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Colonization by Macroinvertebrates of Experimentally Disturbed Stones in Three Tropical Streams Differing in Size

key words: aquatic insects, recolonization, community structure, disturbance, Brazil

Abstract

We experimentally disturbed stones in three streams of different sizes and followed the macroinvertebrate colonization process in terms of abundance, species richness and similarity over 64 days. We hypothesized that colonization in the smallest and in the largest streams would be slower than in the medium-sized stream. The small upstream pool of colonists available in the smallest stream could restrict colonization, while in the largest stream predation by the diverse fish assemblage could restrict drifting colonists. The medium-sized stream did not have these two constraints. We found similar colonization patterns in all three streams, leading to the rejection of the stated hypotheses. Lack of support of the original hypothesis might be due to the weakness of the two hypothesized restrictions on colonization. In addition, colonization by crawling species from undisturbed nearby patches might be of significant importance.

1. Introduction

Disturbance caused by high flow plays a major role in the structure of stream macroinvertebrate assemblages (RESH *et al.*, 1988). During floods, substrates used by benthic organisms such as stones, leaf packs, and wood debris are tumbled and dislocated downstream. In small streams, small waterfalls formed by fallen trees and accumulated leaves, twigs, and sand are ruptured, causing movements of substrate located upstream and the consequent burying of patches downstream. Following a high flow event, densities of individuals are often decreased. Depending on the disturbance event, the total number of individuals can be reduced by up to nearly 100% (SCRIMGEOUR *et al.*, 1988; MATTHAEI *et al.*, 1997).

Recovery is generally fast and original abundance levels can be attained within 30–120 days (MACKAY, 1992; FLECKER and FEIFAREK, 1994). It is thought that fast recovery is due to the presence of unaffected areas or refuges, where individuals accumulate during floods and from which they can disperse to colonize denuded patches after baseflow is restored (LANCASTER and HILDREW, 1993; DOLE-OLIVIER *et al.*, 1997). Recovery can be affected by a number of factors, including distance from unaffected areas or refuges containing potential colonists (GORE, 1982), small-scale bed characteristics (WILLIAMS and SMITH, 1996), and biotic interactions (DIAMOND, 1986).

WILLIAMS and HYNES (1976) assessed the relative importance of drift, aerial sources, upstream migration, and movement up from the substrate during the recolonization process. They concluded that drift was the most important mechanism, accounting for 41.4% of the total number

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of individuals settled in experimental traps. Further support for the importance of drift during the recovery process was provided by TOWNSEND and HILDREW (1976) and MOSER and MINSHALL (1996). However, only part of stream invertebrates are commonly observed in drift. Many species of insects enter drift only during their first larval instar while some others never enter (PRINGLE and RAMÍREZ, 1998). For example, many species of caddisflies are prevented from entering drift due to their heavy, portable cases (*e.g.* Helicopsychidae, Glossosomatidae).

In this study we evaluated whether recovery following an experimental small-scale disturbance differed in three different-sized stream sites within a catchment. Specifically, we tested for each stream at what point in time control densities were reached within a 64-day period of recolonisation. Site 1 was a first-order stream located around 200–300 m downstream from its source. Site 3 was a fifth-order stream and contained a diverse fish assemblage, including benthonic and nektonic insectivorous species that feed either in riffles or pools. We predicted that recovery in these two sites would be slow. In site 1 because the small area located upstream could limit the number of individuals available to drift, and in site 3 because predation by insectivorous fishes could reduce drift rates or at least restrict it (FLECKER, 1992; HUHTA *et al.*, 2000). Site 2, a fourth-order stream, was neither constrained by size of the area upstream nor by presence of insectivorous fishes. As a consequence, we predicted that recovery to original levels in site 2 would be faster than in sites 1 and 3. Additionally, if the restrictions on drift outlined above were true, we would expect that the negative effects on site 1 and 3 would be more conspicuous for drift-prone species than for crawling-prone species. We assessed this prediction by plotting colonization curves for one insect family characteristically drift-prone, the Baetidae (Ephemeroptera), and one characteristically crawling-prone family, the Glossosomatidae (Trichoptera).

2. Methods

2.1. Study Sites

The study was carried out in the Rio do Carmo catchment, at Parque Estadual Intervales (24°18' S, 48°25' W), São Paulo State, Brazil. The vegetation is tropical ombrophilous submontane-montane forest, commonly known as tropical rain forest. The mean annual precipitation in the area is 2040 mm (25 y record). Rainfall is unevenly distributed across two seasons: one rainy (150–400 mm/mo) and warm (15–30 °C) from September through March and another dry (60–150 mm/mo) and cold (0–25 °C) from April to August. The experiment was carried out from July through September 1999, during the dry season. No flood was observed during the period.

At site 1 the stream was 0.5–1 m wide and the streambed consisted mainly of sand and stones (10–40 cm long). The studied reach had several pools and small waterfalls formed by fallen trees and accumulated twigs, leaves, and sand. Discharge was very reduced in the dry season, and during the experiment it was ~0.0034 m³/s. No fish were observed during five years of study in site 1, although small mailed catfish (Loricariidae) may occur. Site 2 was on average 10 m wide, discharge of ~0.408 m³/s, and the streambed consisted of stones and boulders up to 2 m long. Small mailed catfish up to 10 cm long that feed on periphyton (BUCK and SAZIMA, 1995) were common and were often collected together with invertebrates in nets. Site 3 had a streambed similar to site 2, but the width was on average 20 m and discharge ~5.977 m³/s. The fish assemblage in site 3 was quite diverse, and included species that feed on benthic and drifting invertebrates (SABINO and CASTRO, 1990; CASTRO and CASATTI, 1997). Macroinvertebrate assemblages at sites 1 and 2 were partially similar, but quite distinct from site 3. Sites 1, 2, and 3 represent sites 1, 8, and 10, respectively, in Figure 1 of MELO and FROELICH (2001), where additional information on the streams and macroinvertebrate composition can be found.

2.2. Experimental Procedure

At each stream site, 70 stones (~18 cm long) were taken out from a stream reach and cleaned of invertebrates. Stone type and texture varied but reflected the pool of stones present in each studied site.

Each stone was labelled with a small non-toxic ink mark and/or with a small plastic tag attached by angling line. Labelled stones were then randomly placed in riffles in a stream reach of at least 100 m in length. After 1, 2, 4, 8, 16, 32, and 64 days of the start of the experiment, 10 stones were randomly selected and sampled. Invertebrates on 20 undisturbed (control) stones located in adjacent riffles were collected from sites 1 and 2 respectively one day before and two-three days after the start of the experiment. Control stones were not collected in site 3 during the experiment and thus we used available data from stones collected in the same time of the year, but two years before as reference. Riffles selected to sample control stones were very similar to those used in the experiments and were within the same homogenous experimental reaches.

Stones were sampled using an U-net sampler (SCRIMGEOUR *et al.*, 1993). Macroinvertebrates were removed alive from detritus and fixed in ethanol. In the laboratory, individuals were identified to the lowest taxonomic level possible and then assigned to morphospecies.

2.3. Data Analysis

We constructed curves of colonization using mean number of individuals and species per stone. Pooled abundance of all species in each stone were $\log_{10}(x+1)$ transformed. We used an one-way Analysis of Variance (ANOVA) to test for differences among days of colonization, including the control sample. Ten stones randomly chosen from the 20-stones set composed the control samples in these cases. In case a significant difference was found at $p = 0.05$, we compared each treatment level (day of colonization) with the control sample using Dunnett's test (DAY and QUINN, 1989) to identify the day of colonization when there was no significant difference between colonized and control stones.

In order to evaluate recovery of species composition and relative abundances, we computed Sørensen similarity values between the control sample and the seven colonization samples. Each colonization sample was composed by pooling data from the 10 stones collected at each combination of stream and date. Two control samples for each stream were used, each one composed of 10 stones randomly chosen from the 20-stones set available. We evaluated thus the overall similarity using all sampling units (stones) collected at a given time of colonization with the controls. We did so because the species composition on each single stone represents only a small fraction of the species in the community. Similarity among single stones would be thus too low, even among control stones. Reported values are mean similarity between a given treatment sample with each of the control samples. Similarity was also calculated between the two control samples. We used $\log_{10}(x + 1)$ transformed abundances standardized by total abundance in the sample. This prevented the effects of low abundance in samples collected early in the colonization process and allowed the calculation of similarity values based only on species composition and relative abundance. Results are presented graphically.

Our study deals with only one stream site for each of the three treatments (restriction related to the pool of colonists, no restriction, restriction by insectivorous fishes). As the spatial scale of our hypothesis is the stream site, we acknowledge that the study has no true replication, and should thus be interpreted as a study case. The analyses described above avoid direct comparisons between stream sites and are restricted to within site comparisons. Evaluation of the stated hypothesis is done mostly by contrasting values obtained in analyses done for each stream site.

3. Results

3.1. Abundance

Colonization curves for the small- and the medium-sized streams, sites 1 and 2 respectively, were very similar to each other (Fig. 1). Recovery to control level of abundance for these two streams occurred in day 8 and persisted greatly unchanged until the end of the experiment (Table 1). Abundance in stream 3 was consistently higher than in streams 1 and 2. For stream 3, the control level of abundance was attained very soon on day 4. However, the abundance values increased continually until the end of the experiment, attaining values significantly higher than those observed in the control sample after day 32 (Fig. 1; Table 1).

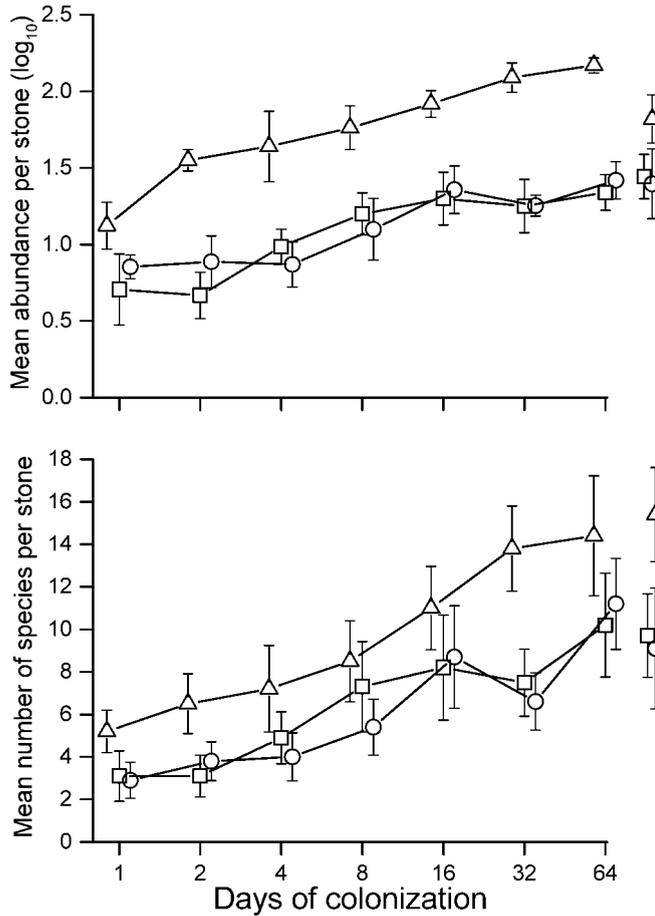


Figure 1. Colonization curves for abundance and species richness (mean and 95% CI). Some symbols are slightly dislocated around sampling days in order to avoid overlap. \square = site 1, \circ = site 2, \triangle = site 3. Symbols placed at the right of the graph and not connected by lines represent control samples.

Table 1. Effects of colonization time on abundance and species richness per stone in the three stream sites studied. One-way analysis of variance includes control sample and seven colonization dates (1, 2, 4, 8, 16, 32, and 64 days after the start of the experiment). For all levels $n = 10$. Dunnett's test is employed to compare each treatment with the control level.

Stream	Metric	Analysis of variance		<i>p</i> -value of Dunnett's test – treatments versus control						
		$F_{7,72}$	<i>p</i>	1	2	4	8	16	32	64
1	abundance	12.97	<0.001	<0.001	<0.001	0.001	0.190	0.722	0.421	0.925
2	abundance	9.65	<0.001	<0.001	<0.001	<0.001	0.058	>0.999	0.705	>0.999
3	abundance	23.26	<0.001	<0.001	0.047	0.332	0.994	0.807	0.032	0.003
1	richness	8.78	<0.001	<0.001	<0.001	0.003	0.312	0.773	0.400	0.999
2	richness	10.85	<0.001	<0.001	0.001	0.001	0.027	>0.999	0.238	0.409
3	richness	15.20	<0.001	<0.001	<0.001	<0.001	<0.001	0.017	0.784	0.972

3.2. Species Richness

Recovery of species richness in stream 1 and 2 were quite similar to each other, as they were for abundance (Fig. 1). However, control levels of species richness were attained in day 8 for stream 1 and day 16 for stream 2 (Table 1). There was a decrease in richness in stream 2 on day 32. However, given the great 95% confidence interval exhibited by samples collected on days 16, 64 and in the control, it is likely that this decrease was due to chance. Recovery in stream 3 took place on day 32, and different from abundance, values on days 32 and 64 were not higher than values observed for the control sample (Fig. 1; Table 1).

3.3. Community Similarity

Similarity between colonization samples and the control samples tended to flatten off around day 16 for the three streams studied (Fig. 2). However, in all three streams similarity values on day 64 were lower than those observed between the two control samples. The difference for stream 1 was small, but was large for streams 2 and 3.

We observed that one species of caddisfly (*Leucotrichia* sp.) was abundant in control samples of stream 2, but not in the experimentally disturbed samples. In order to check if differences in similarity between day 64 and controls were due to the absence of this species, we re-ran the similarity analysis excluding this species from the dataset. New similarity values are plotted as unconnected filled circles in Fig. 2. There was a decrease in the difference between day 64 and the control samples, but of low magnitude.

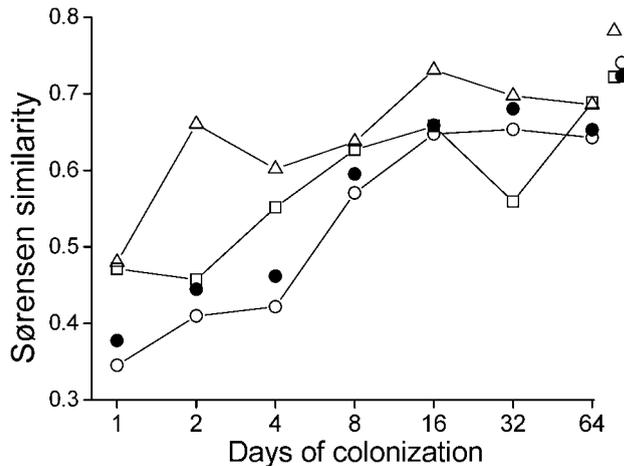


Figure 2. Sørensen similarity between samples collected at different days after disturbance and two control samples. Values for each day are means from the two comparisons with controls. Symbols placed at the right of the graph and not connected by lines represent similarity between the two control samples for each stream site. Some symbols are slightly dislocated around sampling days in order to avoid overlap. □ = site 1, ○ = site 2, ● = site 2 without *Leucotrichia* sp. (see text for explanations), △ = site 3.

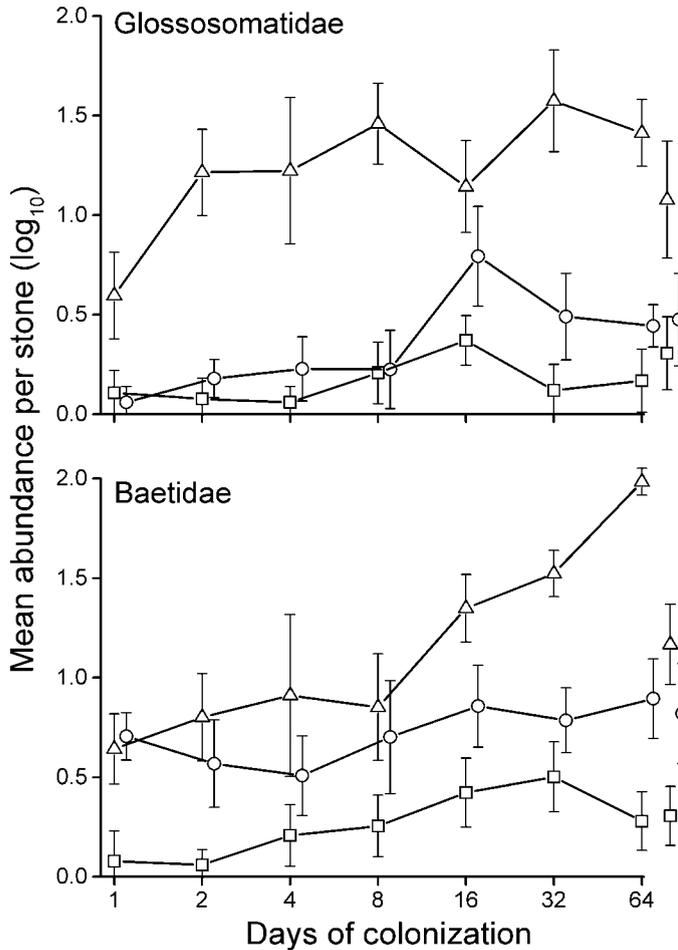


Figure 3. Colonization curves for selected taxa in relation to main mode of colonization (mean and 95% CI). Glossosomatidae (Trichoptera) colonizes substrates mainly by crawling while Baetidae (Ephemeroptera) mainly by drift. Some symbols are slightly dislocated around sampling days in order to avoid overlap. □ = site 1, ○ = site 2, △ = site 3. Symbols placed at the right of the graph and not connected by lines represent control samples.

3.4. Colonization by Drift- and Crawling-Prone Families

There were not consistent differences between colonization curves of drift- and crawling-prone families (Fig. 3). Contradicting the original hypothesis, species of crawling caddisflies larvae (Glossosomatidae) colonized stones as fast as drift-prone species mayflies (Baetidae).

4. Discussion

Colonization patterns did not differ between stream sites 1 and 2, in terms of abundance, species richness, and similarity from undisturbed stones. Recovery in stream 3 was similar

to streams 1 and 2 in terms of species richness and similarity, but differed in relation to abundance. Mean abundance per stone in stream 3 recovered to control levels after only four days of the start of the experiment, attaining values higher than those of the control after 32 days. It is likely that the density of organisms at the time of the collection of control samples in 1997 was lower than the density during the experiment in 1999, although we have no data to assess this suggestion. The original hypothesis that the medium-sized stream 2 would recover to original levels faster than streams 1 and 3 was rejected.

Lack of support for the stated hypothesis might be due to the weakness of the two mechanisms that would generate the expected pattern. It seems that fish presence in stream 3 was not enough to reduce drift to a level low enough to affect colonization of new patches. Also, the upstream pool of colonists in stream 1 does not seem to limit recovery. Additionally, colonization by crawling of nearby individuals might be of significant importance to colonization of small-scale point disturbance (BROOKS and BOULTON, 1991; MARCHANT *et al.*, 1991). In fact, we observed that larvae of Glossosomatidae, a crawling caddisfly, colonized stones as fast as larvae of the mayfly family Baetidae, known to be common in drift samples elsewhere in tropical streams (*e.g.* PRINGLE and RAMÍREZ, 1998).

Our experiment was designed to detect potential differences in colonization rates at a very restricted spatial scale, a single stone. Although small, the spatial scale of our study is similar to most of the colonization experiments in streams described in the literature (*e.g.* MALMQVIST and OTTO, 1987; LAKE and SCHREIBER, 1991; MCCABE and GOTELLI, 2000). BROOKS and BOULTON (1991) suggested that resilience in a small-scale experiment like ours can potentially be higher than that following large scale disturbances affecting streams. In small-scale experiments, the nearby patches are not affected by the disturbance and thus are able to provide much more immigrants than those available when a natural disturbance affects the whole stream reach. In the context of our hypothesis, this would mean that following a natural disturbance, colonization by crawling species dispersing within restricted areas would be low. Colonization thus would depend mostly on drifting immigrants from distant, undisturbed (refuges) patches. In the case of the two constraints to colonization discussed here (small upstream pool and insectivorous fish), it is possible that our hypothesis would be found to be true in experiments encompassing the large spatial scales relevant to natural disturbances (*e.g.* MELO *et al.*, 2003).

Few studies have compared recovery of disturbed stones among streams of different size. MARCHANT *et al.* (1991) did not find differences in colonization rates in five points along a river (stream orders 2–6) in Australia. LAKE and SCHREIBER (1991) found that colonization rates differed among eight stream sections in the Acheron River catchment, Australia, but these differences were not related to stream size. ROSSER and PEARSON (1995) compared colonization on experimentally disturbed stones in two streams located at different altitudes and containing different community structure. They found that recovery in terms of species richness did not differ between the two stream sites, but did so for abundance. In the upland site, abundance levels flattened off around day 21 and remained constant thereafter, while in the lowland site abundance increased indefinitely, not attaining a plateau even after 70 days. In the Brazilian Amazon basin, FREITAS (1998) compared colonization of artificial substrate in the Urubui river and two of its tributaries. Colonization rates were low in his study, assessed using total abundance and number of families. He did not find differences in recovery of abundance among the three areas, but he did so for number of families. In the small tributaries, colonization was lower than in the main channel.

Although abundance and species richness per stone recovered to original levels in 8–16 days, the similarity between samples collected on day 64 and the controls were lower than similarity between controls (Fig. 2). This suggests that species composition and/or relative abundance on samples collected on day 64 were different from the undisturbed stream community. An example of species causing such difference is the caddisfly larvae *Leucotrichia* sp. This species was very abundant in control samples of stream 2, but was absent in the

colonization samples. It seems that this species colonizes stones only by adult oviposition and/or dispersion of first instars larvae. In fact, *Leucotrichia* sp. build or occupy unused houses made of silk attached to the stone surface (MCAULIFFE, 1984). The high cost involved in building or finding an empty case probably prevents larvae from further dispersing after they have settled on a given stone.

This study did not support the hypothesis that recovery in medium-sized streams is faster than in small or large streams. Nevertheless, recovery in the three streams studied was rapid and consistent with results found in the literature dealing with small-scale experiments (DOEG *et al.*, 1989; MACKAY, 1992), supporting the view that stream communities are highly resilient.

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