Colonization routes of benthic macroinvertebrates in a stream in southeast Brazil.

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ABSTRACT: Colonization routes of benthic macroinvertebrates in a stream in southeast Brazil. The colonization of the benthic substrate by macroinvertebrates of a tropical stream was investigated through four routes: downstream movement, upstream movement, movement from the subsurface and colonization by aerial source. Traps were built and installed to quantify separately each route. Samples were removed after 1, 3, 7, and 21 days of colonization. The community showed two main characteristics: the dominance of two groups (Chironomidae and Baetidae) and a progressive increase in richness and density in a temporal scale. Although this dominance occurred at all routes, they differed in relation to the total richness, total density, community composition, and over time. The density of the main groups sampled differed significantly among routes only at the 21st colonization day. When considered the percentage density by each route (only at 21 colonization day) for the ten most common taxonomic groups, three patterns can be pointed out. (1) Seven taxa used the four routes (Chironomidae, Trichoptera, Baetidae, Leptophlebiidae, Copepoda, Leptohyphidae and Elmidae), (2) one taxa used three routes (Annelida), and (3) two taxa used only two routes (Simuliidae and Glossosomatidae). In this study, the four colonization routes were important for replacement of denuded areas. Groups of benthic macroinvertebrates, which used preferential routes, determined the differences in community structure between different colonization routes.
Key-words: dispersal movements, colonization, invertebrates, artificial substratum, experimental manipulation, tropical stream.

RESUMO: Rotas de colonização de macroinvertebrados bentônicos em um riacho do sudeste do Brasil. A colonização do substrato bentônico por macroinvertebrados de um riacho tropical foi investigada através de quatro rotas: movimento rio abaixo, movimento rio acima, movimento de subsuperfície e colonização aérea. Armadilhas foram instaladas para quantificar separadamente cada rota. Amostras foram removidas após 1, 3, 7, e 21 dias de colonização. A comunidade amostrada apresentou duas principais características: a dominância de dois grupos (Chironomidae e Baetidae) e um progressivo aumento na riqueza e densidade numa escala temporal. Embora esta dominância tenha ocorrido para todas as rotas, elas diferiram em relação à riqueza total, densidade total, composição da comunidade e ao longo do tempo de colonização. A densidade dos principais grupos apresentou diferença significativa entre as rotas somente aos 21 dias de colonização. Quando considerado o percentual de densidade (somente do 21° dia) para cada rota para os dez taxa mais representativos, três padrões puderam ser observados. (1) Sete taxa usando as quatro rotas (Chironomidae, Trichoptera, Baetidae, Leptophlebiidae, Copepoda, Leptohyphidae e Elmidae), (2) um taxa usando três rotas (Annelida) e (3) dois taxa usando somente duas rotas (Simuliidae e Glossosomatidae). Neste estudo, as quatro rotas foram importantes para a colonização de áreas desnudas. Grupos de macroinvertebrados bentônicos, os quais utilizaram rotas preferenciais, determinaram as diferenças na estrutura da comunidade quando comparadas as diferentes rotas.
Palavras-chave: movimentos de dispersão, colonização, invertebrados, substrato artificial, manipulação experimental, riacho tropical.

Introduction

Dispersal movements are an important activity in the ecology of benthic macroinvertebrates, and can happen by active movement among stream patches, drift and adult emergence (Smock, 1996). Dispersal movements (active or passive) can occur in response to several factors (Smock, 1996), with water flow acting as an energetically efficient mechanism on this process. Several studies have demonstrated that rates of macroinvertebrates colonization of new substrates differ among taxa, across the year and is affected by the physical characteristics of the substrate (e.g. Smock, 1996).

Colonization of substrates can occur through four routes (Williams & Hynes, 1976). Downstream movement is considered one of the most important ways of colonization in streams, occurring primarily by drift, but also from movement along the sediment (Waters, 1972; Williams & Hynes, 1976). Upstream movement along the sediment occurs in species exhibiting positive rheotaxis (Bishop & Hynes, 1969; Humphries, 2002). A third way of colonization is from subsurface or hyporheic zone (Smock, 1996; Olsen & Townsend, 2005). Finally, aerial colonization is important in all streams (Benzie, 1984; Reich & Downes, 2003 a, b), with oviposition by winged adult insects being the primary mechanism of this colonization path.

If species differ in their preferential mechanisms of colonization, it is plausible that different factors affecting one or more ways of colonization may result in different community structure. We tested this hypothesis in a tropical stream of southeastern Brazil. Although a large body of information for temperate streams in North America and Europe (e.g. Williams & Hynes, 1976) exists, no comparable information is available for tropical streams (but see Benzie, 1984 and Boyero & DeLope, 2002).

Material and Methods

Study area

The experiment was done in Ribeirão da Quinta (23°06'47"S, 48°29'46"W) located at the municipality of Itatinga, São Paulo State, southeast Brazil, at an elevation of 743m. This is a pristine third order stream, located in a cattle raising farm, distant from urban areas. At the experimental site, the stream is partially shaded by a well-preserved riparian gallery forest at the left margin and abundant herbaceous vegetation at the right margin, with a contribution to the system of an autochthonous (periphyton) and an allochthonous (coarse organic matter) source of energy.

The experiment was located in a 6 m long and 4 m wide run, with gravel-sandy substrate. The experiment was conducted in July (dry period), when the run was shallow (10 - 14 cm) and with slow current (14 - 44 cm/s).

Experimental design

An experimental method similar to the one described by Williams & Hynes (1976) was used to analyze the different routes of colonization. Traps were built to quantify separately the downstream, upstream, subsurface and aerial colonization routes (Fig. 1). The traps (30 cm L, 15 cm W and 30 cm H) were made of iron frame and covered with copper screen (mesh 250 mm). Five types of traps were used (Fig. 1): (A) only with the upstream and (B) downstream side opened (without screen), allowing colonization from only one route; (C) all sides closed and the bottom with a screen of 1 cm of diameter allowing vertical subsurface movement; (D) only the top opened for aerial colonization, with plastic bottles attached to each side for flotation; and (E) control traps opened at all sides and with a 1 cm screen at the bottom. All traps, except for the aerial and control, had the top covered with transparent plastic, to allow light transmission.

The area around downstream, upstream and control traps was electrified (Fig. 1), preventing fish access and, in this way, standardizing the condition of those traps with the subsurface and aerial ones. These traps were placed between two parallel copper bars (3/8 of diameter and 1 m L), linked to a 12V electrifier (SpeedriteTM, model Viper 5000). The electrifier was linked to a 95 AH battery, supported by a solar panel, which maintained 3.4 volts. In an experiment conducted before, it was confirmed that this electric field had no effect upon macroinvertebrates (data not-published).

An artificial rocky substrate, made from cement and cobbles was placed in each trap (Fig. 1 F). This artificial substrate was tested before and showed to be adequate for colonization experiments (Carvalho & Uieda, 2004).

Four blocks, each composed by the five kinds of trap were installed in sequence through the stream, 50 cm apart from each other. Twice a week the experiment was inspected to measure the voltage and clean the screens.

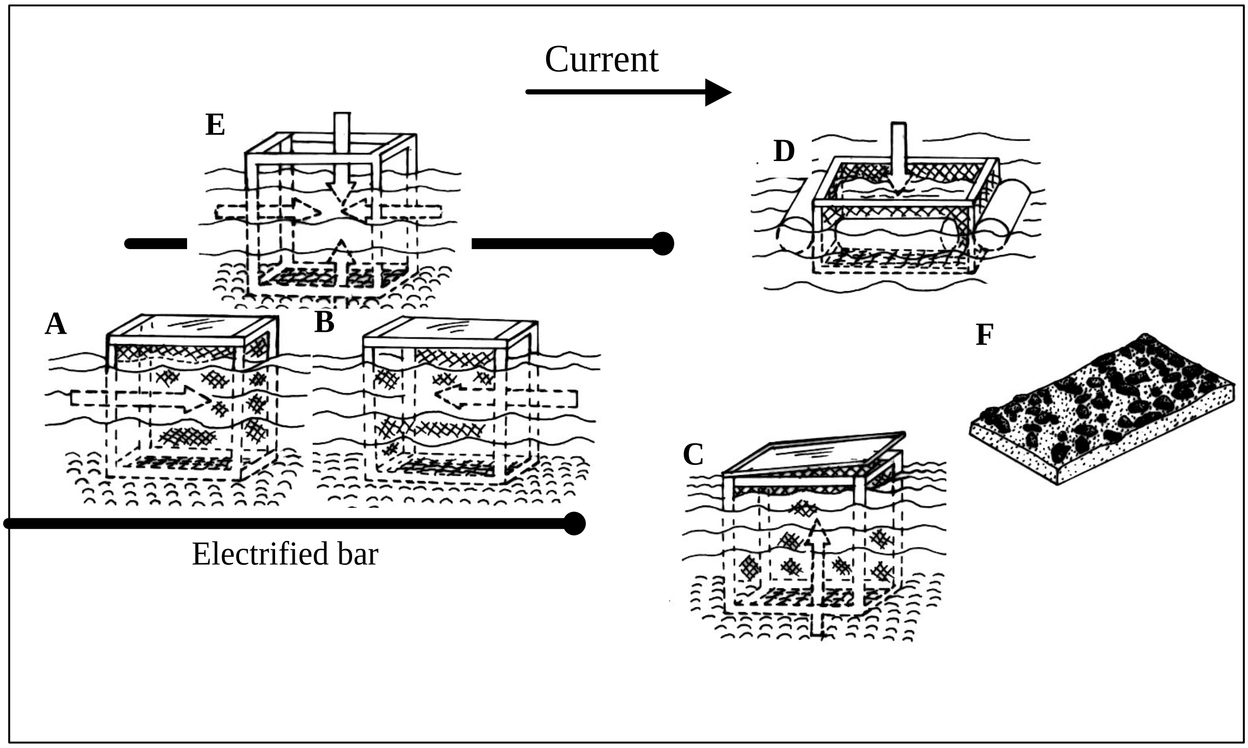

Figure 1: Position of the five recolonization traps (A) downstream movement, (B) upstream movement, (C) subsurface movement, (D) aerial colonization, (E) control, and (F) the artificial rocky substrate used inside the traps. The white arrows indicate the direction of entry of animals into each trap. Two electrified copper bars surrounded three traps (control, downstream and upstream).

Data collection

Four substrates were installed in each trap, and sampled after 1, 3, 7, and 21 days of colonization. The substrate removed from each trap was packed individually and preserved in 70% alcohol. The material was then cleaned and inspected individually at the laboratory. The macroinvertebrates sampled were identified (Pennak, 1978; Lopretto & Tell, 1995; Merritt & Cummins, 1996) and counted, to determine richness and density. The family level was the minor taxonomic level used to taxon determination. For some orders it was not possible to identify the initial instars and pupa phase to family level.

Statistical analysis

Dominance-density curves of species (Brower & Zar, 1984), or species importance curve, were constructed by plotting the log10 (x+1) of absolute density of each species against the corresponding rank, in decreasing order of abundance. Treatments were compared by One-Way ANOVA followed by multiple comparisons (Tukey test; Statistica 5.1, 1996). The data were transformed in $\log_{10}$ (x +1) after testing for normality (Shapiro-Wilks; $a = 0.05$) and homocedasticity (Levene; $a = 0.05$) (Statistica 5.1, 1996).

Results

Thirty-three macroinvertebrates taxa were sampled, being Chironomidae, Baetidae, Glossossomatidae and Leptophlebiidae the most abundant (Tab. I). Control cages had the highest density. Among treatments the highest density was in the aerial treatment. Downstream was the route with the highest taxonomic richness. In terms of taxa composition, the upstream and subsurface treatments presented the same order of group's importance, but the downstream and aerial treatments were similar only for the three first most important density groups (Tab. I).

Taxonomic richness increased through time in all treatments. Highest taxonomic richness was found at downstream treatment for most dates, although the subsurface had a similar richness at 1st and 7th days (Tab. II).

Table I: Density (D = number of individuals / m² of substrate area) and relative density (%) of macroinvertebrates taxa sampled in the control and in the four treatments (sum of four sampling days).

Taxa	Control		Downstream		Upstream		Aerial		Subsurface	
	D	%	D	%	D	%	D	%	D	%
Cnidaria-Hydrozoa	-	-	-	-	4	<1	4	<1	-	-
Platyhelminthes-Turbellaria	-	-	16	<1	-	-	-	-	-	-
Nematoda	-	-	-	-	4	<1	4	<1	-	-
Mollusca-Ancylidae	-	-	12	<1	-	-	-	-	12	<1
Mollusca-Bivalvia	-	-	-	-	-	-	-	-	4	<1
Annelida-Oligochaeta	195	1	563	1	236	1	-	-	414	2
Copepoda-Ciclopoida	-	-	8	<1	90	1	25	<1	176	1
Acarina	4	<1	33	<1	4	<1	-	-	16	<1
Plecoptera-Perlidae	-	-	4	<1	-	-	-	-	-	-
Collembola-Isotomidae	-	-	-	-	-	-	-	-	12	<1
Ephemeroptera-Leptophlebiidae	73	<1	364	1	4	<1	98	<1	17	<1
Ephemeroptera-Leptohyphidae	190	1	305	1	62	<1	244	1	45	<1
Ephemeroptera-Caenidae	-	-	-	-	-	-	-	-	8	<1
Ephemeroptera-Baetidae	5615	22	4693	23	2471	15	3949	17	1562	9
Ephemeroptera pupae	8	<1	8	<1	-	-	-	-	28	<1
Odonata-Libellulidae	-	-	4	<1	-	-	-	-	-	-
Odonata-Gomphidae	-	-	-	-	-	-	-	-	4	<1
Odonata-Calopterygidae	12	<1	12	<1	-	-	8	<1	-	-
Odonata-Coenagrionidae	-	-	8	<1	-	-	-	-	-	-
Trichoptera-Hydropsychidae	16	<1	52	<1	-	-	-	-	-	-
Trichoptera-Hydroptilidae	4	<1	37	<1	12	<1	8	<1	-	-
Trichoptera-Leptoceridae	-	-	-	-	-	-	-	-	12	<1
Trichoptera-Glossosomatidae	147	1	171	<1	4	<1	-	-	-	-
Trichoptera larvae	434	2	487	1	49	<1	179	1	32	<1
Trichoptera pupae	-	-	4	<1	-	-	-	-	12	<1
Coleoptera-Gyrinidae	-	-	-	-	-	-	12	<1	-	-
Coleoptera-Elmidae	69	<1	123	<1	87	1	199	1	87	1
Diptera-Simuliidae	359	1	392	1	-	-	4	<1	-	-
Diptera-Ceratopogonidae	-	-	4	<1	-	-	-	-	-	-
Diptera-Psychodidae	-	-	24	<1	-	-	-	-	-	-
Diptera-Empididae	42	<1	58	<1	-	-	4	<1	-	-
Diptera-Chironomidae	18673	72	11762	71	13539	82	17914	79	14619	86
Diptera-Stratiomydae	-	-	-	-	12	<1	-	-	-	-
Total density	25841		19144		16578		22652		17060	
Richness	15		24		14		14		17	

Table II: Number of taxa, density (D), and relative density (%) of macroinvertebrates sampled in the Ribeirão da Quinta in four dates, during the experiment used to quantify the routes of colonization (treatments).

Treatments	1st day			3rd day			7th day			21st day		
	Taxa	D	%	Taxa	D	%	Taxa	D	%	Taxa	D	%
Downstream	5	1226	41	9	1988	24	11	3286	21	20	12946	27
Upstream	4	381	13	3	2429	30	6	4488	28	12	9283	19
Aerial	3	750	25	4	2012	24	7	3988	25	14	15904	33
Subsurface	5	667	22	3	1798	22	11	4226	26	13	10371	21
Total without control	5	3024	62	12	8227	80	21	15988	82	28	48504	72
Control	8	1869	38	8	2095	20	9	3429	18	14	18450	28
Total with control		4893			10322			19417			66954	

The density increased significantly with time (One-Way ANOVA, $F_{3,76}$ = 153.65; p<0.001). However, densities were significantly different among treatments only at the 21st day ($F_{4,15}$ = 18.88; p<0.001), with predominance of control and aerial colonization route (Fig. 2). The 3, 7 and 13 colonization days showed smaller densities and did not differ significantly among routes ($F_{4,15}$ = 2.83, 0.48, 1.06; p = 0.062, 0.75, 0.41; respectively).

The resemblance among treatments was evident when the dominance-density curves were compared over time (Fig. 3). One of the similarities was the dominance of two groups (rank 1 and 2), determined by Chironomidae and Baetidae. Another similarity was the progressive increase of richness along the colonization process with a greater number of rare groups at the 21st day. On the other hand, two differences could also be observed among treatments.

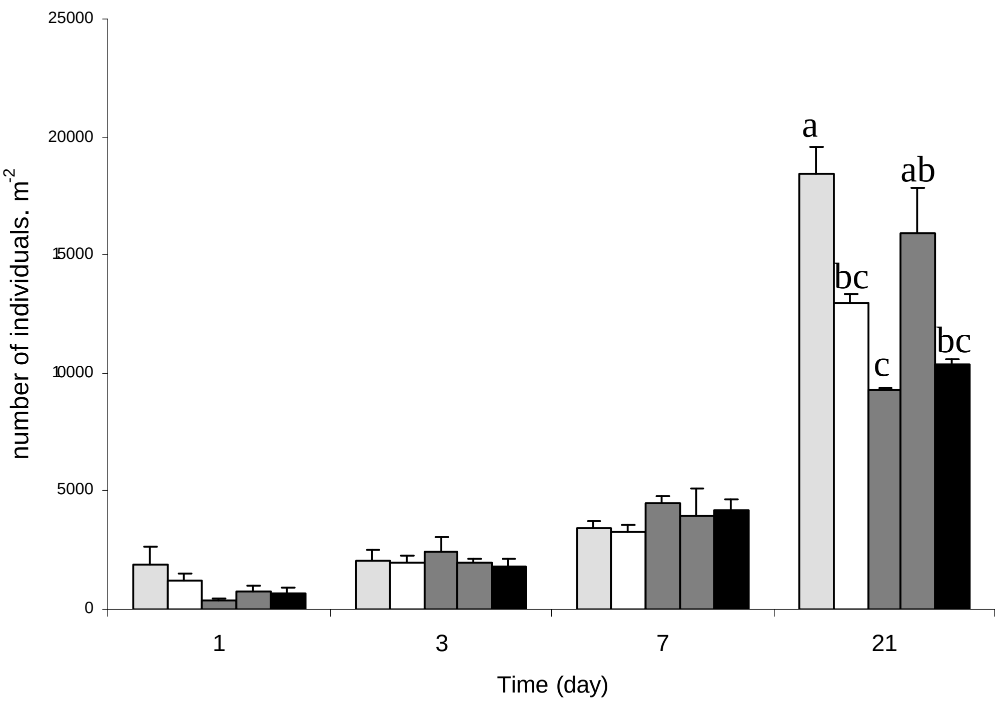

Figure 2: Density (number of individuals / m² of substrate area) of total macroinvertebrates sampled in four dates (mean ± 1 standard error). Different letters indicates significantly different treatments (Tukey test). Control ■ Downstream □, Upstream ■, Aerial ■, Subsurface ■.

First, the greatest richness was found at downstream treatment on every sampling day. Second, at the subsurface treatment most groups were already observed by the 7th day.

For the ten most abundant taxa, considering only the density of the 21st day (when the density by route were significantly different), three distinct groups are visible: (1) seven taxa using the four routes, (2) one taxa using three routes and (3) two taxa using only two routes of colonization (Fig. 3). In the first group, Chironomidae, Trichoptera, Baetidae, Leptophlebiidae and Copepoda showed significant differences when the density by routes were compared (One-Way ANOVA, $F_{3,12}$ = 6.9, 5.22, 13.85, 6.57, 5.6; p = 0.006; 0.015; 0.0003; 0.007; 0.012, respectively). Chironomidae and Trichoptera used mainly the aerial route; Baetidae and Leptophlebiidae mainly downstream and aerial, and Copepoda mainly upstream and subsurface. From the first group yet, Leptohyphidae and Elmidae did not showed significant differences between routes ($F_{3,12}$ = 2.5; p = 0.11 for both). The second group, composed only by Annelida, did not present significant differences when downstream, upstream and subsurface routes were compared (($F_{3,12}$ = 20.46; p = 0.70). In the third group, although Simuliidae and Glossosomatidae showed a preference for downstream colonization, this tendency was not significant.

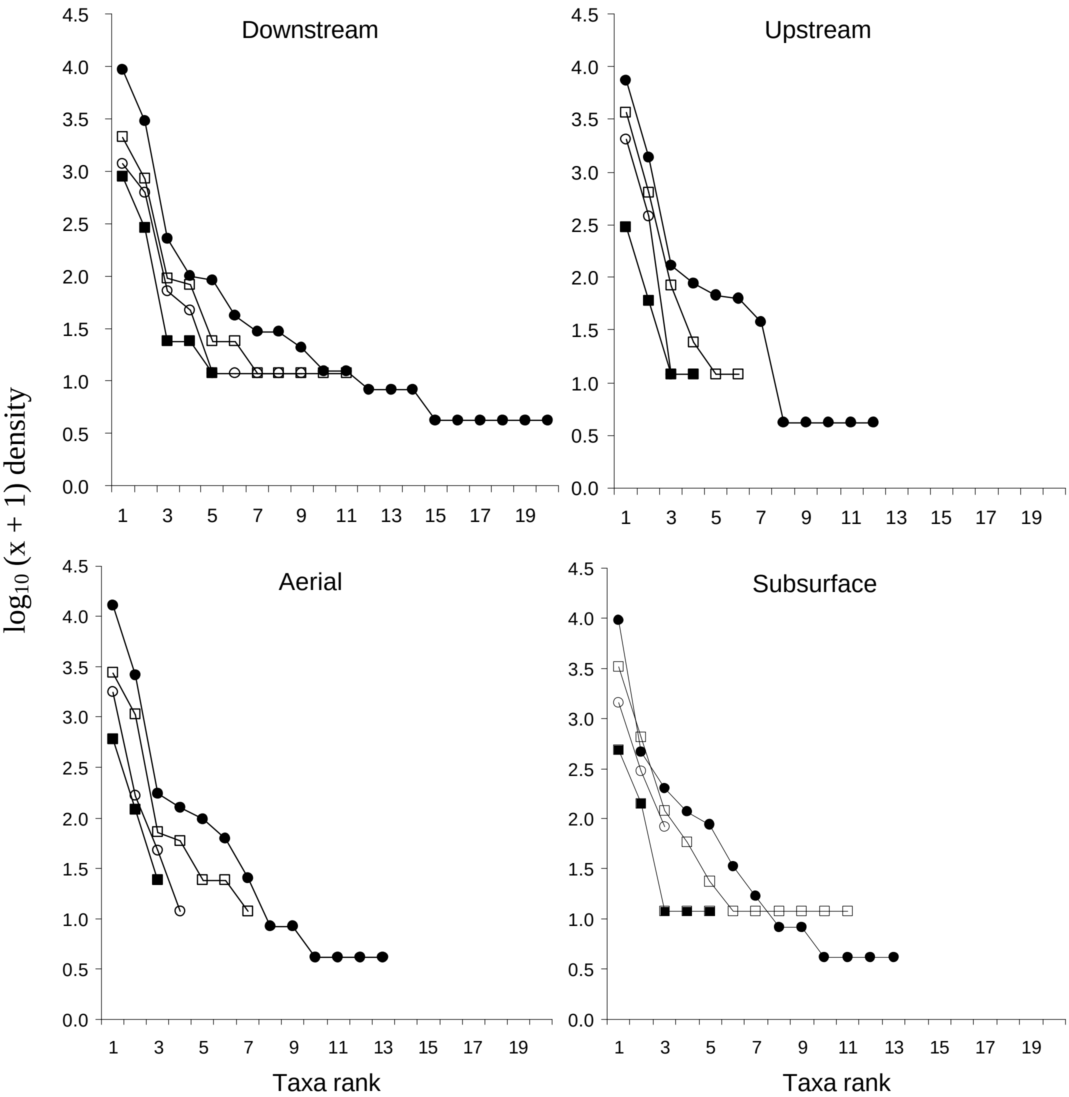

Figure 3: Comparison of the four sampling days by a dominance-density curve of macroinvertebrates for each treatment (log_{10} (x + 1) of the density mean). Comparison of the four sampling days by a dominance-density curve of macroinvertebrates for each treatment (log_{10} (x + 1) of the density mean). Day 1 ■ , Day 3 ○ , Day 7 □ , Day 21 ● .

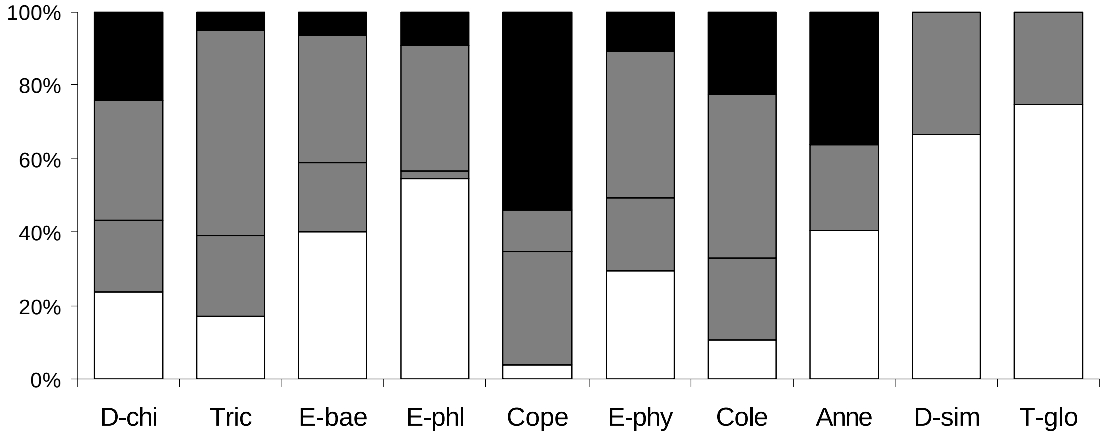

Figure 4: Percentage density of the ten most representative taxa sampled in the 21st colonization day. Diptera-Chironomidae (D-chi), Trichoptera larvae (Tric), Ephemeroptera-Baetidae (E-bae), Ephemeroptera-Leptophlebidae (E-phl), Copepoda (Cope), Ephemeroptera-Leptohyphidae (E-phy), Coleoptera-Elmidae (Cole), Annelida-Oligochaeta (Anne), Diptera-Simuliidae (D-sim) and Trichoptera-Glossosomatidae (T-glo). Downstream □Upstream ▒ Aerial ■ Subsurface ■.

Discussion

Williams & Hynes (1976), analyzing the colonization routes in denuded areas of the benthic substrate of a stream in Canada, concluded that drift constituted the most important colonization route. However, the authors pointed out that the four routes were important for the replacement of the denuded areas and that many groups used preferential routes, arguing that the exclusion of some colonization directions could lead to the establishment of distinct communities.

For the analysis of these different routes, the utilization of a manipulated control, which kept the same characteristics of experimental areas, but allowed the access of the invertebrates to denuded areas by all colonization directions, was more important than a natural control (rocks of the substratum). The efficiency of this control, opened to all routes, was confirmed by the greatest density value found, when compared to other treatments (Williams & Hynes, 1976; present study).

According to Williams & Hynes (1976), theoretically, if the stabilization of the colonization process was not reached by the last sampling day, the control will not reach the sum of the four routes. From the only three works that investigated colonization routes (Williams & Hynes, 1976; Williams, 1977; Benzie, 1984), none reached the hypothesized value for the control. It is possible that this theoretical value might never be reached, not because of the absence of stabilization, but perhaps by the existence of an interaction among groups in the control (Humphries, 2003) or by different opportunity of dispersal on each trap. Limited dispersal may be occurring in the aerial trap, where females laid egg masses and the larger number of hatchlings had limited dispersal from the trap, contributing to the high density in this treatment.

Moreover, the time of stabilization of the community probably depends not only on dispersion of the species for occupation of new areas but also on several other factors. According to Rosenberg & Resh (1982 in Mackay, 1992), the balance or community's stabilization, reached when the relation between species immigration and emigration in an area becomes more or less constant, can be influenced by the experimental model, season, and geographical location.

Colonization Routes

The downstream route includes invertebrates moving downstream by crawling on the substrate and also the ones that move, actively or passively, in the drift. The structure of the downstream trap, closed on the downstream side, could have caused an overestimate of the quantity of invertebrates found there. With this barrier (closed side), some invertebrates that will just pass through the trap will be forced to stay. However, Williams & Hynes (1976) considered the downstream route only as a drift movement, not considering the crawling movement that certainly happened in their experiment. This type of downstream movement could be avoided keeping this trap above the substratum, as accomplished by Doeg et al. (1989). These authors were able to quantify only the drift using a suspended trap and found a low contribution of this route for colonization of the rocky substratum, despite other authors (Waters, 1972; Williams & Hynes, 1976; Williams, 1977) that suggest drift as the main colonization route. However, Boyero & Bosch (2004) suggested that stone recolonization by macroinvertebrates depends on background communities at a "stone scale" and on macroinvertebrates drift at riffle scale. This pattern of displacement of macroinvertebrates depends on animals which move short distances by crawling (stone scale), and long distances by drift (riffle scale). This may be the explanation for different results at the literature about the relative importance of drift. As stressed by Boyero & Bosch (2004), the spatial dimension of the process of stone recolonization by macroinvertebrates has usually been neglected, and opposite patterns found by different authors may be due to a mismatch in the spatial scales of study.

Although oviposition is considered a fast colonization route, there are few data documenting the activity of adult insects and the number of eggs deposited (Mackay, 1992). Some recent works tried to analyze the behavior mechanisms involved on this process, the physical characteristics of oviposition sites, and what features are related to females oviposition sites selection (Peckarsky & Taylor, 2000; Lancaster et al. 2003; Reich & Downes, 2003 a, b). The patterns of oviposition could ultimately influence the large and small scale distribution of certain stream taxa (Peckarsky & Taylor, 2000; Reich & Downes, 2003 a).

Williams (1977), analyzing the colonization routes in two temporary streams in Canada, attributed the lower importance of aerial colonization in the experiments to the low incidence of adult insects in the area. On the other hand, the aerial colonization was second in importance only to drift in Williams & Hynes (1976) experiment. These differences in the importance of aerial colonization route may be related to the period of year, differing among seasons, with a lesser contribution in the winter (Williams & Hynes, 1976). In our study, females laid egg masses in the aerial treatment and the large number of hatchlings had limited dispersal from it, resulting in a high density of first instars inside this treatment. It needs to be emphasized also that the importance of aerial colonization at this type of experiment may be related not only to the lack of subsequent dispersal, but also to protection from predators, and entrance of animals smaller than the mesh net used. These effects may be present at Williams & Hynes (1976) and at our experiment, both utilizing the same aerial trap design. The presence of non-aerial groups at aerial treatment, although in small density, may be a result of water splash or an entrance through the mesh net.

Like for aerial route, the relative importance of vertical colonization, from subsurface or hyporheic zone is less conclusive. In the present work, although subsurface colonization was not an important route, in this trap almost all groups already occurred at the 7th day, 1/3 of the total experimental period. On this route the distance for vertical movement of the organisms to the substrate is smaller, which could facilitate more rapid establishment of the groups. In this way, invertebrates are less exposed to strong flow and predation. Conversely, Olsen & Townsend (2005) showed that hyporheic zone provided refuge during high flows. The decrease of flow caused by the experimental structure can have caused an overestimation of some taxa. Changes in the physical environment of the hyporheic zone may change community patterns according to the habitat requirements of different taxa (Olsen & Townsend, 2005).

Structure of the community

The community structure sampled presented two main characteristics: (1) the dominance of two groups and (2) a progressive increase of richness and abundance at a temporal scale.

The dominance of Diptera and Ephemeroptera on recolonized denuded stones was also reported in other studies in tropical streams in Africa (Hynes 1975; Benzie 1984), Panama (Boyero & DeLope, 2002), and Costa Rica (Boyero & Bosch, 2004).

The progressive increase of richness and density differed between routes.

Downstream route presented the greatest species richness at all sampling dates, most composed by rare species at the end. Subsurface route showed community stabilization at half of the total sampling period, with colonizers proceeding probably from nearby areas. The large number of potential colonists at the surrounded area and the higher mobility of most macroinvertebrates are some good reasons for the fast recolonization of denuded areas (Boyero & DeLope, 2002; Boyero & Bosch, 2004).

The patterns observed for the main taxa, regarding the utilization of different routes, reinforce some previously discussed questions. First, the utilization of all colonization routes by Chironomidae and Baetidae probably should have contributed to their numerical dominance. Second, Simuliidae and Leptophlebiidae used preferentially the downstream colonization route, probably by drift. Third, the predominant utilization of one route occurred mainly by the less abundant species, determining a great similarity among treatments.

Among the colonization route studies, the one of Benzie (1984) showed the closest results to the present study, and shared similar experimental method, period of year (dry) and region (tropical). These similarities reinforce Williams & Hynes (1976) view that the experimental model, the season and the geographical location would be the main factors that define community adjustment.

In the present study, the four colonization routes were important for replacement of denuded areas. Groups of benthic macroinvertebrates, which used preferential routes, determined the differences in community structure between different colonization routes.

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