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Community responses to experimental food depletion: resource tracking by stream invertebrates

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Abstract The regulation of population processes for most organisms depends upon the strength and rate of feedback between resources and consumers. We conducted an experimental manipulation of leaf packs in stream channels, a patchy and ephemeral resource, which is consumed by a number of detritivorous invertebrates. We reduced the number of available food patches (red alder leaf packs) by half and then measured a variety of community responses, including emigration rate, aggregation on remaining food patches, decomposition rate of food patches, and species-specific differences in these responses. Replacement of removed leaf packs with polyester mimics resulted in no statistical difference in emigration rates or aggregation on remaining resources when compared to those removal channels without replacement. These results indicate that leaf packs are not used primarily for refuge. In the removal channels (including those with leaf pack mimics) emigration rate nearly doubled relative to control channels. Those invertebrates that did not emigrate from removal channels aggregated on remaining leaf packs, which led to more rapid decomposition of leaf packs relative to control channels. The increase in emigration rate only became apparent 2–3 days after the manipulation, presumably because animals colonized the remaining leaf packs and did not emigrate until food patch value per individual had been reduced by higher densities or due to increased discharge. Discharge through the channels increased slightly starting 3 days after the manipulation, resulting in increased emigration rates in all channels. Despite the increase in discharge, the effect of the manipulation remained strong. These results show that stream invertebrates colonizing leaf packs responded in predictable ways to a short-term reduction in food resources which would be adaptive in a system which is heterogeneous in space and time.

Keywords Disturbance · Food depletion · Aggregation · Competition · Resource tracking

Introduction

Population models often assume direct and rapid feedback between resource supply and demographic rates (Lomnicki 1988; Murdoch 1994; Turchin 1995). It is now recognized that resources vary greatly in space and time (Fretwell 1972; Southwood 1988; Turchin 1995; Abrams 1997). Increasing evidence of large temporal and spatial variations in resource supply have led to much debate about the ubiquity of population regulation in nature (Wiens 1977; Strong 1984; Grant 1986). The demographic responses of a species to resource variation, such as individual growth, birth and mortality rates, often occur on time scales that are greater than those of their resources. Potential short-term responses to resource variation are primarily behavioral (e.g., Hassell 1978) and include movements of individuals between patches or sub-populations. The connection between short time-scale processes such as behavioral responses and population dynamics across generations is only beginning to be developed either empirically or theoretically (e.g., McNamara and Houston 1987; Mangel and Roitberg 1992; Hik 1995; Abrams 1997; Anholt 1997).

The most relevant field data on behavioral and demographic responses to variation in resource abundance come from food addition experiments. As expected, colonization of food-supplemented plots is typically positive and often rapid, and often leads to increased rates of growth, survival, and reproductive output. (e.g., Boutin 1990; Hart and Robinson 1990; Richardson 1991). Depletion of food resources is expected to produce similar but opposite responses to food additions. However, emi-

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gration from resource-depressed plots or longer-term demographic responses are rarely assessed, perhaps because of the difficulty in conducting population or community level food depletion experiments (but see McMahon and Tash 1988; Wallace et al. 1999).

Rapid resource fluctuations are the hallmark of stream communities, particularly those in lower-order channels (Shortreed and Stockner 1983; Grimm 1994; Power 1995; Whiles and Wallace 1995). In streams both resources and organisms are patchily distributed and temporally shifting (reviewed in Townsend 1989). Such communities are regularly exposed to rain- and meltwater-induced flooding, which can be extreme. During floods, organisms may be displaced from their resources, resources depressed, or animals killed, thus severing any developed link between resource and population abundance (Reice 1981; Winterbourn et al. 1981; Townsend 1989). Drift, the active or passive downstream movement of stream organisms, may be the main process by which lotic organisms respond to variation in their resources. However, the underlying mechanistic basis for drift is still only partially understood and there are several non-exclusive hypotheses (Brittain and Eikeland 1988; Rader 1997). Drift has been linked to changes in the physical environment, such as discharge (Otto 1976; Lancaster and Hildrew 1993), as well as a means of avoiding predators (Soluk and Collins 1988), or moving between patches of resources (Otto 1976; Kohler 1992).

The frequency and intensity of flood-induced disturbance have led some stream ecologists to suggest that lotic communities may only rarely be regulated by biotic factors (Resh et al. 1988; Power et al. 1988; Townsend 1989; Townsend and Hildrew 1994). This is because organisms are often separated from their resources in time and space, thus breaking any link between resource level and population abundance. An alternative view is that, as a result of common disturbances, stream organisms may be particularly well adapted to deal with these disturbances and to have evolved behavioral mechanisms that facilitate tracking of their resource base. Indeed, several lines of evidence suggest that stream organisms have some potential to track resource abundance and distribution. First, studies of stream communities generally reveal positive correlations between food supply and population abundance and these results are generally consistent on a variety of space and time scales (e.g., Grimm 1994). Second, several studies of the colonization of newly available substrates or supplemented food patches have demonstrated rapid aggregation on these resources (e.g., Richardson 1991, 1992b; Dobson and Hildrew 1992). Third, several field studies have experimentally demonstrated matching trends in resource abundance and consumer abundance or growth (reviewed in Feminella and Hawkins 1995). Yet, most of this data was for species feeding on algae rather than detritus. Finally, as leaf packs become depleted due to consumption and decomposition, consumer abundances decline (Cummins et al. 1989; Wallace et al. 1999). Although the latter line of evidence suggests that stream organisms respond to declining resources, no studies include rapid resource depletions. Thus, our evidence for rapid tracking of resource supply is largely unidirectional, and rapid tracking is an assumption of most models of population regulation (Lomnicki 1988; Murdoch 1994; Turchin 1995).

In this paper, we test the hypothesis that movements of stream organisms take place in response to declines in food resources. In particular we predict that an instantaneous reduction in food resources leads to behavioral aggregation of consumers on remaining resource units, thereby, further depleting the resource base, and to increased rates of emigration from food-depressed patches. We also predict that the timing and magnitude of the response differs between trophic groupings, i.e., those species for which decaying leaves are a prime food resource respond to a greater degree than those feeding primarily on other resources. Our approach is experimental, and we focus on responses at a short time scale, and at the level of the community.

Materials and methods

Experimental stream channels

Our food depletion experiment was conducted in six parallel experimental channels, on a floodplain adjacent to Mayfly Creek in the Malcolm Knapp Research Forest of the University of British Columbia. Mayfly Creek is a second-order, dilute, montane stream of approximately 3 m width and a slope of 0.08 m/m. Further details of the chemistry and ecology of streams in this area are given in Feller and Kimmins (1979), and Richardson (1991). Experimental channels (15 m×0.35 m) contained substrates of 3- to 4-cm rounded gravel to a depth of 20 cm, with sand and gravel filling much of the interstitial space. Channels were supplied with Mayfly Creek water that passed through two settling boxes prior to irrigating the channels. Settling boxes removed all but the finest mineral sediment from the flow, without impeding colonization of the channels by the major invertebrate taxa of Mayfly Creek. A series of valved PVC pipes supplied water from the last settling box to each channel. Flow rate per channel ranged from 1.3 to 3.0 l/s over the experiment (even during flood in Mayfly Creek given the restriction of flow through the intake pipe) and was indistinguishable among channels. Water temperatures during the experiment were between 4.5 and 10°C, with a general decline in temperature over the course of the experiment. Further details of the design of these stream channels are given in Richardson (1991). Prior to our experiment stream channels had had no other experimental manipulations for more than 12 months and flow from Mayfly Creek ensured that the community of the channels was similar to that found in Mayfly Creek (Richardson 1991).

Predictions and experimental design

The experiment consisted of two periods, a pre-manipulation colonization period of about 1 month (for leaf pack colonization) and a 9-day post-manipulation period. At the start of the experiment's colonization period we removed all visible coarse particulate organic matter from the channels, of which there was very little. Leaves of red alder were collected from the ground shortly after abscission, dried in the laboratory, and weighed into groups of 5 g (±1%) dry mass for construction of leaf packs tied with nylon monofilament. We added twenty 5-g leaf packs of red alder to each channel on the 29 September and allowed time for their colonization from within the channels and by immigrants from Mayfly Creek. This leaf pack density (20 g/m^2) fell within the range occurring in nearby natural streams (Richardson 1992a), and leaf packs were placed at least 50 cm apart from each other. On 24 October, 3 days before the manipulation, we placed fine-mesh nets (250 µm) over the inflow pipes to stop immigration of animals from Mayfly Creek. On the same day we began sampling emigration from the channels with three consecutive 24-h drift samples. The entire flow from a channel was passed through a 250-µm-mesh net at the downstream end of each channel. At the start of the manipulation (27 October; day 0) we removed ten randomly selected leaf packs of the 20 added from all channels and gently placed them into a separate basin of water for each channel. The leaf packs in each basin were gently rinsed to dislodge as many animals as possible and the animals in each basin were returned to the head of the channel from whence they had been removed; this process was repeated 6 times per basin over a 1.5-h period. This procedure was carried out so that we would not deplete the number of invertebrates in the channels and thereby start the experiment with unnaturally low invertebrate densities. We then applied three treatments: (1) the control, in which ten leaf packs were returned; however, these were a random selection of rinsed leaf packs pooled from all six channels; (2) "removal", in which no leaf packs were returned; and (3) "artificial", in which the ten leaf packs removed were replaced by ten artificial leaf packs. These artificial leaf packs were constructed of stiff polyester cloth in the shape of leaves and provided a surface area within the leaf pack similar to that of an alder leaf pack (as used in Richardson 1992b). We did not "condition" these artificial leaf packs prior to the experiment so that they would not be colonized by detritus and microorganisms that may act as a food source. Therefore, we could clearly distinguish their utility as a habitat from that as a food source. Following this manipulation, we estimated emigration rate as the number of individuals captured in drift nets per unit time. We captured all emigrants from the channels for three consecutive 24-h periods followed by two subsequent 48-h periods. During what would have been the third and final 48-h period our emigration nets backed up and overflowed due to the increased transport of fine particulate organic matter from Mayfly Creek, which was then experiencing a spate (see below), thus we did not use emigration samples from the final period.

At the end of the experiment (day 9; 5 November) we collected the remaining leaf packs to determine their ash-free dry mass and the density of invertebrates remaining on them. We also took six of the artificial leaf packs from each of the two channels containing them. All samples were preserved in formalin. In the laboratory, leaf packs were carefully disassembled and washed to remove invertebrates that were retained on a 100-µm sieve and stored in alcohol. Leaf packs were dried, weighed, burnt at 500°C for 2 h, and reweighed to determine ash-free dry mass. Invertebrate samples from the emigration nets or leaf packs were sorted under a dissecting microscope, identified, counted, and measured using an ocular micrometer.

We predicted that removal of leaf packs would result in increased emigration of consumers from the channels and increased aggregation of consumers on, and further depletion of, remaining food resources. A comparison of responses between control and removal channels tests such an effect. We further predicted that the response to leaf pack removal resulted from a decrease in food abundance, rather than a decrease in refuge habitat or any other hydraulic effects provided by leaf packs. The lack of a difference in responses between removal and artificial treatments, but a significant difference in the contrast with the controls, would indicate a response to food abundance.

Data were analyzed using ANOVA in SYSTAT. Densities of animals per leaf pack or leaf pack mass were tested using one-way repeated measures ANOVA with leaf packs within a channel as the repeated measure. The emigration data were tested using repeated measures ANOVA, with date as the repeated measure. Since we predicted that increased emigration under food depletion would develop slowly after the manipulation we also tested the food depletion by date interaction. Groupings of data by shredders and non-shredders were tested to compare by trophic differences. Particular shredder taxa for which there were sufficient data were also tested separately as above.

Results

Use of artificial leaf packs

We first analyzed our leaf pack data from the two removal and two artificial channels to determine whether there was any effect of replacement of removed leaf packs with artificial leaf packs. Three lines of evidence demonstrate that addition of artificial leaf packs to channels had no significant effect on the behavior of benthos. First, the combined densities of shredders and non-shredders on artificial leaf packs was only 4.5 invertebrates per leaf pack and negligible relative to those of natural leaf packs which were 30-fold greater (see below). Second, there was no significant difference in either shredder (ANOVA, $F_{1,2}=0.57$, $P>0.50$) or non-shredder ($F_{1,2}=0.06$, $P>0.80$) densities on the remaining natural leaf packs between removal channels and those with artificial leaf packs added. Finally, the dry mass of natural leaf packs remaining in channels did not differ significantly between removal channels and those with artificial leaf packs added (ANOVA, $F_{1,2}=1.29$, $P>0.20$). Therefore, for the remaining analyses we combined data from the two removal and two artificial channels to form a single "depletion" category for comparison with control channels.

Aggregation on remaining resources and depletion of leaf packs

Mean shredder densities on remaining leaf packs were about 34% greater in the depletion relative to the control channels (Fig. 1A; ANOVA, $F_{1,4}=24.20$, $P=0.003$). We subdivided the shredder data into the three numerically

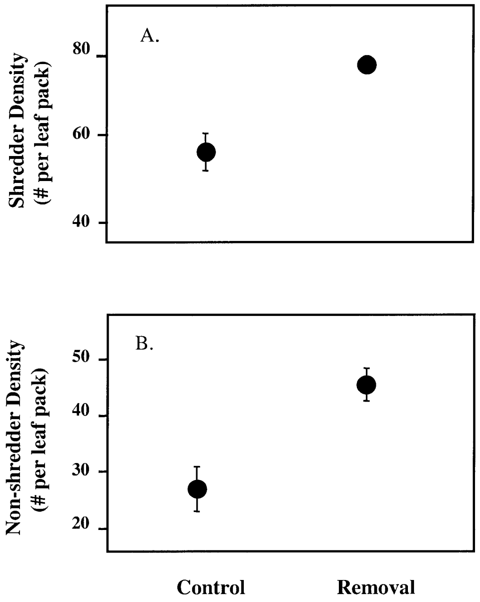

Fig. 1 Density of **A** shredders and **B** non-shredders on remaining red alder leaf packs in removal (n=4) and control channels (n=2). *Points* and *bars* represent means and SEs, respectively

Table 1 The mean proportional increase in density of non-shredders, shredders, and taxa of shredders on leaf packs that resulted from food depletion; the *P*-value is for separate tests (ANOVA) of the effects of food removal on densities on leaf packs. *Zap. Zapada* spp., *Lep. Lepidostoma* spp., *Bril. Brillia retifinis*, *Misc.* remaining shredders

	Non-shredders	Shredders	Shredder taxa			
			Zap.	Lep.	Bril.	Misc.
% Increase due to food removal	66.2	34.3	46.5	146.6	19.2	1.9
Effect of food depletion [*P*-value (ANOVA)]	0.004	0.003	0.415	0.003	0.173	0.454

dominant genera and a miscellaneous group (remaining species) to test for depletion effects (Table 1). Each group increased in density on leaf packs in depletion channels and hence contributed to the total increased densities; however, *Lepidostoma* spp. made by far the greatest contribution. Separate analyses of the effect of food depletion on densities of each group similarly demonstrated that increases were significant only for *Lepidostoma* spp. (Table 1).

We also analyzed a subset of the shredder data to determine if the size composition of each was affected by food depletion. We were not looking for differences in growth over the short period of the reduction, instead we were interested to determine whether different size classes responded differently to the experimental reduction in food supply. Species in our miscellaneous shredder category were excluded because numbers of each species were too small and *Brillia retifinis* were excluded because we could not reliably distinguish smaller instars. We found no significant difference between mean head capsule width in depletion and control channels for any of *Lepidostoma cascadense*, *L. unicolor*, or the nemourids *Zapada haysi* or *Z. cinctipes* (ANOVA, df=1,4; F=2.48, P=0.194; F=0.01, P=0.947; F=1.09, P=0.356; F=1.49, P=0.259; respectively).

Similar to shredders, non-shredder densities were about 66% greater on leaf packs in the depletion channels than those in the control channels (Fig. 1B, Table 1; ANOVA, $F_{1,4}$=19.13, P=0.004). Specific numbers of non-shredders were too low to allow for analyses of treatment effects on size compositions.

The mean dry mass of leaf packs in control channels was about 12% greater than those in depletion channels (Fig. 2; ANOVA, $F_{1,4}$=17.30, P<0.02). The combination of reduced leaf biomass and increased benthic densities means that the effect of food depletion is greater when densities are expressed on a per gram mass of leaf pack basis rather than simply as per leaf pack (as shown above). On a per gram of leaf basis, the density of shredders was actually 50% higher and that of non-shredders was 86% higher on the remaining leaf packs in the food depletion channels than those in the controls.

Emigration

Emigration rates varied between channels, but not between treatments, during the pre-manipulation period. We assume that this may have resulted in part from differences in starting densities in the channels, and that such differences have the potential to bias our results. We first checked for such a bias by comparing mean daily pre-manipulation emigration rates between control, artificial and removal channels. We found no significant differences between treatments and controls for either shredders (ANOVA, $F_{2,3}$=3.124, P=0.118) or non-shredders ($F_{2,3}$=1.407, P=0.371). Moreover, for both shredders and non-shredders, control means were intermediate to means from the artificial and removal treatments. Therefore, to increase the power of our tests, we pooled artificial and removal treatments into a single “depletion” treatment (as above) to compare with the control. Further, we accounted for any channel to channel variation by scaling all post-manipulation emigration rates to proportions of mean daily pre-manipulation rates for each channel.

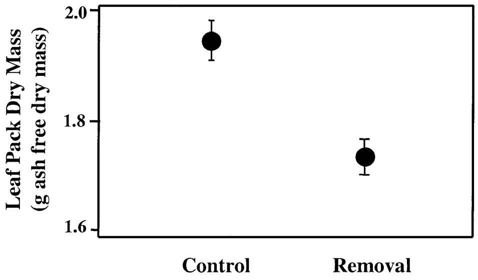

Fig. 2 Ash-free dry mass of remaining leaf packs. *Points* and *bars* represent means and SEs, respectively

There was a strong effect of date on emigration rates, resulting from a storm event that began on the third post-manipulation day (Fig. 3). Discharge through the channels (the same in all channels) only increased to about double the flow in the early part of the experiment, but was sufficient to affect emigration rate. Our analysis revealed a significant effect of date and the interaction between date and food depletion on emigration of shredders (Fig. 3, Table 2). The food depletion term only approached significance. The significant interaction term and inspection of Fig. 3 indicates that the effect of food depletion increased over the course of the 7-day emigration-sampling period. Separate analyses of the data on each date revealed a significant effect of food depletion on emigration of shredders only on the last day of the experiment (P<0.05). Cumulative emigration from food depletion channels was 57% greater than from control channels. We note that each of the three numerically

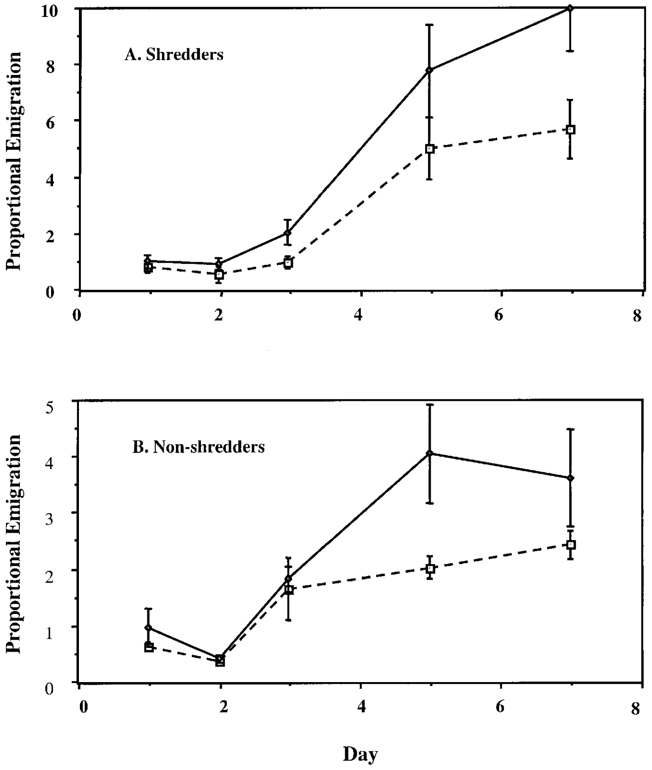

Fig. 3 Proportional emigration rates during the post-manipulation period of **A** shredders and **B** non-shredders. Proportional emigration is the daily emigration rate in a channel during the post-manipulation period expressed as a proportion of the mean daily pre-manipulation emigration rate for that channel (see Results). Mean rates for control channels are shown as *dashed lines* and removal channels are shown as *solid lines*. *Bars* represent SEMs

Table 2 The results from a repeated measures ANOVA of the effects of food depletion and date on mean proportional emigration rates[a] of shredders

	SS	*df*	MS	*F*	*P*
Between subjects					
Food depletion	24.529	1	24.529	5.25	0.084
Error	18.701	4	4.675		
Within subjects					
Date	236.431	4	59.108		<0.001
Food×date	19.354	4	4.839		0.042
Error	24.220	16	1.514		

[a] Daily emigration rate in a channel during the post-manipulation period expressed as a proportion of the mean daily pre-manipulation emigration rate for that channel (see Results)

Table 4 The results from a repeated measures ANOVA of the effects of food depletion and date on mean proportional emigration rates[a] of non-shredders

	SS	*df*	MS	*F*	*P*
Between subjects					
Food depletion	3.843	1	3.843	1.51	0.285
Error	10.122	4	2.531		
Within subjects					
Date	32.221	4	8.055		<0.001
Food×date	3.835	4	0.959		0.242
Error	10.057	16	0.629		

[a] See Table 2

dominant genera of shredders (*Lepidostoma, Zapada, Brillia*) had higher total emigration rates in the food depletion channels than in control channels (Table 3), though the numbers were too small to treat with a full analysis.

Like shredders, there was a substantial increase in non-shredder emigration from food depletion channels (Fig. 3). The date term is significant; however, neither the food depletion term nor the date by food depletion interaction were significant for non-shredders (Table 4). Nevertheless, cumulative emigration from food depletion channels was 65% greater than from control channels (Table 3). Thus we conclude that food depletion may have increased the emigration rate of non-shredders, but if so, we did not have the power to detect the effect in the repeated measures ANOVA.

A small number of invertebrates may not have been washed off our leaf packs and would have reduced the numbers of animals returned to the streams with only ten leaf packs. This potential reduction in numbers would only have served to decrease total numbers in the depletion stream channels and the increase in drift rate would thereby be a conservative estimate of the actual increase.

Discussion

We set out to test the hypothesis that stream invertebrate populations could rapidly track the abundance of their food resource through time and respond accordingly. Our manipulation was meant to mimic the uncoupling of consumer abundance from their resources, as probably happens frequently during disturbance in streams caused by

Table 3 The mean proportional increase in total post-manipulation emigration of non-shredders, shredders and shredder taxa that resulted from food depletion; and the *P*-value for separate tests (repeated measures ANOVA) for the effects of food removal on mean proportional increases in emigration. Abbreviations as in Table 1

	Non-shredders	Shredders	Shredder taxa			
			Zap.	Lep.	Bril.	Misc.
% Increase due to food removal	65.5	57.0	34.9	56.9	0.5	7.7
P-value (ANOVA)	0.035	0.027	0.071	0.082	0.269	0.231

floods (e.g., Lancaster and Hildrew 1993; Whiles and Wallace 1995). Leaf material tends to aggregate in crevices and other low-energy areas in streams, and consumers of these resources in turn aggregate on them. During storm events, both consumer and resource are potentially washed downstream and disaggregated. If storm events are relatively frequent and consumer response times relatively slow, then consumer and resources dynamics are expected to be relatively independent. However, our results demonstrate that shredders do track their resources and do so rapidly. Both groups responded to experimental food depletion by aggregating on remaining resources (Fig. 1), which led to further resource depletion (Fig. 2), and by emigrating from the channels (Fig. 3). These responses occurred within the 7 days following the removal of food. Non-shredders also responded to the removal of leaf packs, perhaps because they feed upon the fine organic matter trapped in leaf packs (Richardson 1992b).

Aggregation of benthos on remaining patches resulted in significant acceleration of the depletion of those resources. The rate of leaf pack loss in the depletion channels during the 9 days of the experiment apparently increased by 17–58% relative to the controls (depending on assumptions of decay models). We found that not only did densities of invertebrates increase on the leaf packs in the food-depleted channels, but the amount of leaf tissue per leaf pack also decreased. The combination of reduced leaf biomass and increased benthic densities means that the effect of food depletion on aggregation on remaining food patches is even greater on a per unit mass basis. This further reinforces our conclusion that the animals aggregate on the remaining patches of food resources.

Debate about the strength of biotic effects in structuring stream communities continues, because of the potentially overwhelming effects of disturbance (Reice 1981; Winterbourn et al. 1981; Power et al. 1988; Resh et al. 1988; Townsend 1989; Power 1995; Townsend et al. 1997). Our results are clearly contrary to the view that storm events prevent any resource tracking by invertebrates. Notably, increasing discharge during a storm event in our experiment was correlated with increased emigration rates, but it did not overwhelm the effect of food depletion. Emigration rate of shredders in the depletion channels relative to the controls continued to be greater, and apparently increasingly so, during the storm event (Fig. 3, Table 2). Similarly, Lancaster (1990) found that predator addition effects persisted through a storm event. Even at low densities of consumers, biotic interactions can be strong (Power et al. 1988) and presumably if resource abundance and consumer density are differently affected by disturbance, consumers could be severely food limited, leading to intense competition.

There are at least two potential mechanisms to account for the observed responses to the depression of food abundance in our experiment. First, there may be interference between the invertebrates and as density increased due to food reduction the rate of interference would have increased. Second, through exploitation of the remaining food resources the amount available per individual fell below some incipient limiting level and individuals sought patches with higher returns. We cannot distinguish between these two behavioral mechanisms from our study.

It is clear that the tendency to aggregate varied among taxa (Table 1). Although all shredders increased in density to some degree on those leaf packs remaining in depletion channels, the range in percentage increase was great (from 2% in the miscellaneous shredder category to 146% in the *Lepidostoma* spp.) and was significant only for *Lepidostoma* spp. (Table 1). Similarly, the tendency to emigrate following food depletion varied among taxa. The percentage increase in emigration ranged from 6% in the miscellaneous shredder category to 70% in *Zapada* spp., and again was significant only for *Lepidostoma* spp. (Table 1). Food limitation, induced by our removal of leaf packs, may have varied between taxa, perhaps due to different responses to inter-specific competition. Based on the large increase in the number of *Lepidostoma* larvae per leaf pack relative to changes in other taxa it may be that *Lepidostoma* are better competitors for access to limited resources. Alternatively, taxa may simply vary in the degree to which they use emigration to escape food limitation.

The effects of our experimental reduction in food abundance on density per leaf pack and emigration rates appeared similar for both shredders and non-shredders. Thus, leaf packs are also a resource for non-shredders, but the mechanisms leading to these results need not be the same. Leaf packs are probably also an important resource for non-shredders and this is likely related to the accumulation of fine organic particles, growth of algae, and high densities of potential prey organisms in leaf packs. A previous experiment showed that the mass of fine particulate organic matter trapped in real and artificial leaf packs was a good predictor of the density of non-shredder invertebrates (Richardson 1992b). Yet, passive accumulation of entrained food on artificial leaf packs must make a relatively small contribution, because non-shredders did not aggregate on artificial leaf packs in this study. The absence of invertebrates on these artificial leaf packs also suggests that the primary reason for colonization of natural leaf packs is feeding rather than refuge (Richardson 1992b; Dudgeon and Wu 1999).

This experiment has shown that short time-scale changes in food abundance lead to predictable behavioral responses of consumers. Addition of food over a 12-month period in the form of added leaf litter resulted in increased growth rates and increased densities through reduced emigration and increased survival rates of detritivores in experimental stream channels (Richardson 1991). The results from our food depletion experiment are opposite in sign to those observed for food supplementation as would be appropriate in a food-limited system. During a 4-year exclusion of leaf inputs to a small stream, more than half the species present exhibited a dramatic decline in density (Wallace et al. 1999).

Taken together, these studies demonstrate behavioral, numerical and life history responses to fluctuations in resource level. The former two classes of response occur on a rapid time scale, while the latter is longer term. In Wallace et al.'s (1999) study, the mechanism underlying the observed reduction in density was unknown. In our study, behavioral responses were clearly implicated, and this suggests that they may have played a substantial role in Wallace et al.'s (1999) results.

Within-generation changes in population size in other animals have been shown to be related to resource abundance, and the mechanisms responsible include emigration and change in body condition (e.g., Hildrew and Townsend 1980; Lomnicki 1988; McMahon and Tash 1988; Richardson 1991). These processes are implied by considerations of self-thinning in other natural populations (e.g., Grant and Kramer 1990). An experimental reduction in food supply to populations of pupfish by halving the food ration resulted in a more than doubled emigration rate and lowered body condition (McMahon and Tash 1988). One question about the role of emigration is why individuals would put themselves at apparent risk from predation or failure to find suitable habitat by emigrating. The observations by McMahon and Tash (1988) of low relative condition in emigrants suggest that fitness of emigrants may be on average higher if they leave than if they were to stay. Our results of manipulation of leaf pack abundance are consistent with a resource-mediated mechanism leading to emigration of stream benthos from stream patches with altered food abundance. However, we did not see any evidence that smaller, perhaps lower-condition, individuals were any more likely to emigrate.

The apparent lag between the manipulation and the emigration response by shredders may be explained by three, non-exclusive processes. First, given that many of these species are not known for drifting (e.g., case-building caddisflies), it may have taken a length of time for animals to move down and out of the 15-m-long stream channels. Second, animals may have sampled remaining patches of food and taken time to assess local densities of competitors and food (indicated by their aggregation on remaining resources) before emigrating. Finally, resources may not have been limited early in the experiment. The aggregation of animals on remaining food patches, leading to higher rates of resource depression and eventually lower per capita resource supply, may then have provoked emigration. As mentioned above, we do not know the behavioral mechanisms by which these stream invertebrates assess and react to resource supply.

The rates at which organisms respond to changes in their environment are critical to an understanding of how feedback through various mechanisms affects population processes and community dynamics (Lomnicki 1988). The responses of our benthic community to variation in food abundance indicate that, at least at some times and in certain systems, those population processes of consumers relative to their food resources are tightly coupled. It is still likely that there is a trade-off between emigrating from a deteriorating (food depleted) patch and the increased risk of mortality potentially associated with movement between patches, and the behavioral mechanisms mediating this trade-off have yet to be addressed.

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