represent direction of water flow.

tory. Snails ($\bar{x} \pm 1$ SE dry mass per individual: 3.24 \pm 0.23 mg, n = 27; 4–6 mm from apex to aperture) were randomly sorted into groups of 10 into two plastic cups, then a group was gently poured into the center of each upstream and downstream half of the substrate. A total of 20 snails per substrate (~ 83 individuals m⁻²) is well within limits of natural densities of P. antipodarum in New Zealand streams (Jowett et al. 1991). Snails were given 10 min to acclimate and disperse before starting flow; an adequate time for dispersal over substrata considering they move at 15-50 mm min⁻¹. A thin film of petroleum jelly spread on the edges of the Plexiglas plate helped deter snails from leaving substrates (see Biggs and Lowe 1994). Tank-flow was then started at 10 cm s⁻¹ (measured 2 cm above substrates) and increased by increments of 10 cm s⁻¹ at 1-min intervals. Maximum flow was 150 cm s⁻¹, a velocity comparable to that encountered in real flood conditions (e.g., Biggs 1995). Numbers of snails on upstream and downstream halves of bed elements, between elements (i.e., crevices) and numbers dislodged were recorded at the end of each 1-min interval. This procedure was replicated 10 times for each substrate type using different snails for each replicate. All snails were used within 48 h of collection. In the few cases where snails glided over the petroleum jelly and off the substrate either during current ramping or the acclimation period, the trial was immediately halted and re-done using a different set of snails. Analysis of variance (ANOVA) (SYS-TAT 7.0) was used to test whether levels of 50% dislodgment (arcsine transformed) were reached at significantly different current velocities among substrates. Regression analysis was used to examine changes in numbers of snails on microsites (i.e., crevices) on bed elements over time.

Artificial stream experiments

Effects of flood duration in stable substrates

Dislodgment and mortality rates of snails exposed to two different durations of simulated floods were compared among four natural substrate types in artificial stream channels between 24 February and 2 March 1997 at the Silverstream Research Facility located 26 km N of Christchurch. Experimental streams were PVC pipe (5.0 m length, 0.25 m diameter) halved longitudinally to produce a U-shaped channel (in cross-section) with an open top (Fig. 1B). A thin layer of sand glued by silicon caulk to the inner surface of each channel helped to simulate bed roughness in real streams. Four parallel channels, spaced 0.5 m apart and sloped at a 1.7% gradient, were placed behind a weir constructed of concrete and radiosa pine that held water diverted from the adjacent Kaiapoi River. Channel heads were placed in half-circles, equal in diameter to channels, cut into the top board of the weir. Another board immediately behind the top board of the weir at the channel heads was used as a valve to regulate discharge in the flow-through channels. At downstream ends of each channel were plastic screens and drift nets. Screens (8 mm mesh) were cut to conform to the half-circle shape of channels and were attached by screws. Screens were large enough to allow dislodged snails to pass into drift nets (mouth 33×33 cm, 1 m length, 153 µm mesh) but were small enough to prevent substrate washing into the nets. Nets were placed to assure capture of all dislodged snails.

Substrates used in channels were rocks hand-collected from the adjacent river. All macroinvertebrates were rinsed and/or hand-picked from rocks, but a thin biofilm of algae (mostly diatoms) was retained to provide more natural conditions and a potential food source for snails. Rocks were then sorted into three types based on particle size: gravels (11-28 mm diameter), pebbles (31-60 mm diameter), and cobbles (63-97 mm diameter). An equal mass (7 kg) of each substrate type was placed in three of the four channels; the channel without added substrate (i.e., gluedsand only) served as a control. Substrates were uniformly spread over a 0.9 m length of channel, starting 3 m from the screen at downstream ends. Gravels were completely submerged ($\sim 2-3$ cm depth) at baseflows (0.2 L s⁻¹); however, tops of some pebbles and all cobbles were exposed to the air. Substrates were tumbled downstream by slowly increasing discharge to 7.5 L s^{-1} to deposit them in a natural, stable configuration at the downstream ends of channels. However, if portions of the substrates were not transported, we gently nudged them by hand so that all rocks would stabilize at downstream ends. After 2-3 min of high flows, discharge was returned to base flow. Our goal in this experiment was to compare the efficacy of the different substrates as flow refugia when sediments were immobilized. It also enabled us to evaluate the generality of the results of the flow tank experiment.

Snails (dry mass: 3.65 ± 0.41 mg; length 4–6 mm) collected from the Kaiapoi River were sorted into groups of 50 in containers and randomly assigned to channels. Snails were gently poured from containers over the entire patch of stabilized substrate to aid in homogenizing initial distributions. After 15 min, \sim 80% of snails in each substrate treatment (except the control) were in rock interstices (i.e., not visible on surface). Discharge was then steadily increased over 10 s in all channels simultaneously to 7.5 L s⁻¹. which generated maximum velocities of 150 cm s⁻¹. Duration of simulated floods was either 1 or 30 min and was determined randomly before snail additions. After flooding, snails were enumerated as: 1) those transported into nets, and 2) those that remained on substrates. Substrates were thoroughly hand-sorted after floods to retrieve all snails, and hence, to help quantify mortality. We assumed unrecovered snails were killed by shifting substrates. Even in stable (non-eroding) rock clusters, smaller particles within the cluster can vibrate greatly during high-intensity flows (Biggs et al. 1997), and presumably cause mortality. Therefore, we assessed mortality by summing these counts and counts of recovered, dead snails. Each flood duration treatment was replicated 8 times for each substrate type, using different snails and rocks for each replicate. Substrate type was randomly assigned to channels after each flood event. Two-way MANOVA (SYSTAT 7.0) was used to assess flood duration and substrate effects on the interdependent response variables, percent dislodgment and mortality (arcsine transformed). Results were then interpreted employing univariate tests for each response variable.

Effects of transport distance and substrate erosion

Substrates often erode in real floods. Thus, in this experiment we evaluated erosion impacts for snails on different substrates. Studies that have tumbled rocks by hand or by mixer have shown that dislodgment rates of benthic organisms increase with tumbling frequency (Reice 1985, Power and Stewart 1987). We wished to determine how tumbling disturbance of different-sized rocks and subsequent displacement of snails affected snail fate. To do this, we tumbled rocks in a linear fashion using increased flows, as in a real flood, and evaluated how amount of rock erosion and tumbling distance affected dislodgment and mortality rates of snails.

Channel setup was the same as in the previous experiment, except length of each PVC channel was extended to 10 m. Kinds and amount of substrate, and assignment procedures to channels, were also as before. However, in this experiment, substrate patches with snails were placed at distances of either 1, 3, 6 or 9 m from downstream ends; substrate patches at the 3, 6 or 9 m distances were separated from downstream ends (screens) by a stretch of sand (glued) equal to that distance, respectively. Transport distance used in each trial was determined randomly and each distance was replicated 8 times for each substrate type. Fifty snails were randomly assigned to each channel and given 15 min to acclimate before flow was increased. As before, most snails moved into rock interstices during the acclimation period. Discharge was increased from 0.2 L/s to 7.5 L/s over 10 s, generating a maximum velocity of 150 cm s⁻¹. Based on results of the previous experiment, we used a 1-min flood duration for all trials. Numbers of snails remaining in channels and transported into nets were counted immediately after each trial. Mortality was assessed as before. Amount of substrate eroded was quantified by collecting and weighing all rocks displaced from the initial 0.9-m-long patch. Percent erosion was calculated by dividing mass of rocks dis-



Fig. 2. Densities of snails in 48 New Zealand streams varying in source and gradient as a function of flood frequency (FRE_3 ; after Clausen and Biggs 1997).

placed by total rock mass used (7.0 kg). Two-way MANOVA tested whether percent dislodgment and mortality (arcsine transformed) were affected by transport distance and substrate. We used correlation analysis to determine whether dislodgment varied with amount of erosion of each substrate.

Results

Field survey

We found that *P. antipodarum* densities were inversely related to flood frequency ($R^2 = 0.154$, P = 0.002) (Fig. 2), though there was considerable variation in this general pattern. Much of the variation was related to source and gradient of the stream. Lake-fed streams and low-gradient streams in foothill regions tended to have fewer, less severe floods and higher snail densities than high-gradient streams in mountain and foothill regions. When each stream type was considered separately, however, snail densities only in steep, foothill streams were significantly negatively affected by FRE₃ $(R^2 = 0.122, P < 0.05)$. Regardless of stream type, snail densities were quite variable in streams with FRE₃ values < 20, thereafter densities were consistently low. Overall, average densities of P. antipodarum rarely exceeded 1000 individuals m^{-2} , even in those streams with infrequent floods.

Laboratory flow tank experiment

Dislodgment profiles of snails varied among substrate types. Probability of dislodgment was higher on mimics of bedrock and large cobbles than on mimics of gravels and pebbles (Fig. 3). Some dislodgment first occurred at current velocities of 30-40 cm s⁻¹ on all substrate types. However, 50% dislodgment was reached at ~90 cm s⁻¹ for "bedrock" and "cobble" substrates while at 110 cm s⁻¹ and 120 cm s⁻¹ for "pebble" and "gravel" substrates, respectively, and this difference was significant $(F_{3,36} = 11.75, P < 11.75, P$ 0.001). No snails withstood velocities of 150 cm s⁻¹ on "bedrock". However, a few snails were consistently able to withstand these flows on the other substrates, particularly on "gravel" and "pebble" (Fig. 3). These data indicated that the particle architecture of these other stabilized substrates provided refugium patches from high flows.

The number of snails present on upstream and downstream microsites on hemispheres generally decreased as near-bed velocities increased (Fig. 4). In contrast, regression analysis showed number of snails in crevices increased significantly until near-bed velocities reached ~ 50 cm s⁻¹ (analyses from 0-50 cm s⁻¹; "gravel": $\beta = 0.117$, $R^2 = 0.98$, P < 0.001; "pebble": $\beta = 0.040$, $R^2 = 0.97$, P < 0.001; "cobble": $\beta = 0.066$, $R^2 = 0.92$, P = 0.002), suggesting snails moved into this microsite as flows increased. Beyond this velocity, numbers in crevices declined steadily. In addition, downstream sides of "cobbles" appeared to



Fig. 3. Dislodgment profiles of snails on artificial "gravel", "pebble", "cobble" and "bedrock" substrates over incremental increases in near-bed velocities (2 cm above substrate) in the flow tank. Shown are means ± 1 SE based on 10 trials per point for each substrate.



NEAR-BED FLOW (cm/s)

Fig. 4. Mean $(\pm 1 \text{ SE})$ number of snails on upstream (\oplus) and downstream (\Box) halves of bed elements and between bed elements (i.e., crevices) (\blacktriangle) on "gravels", "pebbles", and "cobbles" relative to increases in near-bed velocities in the laboratory flow tank (n = 10 trials per point for each microsite).

provide better flow refugium than downstream sides of "gravels" and "pebbles". Snail numbers on downstream sides of "gravels" and "pebbles" decreased as

Table 1. Results of two-way MANOVAs for effects of A) flood duration and substrate type, and B) transport distance and substrate type, on dislodgment and mortality of snails in artificial stream experiments.

Source	df	Wilks' λ	F	Р
A.				
Duration	2,55	0.727	10.31	< 0.001
Substrate	6,110	0.102	39.09	< 0.001
Duration × Substrate	6,110	0.897	1.03	0.441
B.				
Distance	6,222	0.924	1.48	0.184
Substrate	6,222	0.373	23.55	< 0.001
Distance × Substrate	18,222	0.794	1.51	0.089

velocities were ramped from 0 to 50 cm s⁻¹, whereas snail numbers on downstream sides of "cobbles" remained uniform over these velocities.

Artificial stream experiments

Effects of flood duration in stable substrates

Probability of snail dislodgment varied with both flood duration and substrate type (Table 1A, Fig. 5A). Dislodgment rates were slightly, but significantly, higher in



SUBSTRATE

Fig. 5. Average percent (A) dislodgment and (B) mortality of snails in the four substrates in artificial stream channels during 30-min and 1-min floods. Vertical lines are 1 SE; n = 8 trials per substrate for each flood duration.

NUMBER PRESENT



Fig. 6. Average percent (A) dislodgment and (B) mortality of snails from transport distances of 1, 3, 6, and 9 m from the four substrates in artificial stream channels. Vertical lines are 1 SE; n = 8 trials per substrate for each transport distance.

flood conditions lasting 30 min than 1 min ($F_{1,56} = 19.34$, P < 0.001). Dislodgment was far higher from controls (no stones) than from other substrates. Among coarser substrates, dislodgment was greatest from cobbles and lowest from gravels. Increasing flood duration had no effect on dislodgment rates from gravel ($F_{1,14} = 0.846$, P > 0.25) but significantly increased losses from pebbles ($F_{1,14} = 9.159$, P < 0.01) and from cobbles ($F_{1,14} = 6.751$, P = 0.02).

Snail mortality was low (2.2-5.5%) and did not vary significantly between flood durations or substrate types (both P > 0.40, Fig. 5B).

Effects of snail transport distance and substrate erosion Dislodgment rates were related to substrate type but not to distance of the substrate patch from downstream ends (Table 1B). Snail dislodgment from control channels was consistently $\geq 98\%$, regardless of transport distance, and was significantly greater than from coarse substrates ($F_{3,112} = 48.38$, P > 0.001, Fig. 6A). Among coarse substrates, dislodgment was generally higher from cobbles and pebbles than from gravels. Degree of dislodgment was highly correlated with amount of substrate eroded (Fig. 7) (gravel: r =0.895, P < 0.001; pebble: r = 0.602, P < 0.001; cobble: r = 0.621, P < 0.001). Propensity to erode also varied among substrates. On average (± 1 SE), 64.3% (6.1), 34.4% (4.3), and 49.3% (5.8) of gravels, pebbles, and cobbles, respectively, eroded from the initial 0.9-m placement stretches in each flooding event, and this difference was significant ($F_{2,93} = 7.198$, P < 0.001).

Snail dislodgment increased linearly with sediment erosion for all substrates, but differences in physical stability among substrates affected relationships between dislodgment and refugium quality of the substrates (Fig. 7). Among substrates, dislodgment rates of snails were lowest from gravels until ~ 55% of the gravels were mobilized. At this point, snail dislodgment rates "equaled" those from pebbles at 0% erosion (see dashed line, Fig. 7). When ~ 92% of the gravels were mobilized, snail dislodgment rates from gravels "equaled" those from pebbles at 58% erosion and those from cobble at 0% erosion. Thus, the relative quality of a substrate as a refuge from high flows varied with extent of erosion.

Mortality rates varied significantly among substrate types (Fig. 6B; Table 1B). Mortality was higher in cobbles than in other substrates ($F_{3,112} = 5.49$, P < 0.001), but as before, mortality rates were low (1.0–5.7%) in all substrate types. Snail mortality was not related to downstream transport distance ($F_{3,112} = 0.73$, P > 0.50).



Fig. 7. Relationships between snail dislodgment (%) and substrate erosion (%) for gravels (\bigcirc), pebbles (\square) and cobbles (\triangle) in the artificial streams. The relative quality of a substrate as a refugium from high discharge events changes with the amount of substrate eroded. Dashed lines are drawn to help illustrate this relationship (see Results for full explanation). Solid lines are linear correlations for each substrate type.

Discussion

Our results suggest that flow disturbance affects distributions of P. antipodarum on various spatial scales. On a regional scale, snail densities were inversely related to flood frequency in New Zealand streams. However, densities varied considerably in this broad-scale trend, particularly for streams with FRE₃ values < 20. Much of this variation can be explained by source and gradient differences in our diverse array of sample streams. Lake-fed streams, as well as low-gradient streams in the foothills of the New Zealand Alps, tended to flood less frequently than high-gradient streams in the mountains or foothills. Coincidentally, snail densities were generally higher in the lake-fed and low-gradient streams than in the high-gradient streams. In addition, some between-stream variation in densities may be explained by differences in size class distributions among substratum depths. Statzner (1981) found that larger individuals of *Potamopyrgus* tend to be more common in deeper sediments than in upper substratum layers in all seasons except summer. Our samples were taken from relatively shallow depths in late summer and early autumn when some larger individuals could have moved into deeper sediments. Movements by larger individuals to upper sediments after spring floods may be an important recolonization source by which Potamopyrgus populations recover from high discharge events. Despite considerable variation among local densities, our survey data suggest that hydrologic regime influences regional distributions of this snail.

Another factor that may affect the relationship between snail densities and flood frequency is channel form and bed sediment composition. Moderate increases in discharge have relatively little erosive effect in boulder-cobble channels compared to gravel bed channels (Richards 1982). In the latter, increased flows can scour pools and alternatively aggrade and degrade riffles on upstream and downstream sides, respectively (Resh et al. 1988). Only one of 48 streams in our survey had a boulder channel form; the others were gravel to cobble. Parenthetically, the boulder-bed stream had a moderately high FRE₃ (11) yet still supported a relatively high snail density (135 inds. m^{-2}). This observation offers support to the notion that large stable boulders can sometimes provide flow refugia in highmagnitude discharge events that transport smaller-sized bed materials (Suren 1991, Biggs et al. 1997).

Results from both our laboratory flow tank and artificial stream experiments indicate that, at least for snails, finer-grained substrates can provide better refugia from dislodgment than coarser substrates (cobbles) when flows are such that no to moderate amounts of bed movement occur. In the laboratory flow tank where simulated substrates were immobile, dislodgment rates of snails were lowest on "gravels". Further, as near-bed velocity increased, more snails accumulated in crevices

between "gravels" and "pebbles" than in crevices between "cobbles". When roughness elements are relatively close, as they were in the "gravels" and "pebbles", the flow skims across the crests (top) resulting in much slower flows and stable eddies in spaces between the bed elements (Davis and Barmuta 1989). This feature, coupled with the organism's small size and cone-like body shape, likely mitigated hydraulic stress on snails in "gravel" and "pebble" crevices, thereby reducing dislodgment rates. Moreover, the relatively high turbulence between "cobbles", in part, probably contributed to high dislodgment rates from this substrate. Turbulence in "cobble" crevices increases at a significantly higher rate than in "gravel" and "pebble" crevices, particularly beyond near-bed (2 cm from element crests) velocities of ~ 70 cm s⁻¹ (S. Brown and J. Holomuzki unpubl.). Bouckaert and Davis (1998) similarly found that turbulence is highest in wake regions of boulders (streamwise direction) relative to other microsites (e.g., upstream face). Flow separation and wake interference (i.e., vortices produced by upstream elements that affect downstream elements) probably occurred as near-bed velocities increased, increasing turbulence (Carling 1992). Shear stress also likely contributed to higher snail dislodgment from "cobbles", considering that turbulence associated with accelerating flows can produce high shears (Tennekes and Lumley 1972, Bouckaert and Davis 1998).

Similar differences in refugium effects were observed among real substrates. In the flood duration experiment, in which substrates were deposited downstream before increasing discharge, gravels provided better conditions for resisting dislodgment during high flows than coarser substrates. Significantly more snails were dislodged in 30-min floods in pebbles and cobbles than in gravels. Even in the transport experiment where substrates were erodible, mortality and dislodgment rates were generally higher from cobbles than from gravels and pebbles. Larger, heavier cobbles are apparently more likely to crush snails during entrainment than smaller, lighter substrates. Further, natural cobbles have greater distances between stones than smaller substrates like gravels and pebbles. Greater spacing of roughness elements creates a hydraulic environment with relatively high flows in the spaces between elements (Morris 1955, Gordon et al. 1992), thus increasing the chance of snail wash-out. However, large homogeneous patches of cobble are rare in real streams; cobble interstices are typically filled with finer particles. Studies that use more realistic combinations of particle sizes and arrangements will provide a better assessment of how hydraulic forces influence spatial distributions of snails and allow us to more reliably extrapolate results from highly controlled experiments to real stream conditions.

Gravels may not always provide the best refugium from hydraulic stress. The smaller size and associated

relative lightness of gravels enhance their potential for entrainment during high discharge events. Thus, it would be advantageous to reside on larger, more stable substrates (e.g. boulders) in high-erosion floods that mobilize finer-grained sediments. As Fig. 7 suggests, the relative quality of a substrate as a dislodgment refuge from flow disturbance depends on the degree of sediment movement. Death and Winterbourn (1994) similarly found that the physical stability of bed sediments was strongly linked to macroinvertebrate persistence in New Zealand streams. Variation in factors such as embeddedness, particle shape (sphericity, angularity), and arrangement (packing) will certainly affect stability thresholds of sediments, and hence their propensity to erode (Gordon et al. 1992). Like other studies (e.g., Richards 1982, Grimm and Fisher 1989, Dole-Olivier et al. 1997), we found that larger-sized substrates (i.e., cobbles and pebbles) were less likely to erode than gravels. However, we add that the best refugium conditions are not necessarily linked to larger substrate size. Further studies that explore what substrate features and patterns promote the best refugium conditions will help us predict how aquatic ecosystems respond to flow disturbance.

Incremental increases in near-bed velocity affect the movements of snails on surfaces of bed elements, as observed in the flow tank experiment. Snails moved from high- to low-velocity patches (i.e., crevices) as velocities slowly increased. Hart et al. (1996) have similarly reported that black fly larvae make small-scale positioning adjustments to avoid hydraulic forces in high flow events. These very short-term reactions to individual flow events may be critically important in preventing dislodgment, and subsequent transport downstream.

Our work suggests that distance transported downstream is not linked to snail mortality rate. It is possible that our testing procedure influenced this finding considering that distance transported (maximum 9 m) and length of substrate patches (0.9 m) were relatively short. Yet, how far benthic organisms are actually transported in real floods remains to be investigated, as well as how transport distance affects mortality. Clearly, hydraulic features such as velocity, turbulence and dead-zones (i.e., areas such as eddies and wakes little impacted by the bulk flow), as well as organismal features such as body size and form, will affect downstream transport distance (e.g., Elliott 1971, Ciborowski 1983, Lancaster et al. 1996). Additionally, our results suggest flood-induced mortality of snails is affected more by substrate type than by transport distance. The modest mortality rates observed in this study indicate that flooding may alter local snail densities by moving and relocating individuals rather than by killing them. Considering that high densities of P. antipodarum can significantly affect algal biomass and assemblage (Winterbourn and Fegley 1989, Biggs and Lowe 1994), transport and

subsequent relocation of these grazers to downstream reaches or lakes may greatly impact these habitats. Of course, re-dispersal (i.e., upstream movements) of snails during non-flood periods (Huryn and Denny 1997, Poff and Nelson-Baker 1997) may mitigate snail impacts in downstream habitats. Needed are studies that assess both flow-induced downstream transport and subsequent re-dispersal to predict snail impacts on ecosystem processes.

In conclusion, flow disturbance appears to be important in shaping distributions of P. antipodarum at the rock face, substratum and drainage basin scales. Further, disturbance effects on local densities may be influenced more by substrate type and downstream transport than by mortality. Closer examination of relationships between geomorphology, sediment size distribution and architecture, and disturbance regime may help us predict patterns of local establishment of this species. Such studies are particularly relevant considering this snail has been widely introduced geographically and has the potential to alter community structure and function in some habitats. Finally, study of refugium patches and features that promote the best refugium conditions will further our understanding of patch dynamics and community resistance and resilience in stream ecosystems.

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