Longitudinal variation in recolonization rates of macroinvertebrates along an upland river in south-eastern Australia

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SUMMARY. 1. Recolonization rates of benthic invertebrates were estimated at five sites in the catchment of the Acheron River, in spring (October) and in summer (January). The sites ranged from those that experience short floods and high shear stress at the streambed (upstream sites) to those that experience prolonged floods and low shear stress (downstream sites). We hypothesized that these differences should affect recolonization rate.

2. In October, absolute rates of recolonization of taxa (number of taxa $0.05 \text{ m}^{-2} \text{ d}^{-1}$) onto 1-m² patches of substratum, which had been raked to remove fauna, did not vary between the three sites studied, nor did the relative rates of recolonization of taxa (absolute rate/mean number of taxa in control samples, which were taken from adjacent undisturbed patches of substratum). Absolute rates of recolonization of individuals (number of individuals $0.05 \text{ m}^{-2} \text{ d}^{-1}$) were proportional to the mean number of individuals in control samples; relative rates of recolonization of individuals (absolute rate/mean number of individuals in control samples) did not vary between sites.

3. In January, absolute rates of recolonization either of taxa or individuals were positively correlated with the mean densities of taxa or individuals in control samples; relative rates did not vary between the four sites studied.

4. We conclude that the benthic invertebrate communities at the various sites do not adapt to variations in flooding regime by altering relative recolonization rates. Absolute recolonization rates are directly proportional to the prevailing number of taxa or individuals at a site.

Introduction

We have previously investigated the effects of physical disturbance on the recolonization of

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macroinvertebrates onto patches (1 m²) of riverbed at a single site on the Acheron River, Victoria (Doeg, Lake & Marchant, 1989; Lake, Doeg & Marchant, 1989). Two important features influencing subsequent patch recovery are the degree to which the benthic fauna is reduced by the initial disturbance (i.e. resistance of the

fauna) and the rate of recovery (i.e. resilience of the fauna) both in absolute and relative terms (i.e. relative to control densities of taxa or individuals). The aim of this paper is to compare resistance and resilience at a series of sites along this river.

Floods are the most common form of physical disturbance in the Acheron River. Potentially, it seems likely that the previously mentioned features of patch recovery might vary with distance downstream because different sites experience different flooding regimes: upstream sites experience floods of short duration because they drain small catchments, whereas downstream sites experience longer lasting floods because they drain larger areas. Thus, the benthic fauna at sites that experience more prolonged flooding (which would tend to reduce the fauna) may be adapted to this situation by exhibiting high (absolute and relative) recolonization rates. Downstream sites also generally experience lower shear stress at the streambed compared with upstream sites (Townsend, 1980; Statzner, Gore & Resh, 1988). As shear forces are most probably responsible for dislodging the benthic fauna during floods, variations in shear stress along a river may affect characteristics of recovery such as resistance to initial disturbance.

Some similar work has already been carried out in the Acheron catchment (Lake & Schreiber, 1991): in this case the recolonization rates of individual scrubbed rocks by macroinvertebrates were measured; resistance to disturbance was not determined. In the current study the areas of streambed investigated were about two orders of magnitude larger than the areas of the individual rocks used by Lake & Schreiber. Thus, a subsidiary aim was to examine the consequences of a different spatial scale on patch recovery after disturbance.

Methods

Five sites were studied in the Acheron catchment (Table 1), approximately 75 km northeast of Melbourne. The uppermost three sites (1−3) were located in forest dominated by *Eucalyptus regnans* F. Muell. and *E. obliqua* L'Hérit. and were heavily shaded and fairly narrow (3−7 m wide). The lower two sites (4, 5) were in cleared land used for grazing; riparian vegetation was present but neither site was well shaded (width=15−20 m). More detailed descriptions of sites 1 and 3 and of the Acheron River in general can be found in Lake & Doeg (1985) and Doeg *et al.* (1989a).

Slope (Table 1) refers to the slope of the water surface of the river and was measured over at least five transects (parallel to the bank) at each site with a carpenter's level (a 10-m plastic tube filled with water and attached to metre rulers at either end). Water depth was measured at baseflow during summer at 5−10 points at each site; an estimate of water depth at bankfull discharge was made at the same time by measuring to the top of rocks or vegetation that were usually just submerged by an average flood (sites 1 and 2) or to the top of the adjacent bank (sites 3−5).

Shear stress was calculated (in newtons m^{-2}) from depth and slope using the formula given by Smith (1975). Shear stress (Table 1) was highest at the upper sites, but increased more ($\times$ 2.5−3.2) at bankfull discharge at the lower sites than at sites 1 and 2 ($\times$ 1.4−2.1). This amplifies our original suggestions about the effects of different flooding regimes at different sites: downstream sites also experience a greater relative increase in shear force at the streambed during a flood than do upstream sites.

At each site, recolonization was studied in riffles (up to 150 m long) consisting largely of

TABLE 1. Physical characteristics of the study sites

Site	Stream order	Slope (m 100 m^{-1})	Altitude (m)	Water depth (cm)		Shear stress (N m^{-2})	
				Baseflow	Bankfull	Baseflow	Bankfull
1	2	3.5	680	15.0	31.0	51.5	106.3
2	2	1.8	400	17.1	23.9	30.2	42.2
3	4	0.5	360	13.6	43.6	6.6	21.0
4	6	0.3	240	23.9	70.9	7.0	20.8
5	6	0.4	200	30.9	75.9	11.2	27.5

gravel, pebbles and cobbles. Mean grain size (measured from substratum collected in Surber samples) varied from 21 to 49 mm with the least variation at sites 1−3 (27−36 mm). The disturbance of the riverbed that occurs during estimation of recolonization rates does not alter mean grain size (as demonstrated by Doeg *et al.*, 1989a).

Recolonization rates were measured in October 1988 (spring, when discharge is high) at three sites (1, 3 and 4) and in January 1989 (summer, when discharge is low) at four sites (1, 2, 4 and 5) using an experimental technique described in detail by Doeg *et al.* (1989a). In October, fifteen stakes (or rocks >30 cm in diameter, site 4) were placed at random in the riffles at each site to mark individual plots. On 6 October (day 0), one side of each stake (or rock) was selected at random as a control plot and on the other side an area of about 1 m^2 was disturbed by kicking and raking. Five stakes were selected at random and Surber samples (area=0.05 m^2, mesh size=150 μm) were taken from the control and disturbed plots alongside each, beginning at the most downstream stake. (On day 0, to avoid interference, a control plot was sampled before a disturbed plot was raked). Sampling was repeated 11 days and 20 days after day 0, with no stake being sampled more than once. Absolute recolonization rates were calculated from differences in the density of taxa or individuals in disturbed plots on consecutive sampling days; relative rates were calculated by dividing absolute rates by mean densities in control samples. An index of organic matter in each sample was measured by burning organic material at 500°C as described by Doeg *et al.* (1989a).

In January the experimental technique was somewhat modified. Only five stakes (or rocks, sites 4 and 5) were used at each site. As before, one side was selected as a control plot and the other side was disturbed; in this case, however, an area of about 2−4 m^2 was disturbed by kicking and raking. This increase in area enabled two Surber samples to be taken from the disturbed plot, one on day 0 (16 January) and one on day 7. Control samples were taken on both days being careful to avoid resampling on day 7 the same control patch as was sampled on day 0, i.e. the two control samples were taken on the same side of the stake (or rock) but were spaced 10−20 cm apart. In this way five inde-

pendent estimates of recolonization rate were obtained on day 7 per site whereas, in the previous set of experiments, only one estimate was obtained per site on day 11 and one on day 20 because stakes were not resampled.

Macroinvertebrates were picked from a 10% subsample of each sample (as per Marchant, 1989) and identified under low magnification. Within each of the major taxa (except Oligochaeta) identifications were taken to the level of species or presumptive species (based on voucher specimens held at the Museum of Victoria); henceforth, these taxonomic units are termed taxa. Apart from Oligochaeta and a few chironomid taxa no taxon occurred in sufficient abundance at all sites to justify detailed consideration.

Recolonization was thus measured only in terms of the rate of increase in the number of taxa (T) or the number of individuals (N) at a site. The numbers of individuals (or quantities of organic matter) per sample were transformed to $\log_{10}$ before statistical analysis; the numbers of taxa per sample were not transformed. Percentages were transformed to arcsines.

Results

During both experimental periods, discharge (measured just above site 5) remained fairly constant (862−1360 Ml d^{-1} in October; 367−514 Ml d^{-1} in January). Water temperatures (Table 2) increased downstream and were highest in summer, as expected, whereas water velocities tended to vary more at the upstream sites. In October, the amount of organic matter was reduced on day 0 by 40−60% at each site, but increased quickly so that there were no

TABLE 2. Ranges of water temperature and velocity based on spot readings taken during the experiments

Site	Temperature (°C)	Velocity (m s^{-1})
October		
1	6.5−8.5	0.51−0.90
3	9.5−10.5	0.64−1.13
4	10.2−11.5	0.87−1.05
January		
1	11.0−12.5	0.19−0.95
2	12.0−14.5	0.34−0.83
4	15.0−18.0	0.71−0.82
5	15.0−17.5	0.59−0.63

significant differences in amounts (paired *t*-tests, $t=0.13-2.68$, df=4) between control and disturbed plots on days 11 and 20. Mean quantities in control plots ($7.5-9.3$ g organic matter 0.05 m^{-2}) did not vary during the course of the experiments at any site (one-way ANOVAS, $F=0.017-0.483$, df=2, 12) nor did they vary between sites ($F=0.314$, df=2, 42). As the effect of the initial disturbance on the quantities of organic matter did not last long, they were not measured in January.

Composition of the fauna

Representation of major taxa differed somewhat between sites (Fig. 1). Plecoptera (largely Gripopterygidae) were most frequent at the coolest upstream site (1). Ephemeroptera were common at all sites and were dominated by Leptophlebiidae (species of *Austrophlebioides* and *Nousia*) in October; in January, *Baetis* spp. had higher percentage abundances at sites 2–5 whereas Leptophlebiidae still dominated at site 1. Coleoptera (mostly Elmidae) became more dominant at the lower sites, as did the Simuliidae (in others). During both experimental periods, Chironomidae and Oligochaeta numerically dominated all sites, except site 4 where only the latter was abundant. Other Diptera including Ceratopogonidae, Tipulidae and Empididae (all in others) occurred in low numbers at all sites. The representation of Trichoptera varied irregularly between sites; a number of families was present, i.e. Hydropsychidae, Hydroptilidae, Hydrobiosidae, Coenosucidae, Calocidae, Leptoceridae, Philoreithridae and Philopotamidae.

Spring experiments

Recolonization in October showed few consistent trends. The number of taxa (*T*) per sample in control plots varied between sites (Table 3, $F=9.3$, df=2, 42, $P<0.001$), but not within a site during the 20 days of an experiment ($F=0.68-2.69$, df=2, 12). The percentage of *T* remaining after the initial disturbance, i.e. the resistance of the fauna (Table 3), did not vary between sites ($F=1.03$, df=2, 12). Mean *T* per sample was reduced by 45–60% in disturbed plots at each site on day 0 (paired *t*-tests, $t=2.96-4.36$, df=4, $P<0.05$). Recovery was rapid with no site showing a significant differ-
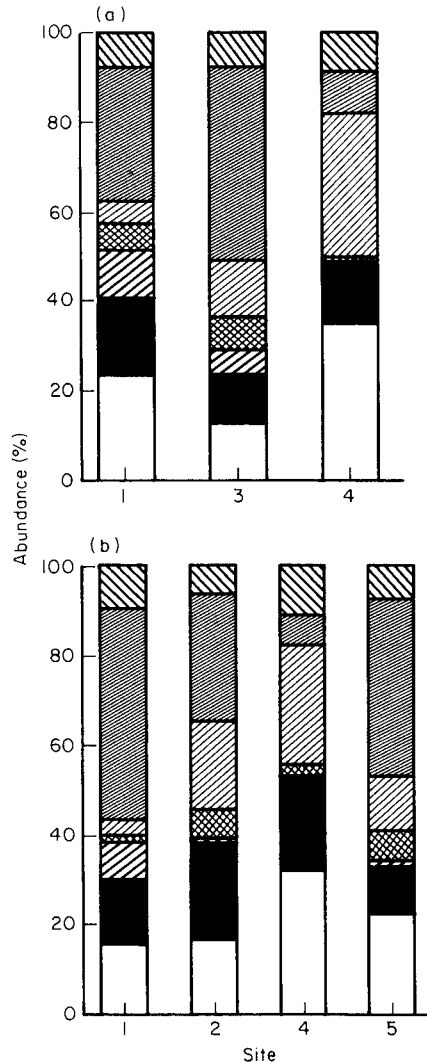

FIG. 1. Percentage abundance of the major taxa at the various sites in (a) October and (b) January. These percentages were based on the mean abundances in the control samples during a particular experiment: Oligochaeta (□); Ephemeroptera (■); Plecoptera (▨); Trichoptera (▧); Coleoptera (▨); Chironomidae (▨); others (◨).

ence in *T* between control and disturbed plots on day 11. Absolute recolonization rates (Table 3) were calculated as the difference between the mean *T* per sample on consecutive sampling days in disturbed plots divided by the sampling intervals in days. Confidence limits (95% CL) for these estimates were calculated from the

TABLE 3. Results of colonization experiments in October 1988. Figures in brackets are $\pm$ (or $\overset{\times}{\div}$ 95% confidence limits. For mean T or N, $n=15$

	Site 1		Site 3		Site 4	
Number of taxa (T)						
Mean number of taxa (T 0.05 m^{-2}) in control plots (a)	15.7	(2.0)	22.8	(3.0)	18.6	(2.5)
Resistance of fauna (%)	38.2		56.1		37.6	
Rate of recolonization (b) (T 0.05 m^{-2} d^{-1})						
day 0 – day 11	0.75	(1.01)	0.45	(0.46)	0.89	(0.45)
day 11 – day 20	0.02	(1.44)	0.44	(0.80)	0.18	(0.64)
Relative rate of recolonization (b/a) (% d^{-1})						
day 0 – day 11	4.8	(4.8)	2.0	(1.5)	4.8	(1.8)
day 11 – day 20	0.1	(6.6)	1.9	(2.5)	1.0	(2.5)
Number of individuals (N)						
Mean number of individuals (N 0.05 m^{-2}) in control plots (a)	359	($\overset{\times}{\div}$ 1.2)	767	($\overset{\times}{\div}$ 1.3)	1954	($\overset{\times}{\div}$ 1.2)
Resistance of fauna (%)	30.1		32.6		12.8	
Rate of recolonization (b) (N 0.05 m^{-2} d^{-1})						
day 0 – day 11	13.5	($\overset{\times}{\div}$ 4.6)	19.1	($\overset{\times}{\div}$ 1.5)	76.9	($\overset{\times}{\div}$ 1.7)
day 11 – day 20	9.1	($\overset{\times}{\div}$ 4.1)	17.6	($\overset{\times}{\div}$ 1.4)	74.7	($\overset{\times}{\div}$ 1.4)
Relative rate of recolonization (b/a) (% d^{-1})						
day 0 – day 11	3.8	(6.0)	2.5	(0.9)	3.9	(1.8)
day 11 – day 20	2.5	(3.5)	2.3	(0.7)	3.8	(1.2)

variance of a difference between two variables (Sokal & Rohlf, 1981). These limits were fairly wide, especially at site 1, but indicate that no significant variation in absolute recolonization rate occurred between sites during either experimental period. Relative recolonization rates (i.e. absolute rates expressed as a percentage of the mean T at each site) displayed no significant variation between sites during either sampling interval, as judged by the width of their 95% CLs (these limits were derived from the variance of a quotient of two variables; Kendall & Stuart, 1961).

The number of individuals (N) per sample in control plots also varied between sites in October (Table 3, $F=69.70$, df=2, 42, $P<0.001$). However, at a single site there was no variation in N per sample from control plots during an experiment ($F=1.47-3.36$, df=2, 12). The percentage of N remaining after the initial disturbance, i.e. the resistance of the fauna (Table 3), did not vary between sites ($F=0.75$, df=2, 12). Mean N decreased by 70–90% in disturbed plots on day 0 (paired t-tests, $t=2.90-$

5.60, df=4, $P<0.05$), but by day 11 was not significantly different from that in control plots at sites 1 and 3; at site 4, N per sample remained significantly different ($t=4.33$, df=4, $P<0.01$) even on day 20, indicating, in terms of N, that recovery was still occurring. Rates of recolonization, both absolute and relative, and their 95% CLs were calculated in a similar way to those based on number of taxa. Absolute rates increased significantly downstream (as judged by the widths of their 95% Cls) as mean N increased, in both sampling intervals. Relative rates of recolonization, on the other hand, showed no significant change between sites during either experimental period.

Summer experiments

In January, experiments were run for 7 days at each site. Previous work in the summer (Doeg *et al.*, 1989a) indicated that rapid recolonization should occur in this interval. As the same stakes were sampled on both sampling occasions paired t-tests were possible between

days 0 and 7 for the T or N values. These tests demonstrated that there were no significant changes in T or N per sample in control plots at any site during the 7 days ($t=0.14-1.53$, df=4) but that there was significant recolonization of the disturbed plots ($t=3.23-6.20$, df=4, $P<0.03$). At site 1 t-values for the disturbed plots were not quite significant ($t=2.15-2.45$, df=4, $P=0.07-0.10$); two plots were not re-colonized (for no obvious reason) during the interval.

Paired t-tests were also possible between control and disturbed plots on each sampling day with this experimental design. These tests show that the initial disturbance always caused a significant reduction in T or N on day 0 ($t=2.78-7.25$, df=4, $P<0.05-0.002$). On day 7, however, no significant differences were found ($t=0.69-2.47$, df=4) indicating that the fauna recolonized quickly. The percentage of T or N remaining after the original disturbance (i.e. the resistance of the fauna, Table 4) did not differ between sites.

Absolute recolonization rates were calculated from differences in T or N of single disturbed plots on the two sampling days. Thus, five estimates were available at each site for both measures. These estimates (as total numbers returning over 7 days) were positively correlated with the mean values for T or N per sample in control plots (Fig. 2). Relative rates of recolonization (Table 4), which were calculated by dividing absolute rates by mean T or N (for a single stake or rock), again showed no significant difference between sites. This is also clear from their 95% CLs, which were calculated from the five estimates of recolonization rate at each site. Relative rates were slightly higher in January than in October, presumably as a result of the greater activity of the fauna at the warmer summer temperatures.

Discussion

It is clear from these experiments that there were no obvious differences in relative rates of recolonization or in the resistance of the benthic fauna to disturbance at various points along the river (stream orders 2−6). Absolute rates of recolonization, on the other hand, were directly proportional to the background levels of T or N. In October and January, absolute rates for individuals were positively correlated with N,
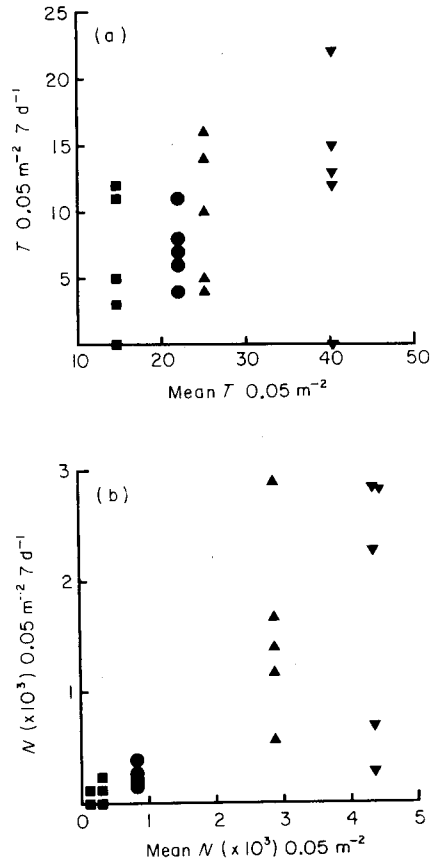

FIG. 2. Total numbers of (a) taxa and (b) individuals returning to the disturbed plots over 7 days at the four sites in January versus mean number of taxa (T) or mean number of individuals (N) per sample: site 1 (■), site 2 (●), site 4 (▲), site 5 (▼). For (a) $r=0.64$ ($P<0.01$) provided the zero value for site 5 is omitted; for (b) $r=0.73$ ($P<0.01$).

which varied significantly between sites. The absolute rate for taxa was positively correlated with background levels of T in January, but not in October; although background levels of T varied significantly between sites in October the degree of difference was not great. These differences in absolute rates of recolonization were still apparent despite the sometimes wide confidence limits associated with the estimates.

Our results are similar to those obtained by Lake & Schreiber (1991) who examined the recolonization of individual rocks (approximately 10 cm in diameter) by invertebrates at eight sites (stream orders 2−6) in the Acheron

TABLE 4. Results of recolonization experiments in January 1989. Figures in brackets are 95% confidence limits. *F* values are from one-way ANOVAS across sites; df=3, 16 in all cases except for mean *T* or *N* where df=3, 36. For mean *T* or *N*, *n*=10

	Site 1	Site 2	Site 4	Site 5	*F*	*P*
Number of taxa (*T*)						
Mean *T* 0.05 m^{-2} in control plots	14.6	22.0	25.1	40.3	35.84	<0.001
Resistance of fauna (%)	33.3	54.3	56.0	60.5	0.73	0.55
Relative rate of recolonization (% d^{-1})	5.6 (0.01–13.4)	5.2 (0.7–9.4)	5.5 (2.0–9.6)	3.7 (0.3–9.0)	0.20	0.90
Number of individuals (*N*)						
Mean *N* 0.05 m^{-2} in control plots	305	826	2879	4357	89.67	<0.001
Resistance of fauna (%)	24.1	23.6	16.0	36.2	1.41	0.28
Relative rate of recolonization (% d^{-1})	4.0 (0.2–12.7)	5.4 (0.8–11.3)	8.0 (2.6–12.9)	5.5 (1.0–11.0)	0.46	0.71

catchment. They found that absolute rates of recolonization were positively correlated with background levels of *T* or *N* but that relative rates were negatively correlated. The ranges of the background levels in *T* or *N* that they encountered were greater than we found. However, for certain ranges of relative recolonization rate, e.g. 4.5–6.2 %d^{-1} for taxa and 4.1–5.5 %d^{-1} for individuals, they found no significant differences between sites. These relative rates are comparable with those we measured in January. In our experiments the areas of the patches being recolonized were approximately two orders of magnitude greater than those studied by Lake & Schreiber (100 cm^2, 1991), yet the response of the fauna was similar in both cases. This suggests that the characteristics of recolonization do not depend greatly on the scale at which these sorts of experiments are run, at least for areas between 100 cm^2 and 2–4 m^2.

In both studies, shear stress was higher upstream than downstream. Lake & Schreiber, like us, found a greater relative increase in shear stress during flooding at lower sites than at upper sites. Their values for shear stress were comparable with ours, although values at their highest sites (>1000 m) with steep gradients were up to twice as high. In neither study was a hump-shaped pattern evident for variation in shear stress along the river, as described by Statzner *et al.* (1988) for streams with catchments <300 km^2 (the catchment of the Acheron River above site 4 is just >400 km^2). If such a hump-shaped transition zone is present, Statzner & Higler (1986) predict that marked changes in the composition and the resilience of the macroinvertebrate communities will occur. In this catchment neither occurred.

Previous work at site 3 on the sources of recolonizing invertebrates (Doeg *et al.*, 1989b) indicates that drift contributes only 36% of the individuals that recolonize gravel and 25% of those that recolonize stones. Therefore, the majority of the fauna apparently recolonizes from the streambed immediately surrounding the disturbed area. This offers a simple explanation for the positive correlation between ambient levels of *T* or *N* and the absolute rates of recolonization evident in this study and in that of Lake & Schreiber (1991). This conclusion combined with the fact that physical disturbance does not seem to favour colonization by particular taxa in this river (Doeg *et al.*, 1989a; Lake *et al.*, 1989) suggests that these invertebrate communities are 'mobility controlled'. Townsend (1989) used this term to describe stream communities in which move-

ment of organisms is so high that competition is not an important feature in community organization.

Although our results corroborate those found at a smaller scale (stones) by Lake & Schreiber (1991) they may not apply to disturbance at a larger scale. Brooks (1989) compared the re-colonization dynamics of macroinvertebrates onto small artificially disturbed patches (0.05 m^2) with those found after a major flood. Not only did he find significant differences in the pathways used in recolonization but also differences in the rates of colonization. The small patches were largely colonized by surface movement from adjacent intact areas whereas areas damaged by the flood were largely colon-ized by vertical movement from the hyporheic habitat. As we have stressed previously (Doeg *et al.*, 1989a; Lake *et al.*, 1989), the degree of disruption to the riverbed produced by our ex-periments may only mimic the effects of small floods in the Acheron River.

We conclude that the recolonization charac-teristics of benthic invertebrate communities in the Acheron River are not specifically adapted to differences in flood duration or shear stress between sites. On the contrary, it seems that the recovery of these lotic communities from the effects of physical disturbance is indepen-dent of longitudinal differences in flooding regime.

Acknowledgments

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