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The influence of initial colonization by hydropsychid caddisfly larvae on the development of stream invertebrate assemblages

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Abstract

Many aspects of the colonization history of a disturbed site can influence the development of a biological community. Initial colonization is known to play a significant role in community development because of the facilitative or inhibitory effects that 'pioneer' species can have on subsequently arriving taxa. We performed an experiment to assess how initial colonization by two species of benthic invertebrates (Trichoptera: Hydropsychidae) might influence the development of stream faunal assemblages. Substrate baskets initially colonized by either *Hydropsyche depravata* or *Ceratopsyche bronta* were placed alongside control baskets in a recently flooded stream. After baskets had colonized for 30 days, we found that species composition in treatment baskets was identical to that in control baskets, indicating that the caddisfly taxa had no selective effects on colonization of other macroinvertebrate species. We did, however, find that *C. bronta* facilitated the recruitment of all species in the colonist pool leading to greater overall abundance and biomass of macroinvertebrates in the final assemblages. In contrast, *H. depravata* had no effect on the abundance or biomass of colonizing invertebrates. The differential effects of these two taxa on abundance and biomass may have been related to differences in microhabitat complexity created by the construction of their retreats and catchnets. The results of this study support the growing recognition that colonization history does influence the structure of lotic communities, but they also suggest that even closely related taxa can play different roles as initial colonists in community development.

Introduction

Biological communities are assembled by the continuous and sequential processes of colonization and extinction. As such, they are inherently a function of the historical processes that underlie their development. The successful establishment of colonizing species has long been thought to depend on the resident biota of the community (Diamond, 1975; Roughgarden, 1989), and indeed, there is a growing body of theoretical and empirical work demonstrating that the sequence of colonization can greatly influence the trajectory and final state of a developing community (McCune & Allen, 1985; Gilpin et al., 1986; Robinson & Dickerson, 1987; Robinson & Edgemon, 1988; Drake et al., 1993; Holland & Jenkins, 1998, and many others).

Initial colonization is one of many aspects of colonization history that can govern how a community develops over time. Initial colonizers can influence the assembly of a community by either facilitating or inhibiting the establishment of other species (Belyea & Lancaster, 1999). Facilitation can occur via trophic interactions (e.g. predators require prior colonization by prey) or via physical modification of a habitat's suitability (Connell & Slater, 1977). Inhibition often results from 'priority effects' whereby initial colonizers limit the establishment of potentially competing species (Alford & Wilbur, 1985; Drake, 1991; Ehmann & MacMahon, 1996). Understanding the net effect of facilitation and inhibition by initial colonizers is crucial to understanding how and why communities develop as they do.

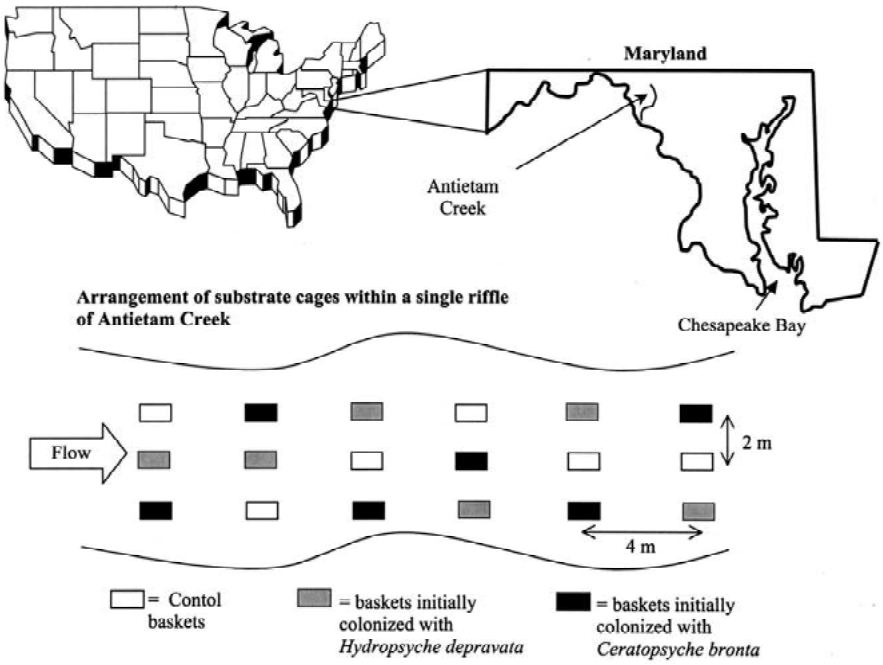

Figure 1. The location of the study site, Antietam Creek, and arrangement of experimental units within a single riffle of the stream.

Like many ecosystems, streams are characterized by periodic disturbances that renew ephemeral resources and reset the trajectory of community development (Resh et al., 1988). As such, initial colonization is likely to play an important role in the dynamics of stream communities following disturbances. Several stream organisms have the potential as initial colonists to influence the establishment of other taxa. Among these are the net-spinning caddisflies from the trichopteran family Hydropsychidae. Several studies have shown that hydropsychid caddisflies can facilitate the colonization of other invertebrates (Diamond & Reice, 1985; Diamond, 1986; Englund, 1993), and this is thought to be related to the habitat complexity generated by the construction of larval retreats and catchnets (Diamond, 1986; Englund & Evander, 1999). Larval hydropsychids can also inhibit the colonization of potential competitors. Caddisflies are aggressive and territorial, and they often compete for space in the benthic habitat of streams (Englund & Olson, 1990; Englund, 1991). Research has shown that competitively superior taxa sometimes inhibit the establishment of populations of competitively inferior species (Hemphill, 1988; Morin, 1991; Englund, 1993).

Given that hydropsychid caddisflies can both inhibit and facilitate the colonization of stream fauna, we asked: (1) What is the net effect of initial hydropsychid colonizers on the development of stream invertebrate assemblages, and (2) Do different species of hydropsychids have different consequences as initial colonizers for the development of stream invertebrate communities? To address these questions, we performed a field experiment in which we manipulated the initial hydropsychid colonizer, either *Hydropsyche depravata* or *Ceratopsyche bronta*, in baskets of stream substrates. *H. depravata* larvae range from 2 to 4 times larger than *C. bronta* larvae, are more aggressive when competing for limited space, and construct catchnets that are c.a. 20% larger (Cardinale, unpublished data). Thus, we suspected that the effects of *H. depravata* on the establishment of macroinvertebrate fauna might differ from the effects of *C. bronta*. Substrate baskets initially colonized by *H. depravata* or *C. bronta* were placed alongside control baskets in a recently flooded stream and allowed to colonize for 30 days. Following this period, we compared the composition and structure of the macroinvertebrate assemblages between the control baskets and those initially colonized by the two different species.

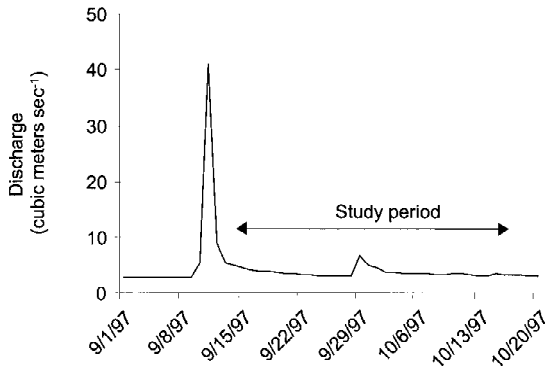

Figure 2. Discharge during the period of the study. Data are from USGS station # 01619500 approximately 500 m from our study site.

Methods

Study site

The experiment was performed in Antietam Creek – a third order tributary of the Potomac River located in the Appalachian Mountains of Western Maryland (39° 27′ N, 77° 43′ W, see Fig. 1). The stream was approximately 20 m wide at the study site and had a cobble/boulder streambed. The experiment was initiated after a flood (recurrence interval ≈1 year, see Fig. 2) left stream substrates denuded of macroinvertebrate fauna (pers. obs.). Performing the experiment after a flood minimized the possible 'swamping' of treatment effects that is common in systems characterized by high dispersal and species turnover (Palmer et al., 1997). Data from a nearby gauging station (USGS # 01619500) indicated that discharge remained relatively constant during the study period (see Fig. 2).

Initial colonization of experimental units

Eighteen, 1000 cm^3 baskets were constructed of 1-cm wire mesh and filled with an equal volume of three particle sizes of natural stream substrates (8–16 mm, 16–32 mm and 32–64 mm diameter) that had been defaunated by ashing. In the lab, baskets were placed in individual containers of circulating stream water. Six baskets were randomly assigned to one of two treatments (initial colonizer = *Ceratopsyche bronta* or initial colonizer = *Hydropsyche depravata*) or designated to serve as controls (no larvae added). An equal biomass (500-mg) of fourth and fifth instar larvae, collected from Antietam Creek 2 days prior to the flood, was added to treatment baskets to approximate naturally occurring biomass in this site. Because *H. depravata* is larger than *C. bronta*, the number of larvae added to each basket was greater for the *C. bronta* treatment (105±SE 16.1) than for the *H. depravata* treatment (30±SE 1.27). The choice of standardizing experimental treatments by abundance or biomass has been a controversial topic in ecological research for many years. In this experiment, we felt that standardizing by biomass would more closely approximate natural recolonization processes where recruitment of stream invertebrates is often inversely proportional to body size (Allan, 1978; Allan & Feifarek, 1989). After larvae were added to the substrate baskets in the lab, they were given 48 h to construct retreats and catchnets. Observations suggested that larvae built normal, functioning structures within this period and were visibly using their retreats.

Placement and subsequent colonization of baskets in the stream

After adding hydropsychid larvae to the baskets in the lab, baskets were transported in individually aerated containers to the study site where they were secured flush to the surface of the streambed with tent stakes. During placement, baskets were surrounded with a PVC pipe (35-cm dia.) to reduce flow so that animals would not be dislodged. The pipe was removed after a brief period of acclimation (approx. 5 min.). Because we wanted all baskets to be exposed to a similar colonist pool, all were placed in a single riffle with one basket of each treatment randomly assigned to a position in each of six rows (Fig. 1). Baskets were allowed to colonize naturally with stream biota for 30 days before the experiment was terminated because of an impending storm.

Retrieval of baskets and data collection/analysis

After 30 days, baskets were again surrounded with a PVC pipe to prevent dislodgment of animals and removed from the streambed. They were placed in individually aerated containers and transported to the lab in coolers with ice to minimize invertebrate activity. In the lab, macroinvertebrates were scrubbed from the substrates and rinsed onto a 500-μm mesh sieve. All animals were preserved in formalin and later enumerated, identified to morphospecies, and then dried and weighed.

Six metrics were used to compare the macroinvertebrate assemblages in the control and treatment baskets. Total abundance, total biomass, species richness and species evenness (as Simpson's index) were

used to compare the structure of the macroinvertebrate assemblages. To assess the similarity of species composition, we calculated the proportion of shared species between the different assemblages (as Sorensen's coefficient) and the similarity of the relative abundances of shared species (as the 'proportional similarity' index, Brower et al., 1998). Because replicates were not paired in our experimental design, unbiased estimates of Sorensen's coefficient and the proportional similarity index required that these indices be calculated for all possible combinations of replicate baskets. For example, a comparison of the proportion of shared species between the controls and *H. depravata* treatment involved 36 estimates of Sorensen's index (6 replicate baskets for the controls × 6 replicate baskets for the *H. depravata* treatment).

ANOVA was used to test for differences in each of the six dependent variables (abundance, biomass, richness, evenness, proportion of shared species and the similarity of the relative abundances of shared species) between controls and treatments. When main effects were significant, pair-wise comparisons were made using *t*-tests. Assumptions of normality and homogeneity of variance were verified for all tests. We were careful to exclude the abundance and biomass of the initial hydropsychid colonizers from all analyses because we could not preclude the possibility of differential emigration of the two initial colonizers from the treatment baskets after placement in the stream. Thus, we focus only on the effects of the two treatment taxa on the remainder of the macroinvertebrate assemblage. Interestingly, we have analyzed the data with and without *H. depravata* and *C. bronta* included and the results are qualitatively identical.

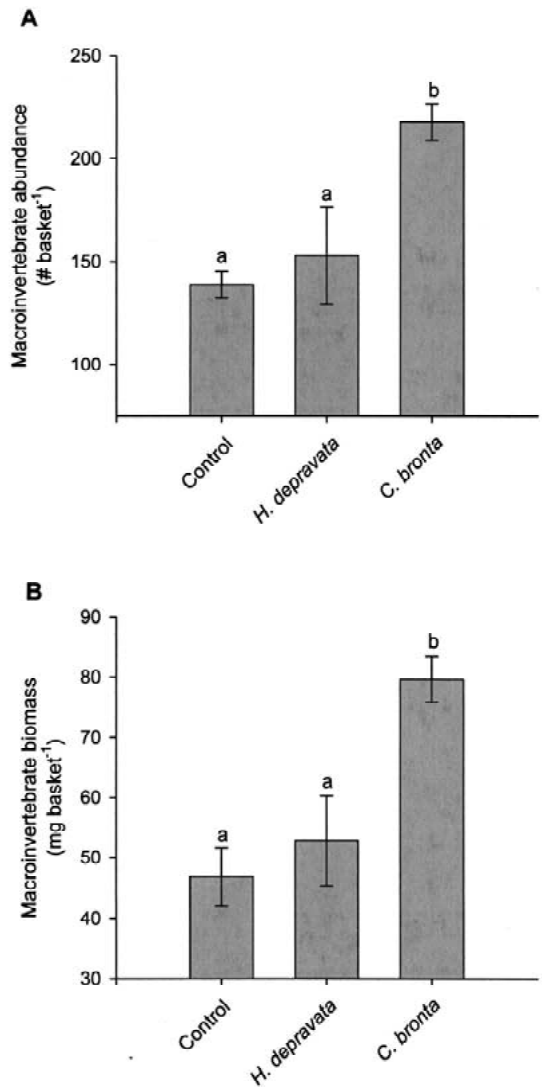

Figure 3. The abundance (A) and biomass (B) of macroinvertebrates in control cages and treatment cages initially colonized with two different species of hydropsychid larvae. Data are the mean ± SE of six replicate cages. The abundance and biomass of the two initial colonizers are not included in these values. Unique letters denote significant (p<0.01) differences.

Results

After 30 days of colonization, substrate baskets initially colonized with *Ceratopsyche bronta* had higher overall macroinvertebrate abundance (see Fig. 3A, $p < 0.01$) and biomass (see Fig. 3B, $p < 0.01$) than did the control baskets or those initially colonized by *Hydropsyche depravata*. The *H. depravata* baskets, however, did not differ from the controls. Greater biomass of macroinvertebrates in the *C. bronta* treatment could have resulted from either (1) greater overall abundance of macroinvertebrates, or (2) larger animals establishing in these baskets. When total biomass was standardized by abundance there was no difference between control and treatment baskets ($p = 0.63$), indicating that higher biomass resulted from greater overall abundance.

In contrast to the differences in abundance and biomass, there were no differences in the composition of the macroinvertebrate assemblages between the control and treatment baskets, or between the two treatments. A total of 26 morphospecies colonized the baskets during the study period (see Table 1). Taxa richness was nearly identical among control and treatment baskets with an average of 16 morphospecies (p

Table 1. The abundance of each morphospecies in control and treatment cages after 30 days of colonization. Data are given as the number of animals per substrate basket. Each basket had a volume of 1000 cm^3

Taxa	Controls		*C. bronta*		*H. depravata*	
	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
Ceratopsyche morosa	8.00	4.20	11.17	5.78	5.6	72.42
C. sparna	0.17	0.41	0.33	0.82	1.33	2.42
C. bifida	0.00	0.00	0.17	0.41	0.00	0.00
Hydropsyche simulans	16.33	13.03	34.33	13.43	28.17	12.70
H. scalaris	1.17	0.75	2.17	1.83	2.67	2.88
H. decantha	8.33	7.97	10.50	5.09	5.83	5.19
H. leonardi	1.50	1.38	1.83	1.72	0.67	0.82
H. sp. *E*	5.00	5.10	9.83	11.41	5.33	5.72
H. sp. *F*	3.67	3.39	7.00	6.23	2.83	0.75
H. sp. *G*	0.33	0.82	0.33	0.82	0.00	0.00
Cheumatopsyche sp. *A*	2.33	2.58	5.17	3.19	2.33	3.61
Ch. sp. *B*	1.17	0.75	3.67	3.83	2.33	2.73
Ch. sp. *C*	0.83	2.04	2.00	2.10	1.83	1.17
Ch. sp. *D*	0.00	0.00	0.17	0.41	0.17	0.41
Ch. sp. *E*	0.00	0.00	0.17	0.41	0.17	0.41
Chimarra sp.	5.33	3.50	7.83	3.13	3.67	2.80
Heptagenia stenonema	4.00	2.00	5.00	1.55	6.17	1.60
H. stenecron	0.50	1.22	0.00	0.00	0.00	0.00
Seratella sp.	25.33	14.09	35.67	13.46	21.33	15.23
Attenella sp.	13.33	16.66	22.83	18.83	13.50	14.73
Baetis sp.	2.00	1.90	2.00	2.28	1.33	1.75
Isonichia sp.	0.33	0.52	0.00	0.00	0.67	1.03
Gammarus sp. *A*	38.67	10.01	54.67	28.12	46.83	32.42
Gammarus sp. *B*	0.33	0.52	0.00	0.00	0.00	0.00
Unidentifiable	0.17	0.41	1.00	1.67	0.00	0.00

= 0.98, see Fig. 4A). There was also no difference in the taxonomic evenness of species comprising the assemblages ($p = 0.61$, see Fig. 4B).

On average, baskets had 80% of their colonizing taxa in common with no significant difference in the proportion of shared species found between control and treatment baskets, or between baskets initially colonized by the two hydropsychid species ($p = 0.52$, see Fig. 5A). There was also no difference in the relative abundance of shared species between the control and treatment baskets or between baskets of the two treatments ($p = 0.23$, see Fig. 5B). Collectively, these data indicate that (1) control and treatment baskets had identical community composition, with the same species all having the same relative abundance, but (2) *C. bronta* facilitated, either directly or indirectly, the rate and/or magnitude of recruitment by the entire macroinvertebrate assemblage.

Discussion

Colonization history is known to play an important role in the development of communities, particularly in ecosystems that experience periodic disturbances (Diamond, 1975; McCune & Allen, 1985; Robinson & Edgemon, 1988; Drake, 1990; Drake et al., 1993; Ehmann & MacMahon, 1996, and others). Because disturbance is a distinct characteristic of stream ecosystems (Resh et al., 1988), it is likely that colonization history is a critical factor that determines how communities develop after flooding in a stream. Despite this, few studies have attempted to characterize the role of colonization history in natural stream environments.

Our study focused on one aspect of colonization history, initial colonization, thought to be a critical determinant of how a community develops. Through their competitive interactions with other taxa, initial

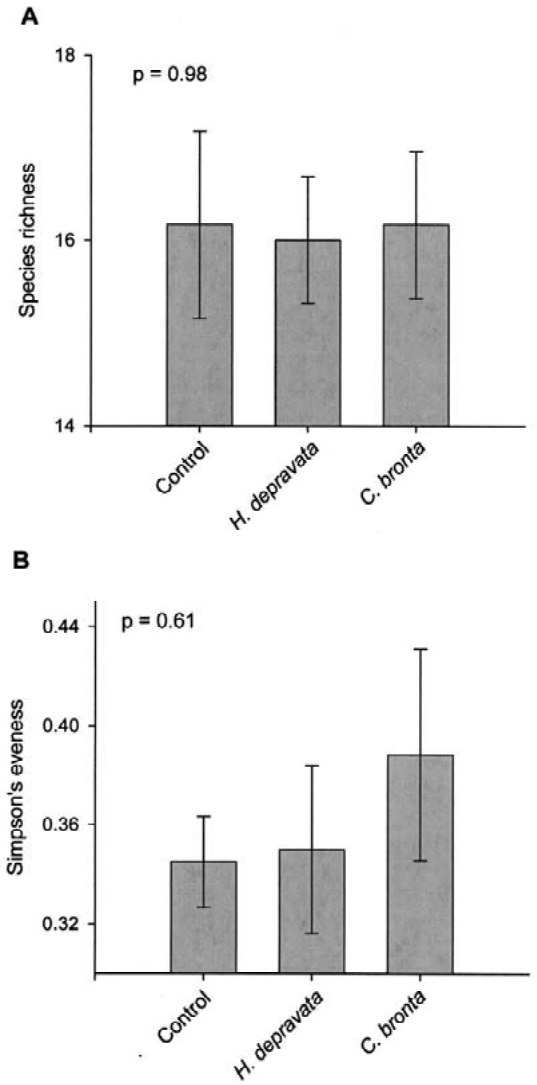

Figure 4. Species richness (A) and species evenness (B) of macroinvertebrate taxa in control cages and in treatment cages that were initially colonized with different species of hydropsychids. Data are the mean ± of six replicate cages.

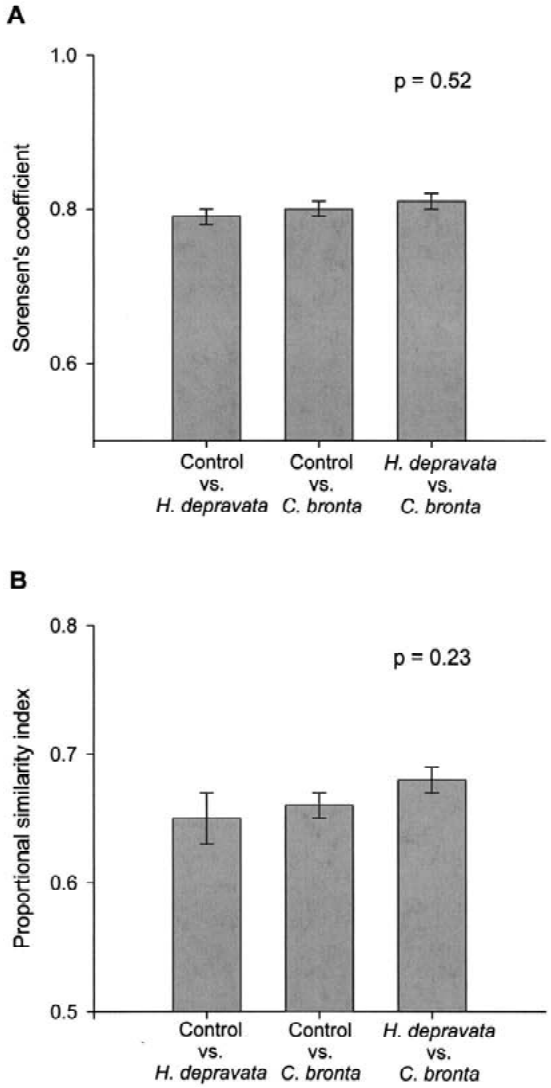

Figure 5. The proportion of shared species (A) and the similarity of the relative abundance's of shared species (B) between control and treatment cages. Data are the mean ± SE of the 36 possible combinations of replicates (see text for an explanation).

colonists can influence the numbers and types of species in a final community (Gilpen & Case, 1976; Alford & Wilbur, 1985; Drake, 1991). Hydropsychid caddisflies compete aggressively for space (Englund & Olson, 1990; Englund, 1991), and they can inhibit the colonization and establishment of other fauna that are potential competitors (Hemphill, 1988; Morin, 1991; Englund, 1993). Because well-established species typically have a competitive advantage over recruiting species (Moyle & Light, 1996), we had expected that the initial colonists used in this study might reduce the diversity of potential competitors relative to control baskets. Yet, we found no evidence for such inhibitory effects. Both treatments were indistinguishable from control baskets with respect to taxa richness, taxa evenness, the number of shared species and the relative abundance of shared species. Many taxa that colonized the substrate baskets were filter feeding hydropsychid taxa that are ecologically similar to the two initial colonizers. Thus, it is perhaps surprising that the initial colonists had no inhibitory effect on the recruitment of any taxa during this experiment. It is, however, quite

possible that resources did not become limited over the short duration of this experiment, and the competitive interactions that lead to inhibitory effects were precluded.

Initial colonists can also influence the absolute and relative abundances of species in a final community through their facilitative effects on species recruitment (Belyea & Lancaster, 1999). Several studies have shown that hydropsychid caddisflies can facilitate colonization by certain types of invertebrates, particularly those that respond to increasing complexity of the benthic habitat commonly associated with the construction of larval cases and catchnets (Diamond & Reice, 1985; Diamond, 1986; Englund, 1993; Englund & Evander, 1999). One of the two hydropsychid taxa in this study facilitated the recruitment and/or establishment of all macroinvertebrates in the stream assemblage. Total abundance and biomass of macroinvertebrates was higher in experimental units initially colonized by *C. bronta* than in control baskets. This difference was not the result of increased abundance of any particular taxon, but rather, resulted from a proportional increase in the colonization and/or establishment of all taxa in baskets of the *C. bronta* treatment. This is the first evidence, to our knowledge, that the initial colonizer in a disturbed stream site may facilitate recruitment of an entire assemblage of organisms. Total community abundance and biomass can exert strong controls on numerous stream processes including the uptake and retention of organic matter (Covich et al. 1999), the rates of primary productivity (Lamberti & Moore, 1984) and the transfer of energy to fish assemblages (Healy, 1984). Thus, one implication of our research is that ecological processes in streams may be affected by which species is the first to establish itself after flooding.

Despite the facilitation of invertebrate colonization by *C. bronta*, it was interesting that *H. depravata* had no effect as an initial colonist on the recruitment of other macroinvertebrate fauna. The lack of any effect was evident from the fact that invertebrate assemblages in the *H. depravata* treatment had equal abundance, biomass and composition to control baskets. It is, perhaps, surprising that the two initial colonists had such different effects given their close taxonomic and ecological similarity. Although this study was not specifically designed to assess why the two initial colonizers might have differential effects on colonization, we speculate that two factors – microhabitat complexity and larval distribution, contributed to the results. Structural complexity at the microhabitat scale is known to govern the density and biomass of lotic invertebrates (Downes et al., 1998). Hydropsychid larvae are generally thought to increase structural complexity through the construction of their retreats and catchnets, and this can increase the abundance of other invertebrates (Diamond, 1986; Englund & Evander, 1999). Due to differences in body size, baskets initially colonized with *C. bronta* contained more larvae (75 more on average) than those colonized with an equal biomass of *H. depravata*. More larvae likely corresponded to a greater number of catchnets which, in turn, could have increased microhabitat complexity in the *C. bronta* baskets relative to that in the *H. depravata* baskets. The difference in abundance does not negate the facilitative effect of *C. bronta* on invertebrate assemblages relative to control baskets, however, it is possible that the differential effects of *C. bronta* and *H. depravata* was partly influenced by our decision to standardize treatments by biomass rather than by abundance. We chose to standardize by biomass because the rates of recruitment of stream invertebrates are often inversely proportional to body size (Allan, 1978; Allan & Feifarek, 1989). To the extent that smaller bodied taxa are most common in post-disturbance drift, or that smaller bodied taxa are more likely to settle into a recently disturbed site, then our treatments would be representative of natural recolonization processes.

Differences in microhabitat complexity cannot fully account for the results of this study since baskets initially colonized by *H. depravata* would also have had increased complexity relative to the initial conditions of the control baskets. Why then did invertebrate assemblages in *H. depravata* baskets not differ from those in control baskets? One possibility is that the microhabitat preference of *H. depravata* precluded it from having an influence on the other colonizing fauna. Filter feeding caddisflies often exhibit specific flow preferences with larger species preferring areas of higher flow velocity (Cummins, 1964; Voelz & Ward, 1996). During our study, we observed that *H. depravata* typically constructed catchnets on the tops of rocks where velocity was presumably highest. Many of the other taxa that colonized the baskets are not adapted for such high flow conditions and tend to inhabit interstitial spaces on the undersides of substrata. Thus, *H. depravata* may have had little influence on the remainder of the macroinvertebrate assemblage because it utilized a microhabitat that is not extensively used by other stream fauna. In contrast, *C. bronta* typically constructed nets on the underside of rocks where the

other invertebrates are common. Thus, facilitation of recruitment by *C. bronta* via increased habitat complexity would have been more likely. To the extent this hypothesis is true, it illustrates how slight differences in the body size and/or behaviour of ecologically similar species could lead to very different effects of an initial colonizer on a developing community.

In summary, this study has provided evidence that initial colonization can be an important historical factor influencing the development of biological communities in stream ecosystems. Our results demonstrated that an initial colonizer can facilitate the recruitment of an entire assemblage of organisms leading to greater overall abundance and biomass in a site that is recovering from a flood. However, we also found that even ecologically similar taxa can have very different effects as initial colonists on community development. This suggests that differences in the colonization history of disturbed stream sites may contribute to the spatial and temporal variation that is commonly observed in the structure of lotic communities.

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