An experimental test of the effects of food resources and hydraulic refuge on patch colonization by stream macroinvertebrates during spates

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Summary

1. The passive or active movement of organisms between habitat patches plays important roles in achieving ecosystem resilience to disturbance and long-term control of population levels. However, causal mechanisms of disturbance-induced movements of mobile biota across heterogeneous habitat patches at a relatively short time-scale are little understood.

2. We experimentally tested the effects of food resource values on macroinvertebrate colonization of hydraulic refugia from spates in a second-order creek. Experimental cages were colonized by macroinvertebrates with combinations of resource types (natural or polyester leaves), and extent of exposure to stream flow (exposed to or sheltered from current); one half of each set was collected before and after a spate. This experiment was repeated over three spates of varying magnitude and seasonal contexts.

3. Pre-spate colonization was consistently greater for the cages with natural leaves relative to artificial leaves regardless of the extent of flow exposure. Two autumn spates with relatively low and stable antecedent flow conditions caused large movements of organic matter and macroinvertebrates across the stream, showing community-level accumulations into hydraulically sheltered patches independent of food treatment. The smallest spate with high and variable antecedent flows during winter resulted in negligible responses, which we interpret to be a result of depletion of easily transportable organic matter and organisms.

4. Two detritivorous taxa, the mayfly *Paraleptophlebia* spp. and stonefly *Despaxia augusta* (Banks) were the most responsive to autumn spates, and had disproportionately higher colonization rates of cages when provided with natural leaves during the largest autumn spate. Preferential settlement in food-enriched hydraulic refugia was attributable to taxon-specific mobility related to efficient acquisition of detritus resource, whose availability varies spatially and temporally.

5. Our findings suggest (1) detritivorous macroinvertebrate colonization of hydraulic refugia can be influenced by hydraulic controls as well as food resource value, and (2) pre-spate environmental conditions in terms of resource distribution and availability may pre-condition organisms' susceptibility to spates and also affect refugium usage, at least in food-limited, detritus-based stream systems.

Key-words: detritus, disturbance, flow refugia, food-limited stream system, patch dynamics

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Introduction

A prevailing tenet in ecology is that disturbance plays a key role in forming structure and function of dynamic natural ecosystems (Sousa 1984). Disturbance imposes patchy influences across the receiving environment

and inhabiting communities, creating structurally and functionally diverse ecosystems (Sousa 1984; White & Pickett 1985). Furthermore, the movements of organisms across heterogeneous patches during and/or following disturbance events may affect the persistence and long-term productivity of natural communities (Pickett & White 1985; Pulliam 1988). Heterogeneity of populations within patches related to disturbance have been relatively well studied for sessile organisms, including grasses and trees in terrestrial systems (White 1979; Salo *et al*. 1986; Aguiar & Sala 1999), intertidal communities on rocky shores (Paine & Levin 1981), and algae on stream substratum (Power & Stewart 1987; Peterson & Stevenson 1992). In contrast, disturbance-induced responses of relatively mobile organisms across heterogeneous environments have been poorly understood. Although the patchy distribution of mobile biota and their resources, and the importance of patch arrangement in their resource acquisition has been increasingly recognized and tested for lotic systems (e.g. Pringle *et al*. 1988; Palmer *et al*. 2000), empirical understanding of population dynamics involving the movements between patches at relatively short time-scales is still elusive.

Continuous variation and occasional extremes of flow discharge have been considered among the major agents in stream community organization (Resh *et al*. 1988; Townsend 1989; Poff *et al*. 1997). While base flow provides a means of continuous dispersal of individuals (e.g. Waters 1972), exceedingly high flow events likely decrease populations of stream biota through direct washout of individuals or displacement of substrate materials (e.g. Grimm & Fisher 1989; Biggs, Smith & Duncan 1999). Nevertheless, stream communities exhibit persistence against flow disturbance through refugia mechanisms operating at various temporal and spatial scales (Sedell *et al*. 1990). The community persistence that occurs over durations shorter than an organisms' generation time has been related to the heterogeneity within a stream channel (e.g. Pearsons, Li & Lamberti 1992; Negishi, Inoue & Munokawa 2002). Lancaster & Hildrew (1993a) demonstrated that the influence of high flow disturbance is heterogeneous across stream channels due to the existence of hydraulically sheltered patches. Geomorphic features such as woody debris (Palmer *et al*. 1996), backwaters (Negishi *et al*. 2002) and inundated channel margins (Matthaei & Townsend 2000; Negishi *et al*. 2002) have been suggested to be important in providing such hydraulic refugia for stream macroinvertebrates.

Mechanisms by which macroinvertebrate communities achieve their refugia-dependent persistence over high flow events have attracted much research interest. The conceptual 'catastrophe avoided' model (see Robertson, Lancaster & Hildrew 1995) argues that dislodged individuals from disturbed patches move into hydraulically sheltered patches and potentially become colonizers following the events. This model is particularly important because it involves no catastrophic loss of individuals and thus community productivity and

structure may be best preserved over time. Several previous findings partially support this model, i.e. distributional shifts across sheltered and disturbed patches over periods of high flow events (e.g. Lehmkuhl & Anderson 1972; Lancaster & Hildrew 1993b; Winterbottom *et al*. 1997). However, all of those field studies have examined distributional shifts over more than 7 days without necessarily sampling immediately before and after an event. Therefore, one is unable to attribute fully distributional shifts to induction by high flow events. A recent laboratory study aided by visual observations provided further support for the view that hydraulically benign patches accumulate macroinvertebrates (Lancaster 1999). Nevertheless, other potentially important factors in natural settings were not included in the necessarily simplified indoor experiments using artificial flumes.

Prior studies have suggested that disturbance may result in the heterogeneity in populations of mobile animals not only by directly damaging individuals, but also by indirectly eliminating or redistributing food resources on which organisms are dependent (Ehrlich *et al*. 1980; Waide 1991). Detritus constitutes an important energy source for detritus-feeding organisms and generates the major flow of energy in most ecosystems (Polis & Strong 1996). In forested streams, where macroinvertebrate communities are typically detritus-based and food resource limited (Richardson 1991; Dobson & Hildrew 1992), their distribution and production are strongly related to the spatial and temporal availability of detritus (see Wallace *et al*. 1999). High flow events affect not only consumers but also their detritus food resource (e.g. Cuffney & Wallace 1989; Wallace *et al*. 1995). Therefore, the timing of litter input and ambient flow level could affect the amount and spatial distribution of organic detritus and organisms across the stream channel (King *et al*. 1987; Richardson 1992a) and it in turn could influence their responses to a subsequent disturbance. Hydraulically benign refugia patches likely promote passive accumulation of not only organisms but also detritus leading to patches of relatively abundant detritus food resource. Therefore, effects of hydraulic controls could mask the potential effects of food resource value on macroinvertebrate accumulation into refugia. Rigorous testing of this question has been hampered by relatively long sampling intervals (e.g. Lancaster & Hildrew 1993b) or the nature of systems in which food resource abundance was not a strong limiting factor (Winterbottom *et al*. 1997).

Our objective was to examine whether the rates of macroinvertebrate colonization on hydraulically sheltered patches during spates is partly dependent on food resource values available within patches. We tested the following hypotheses: (1) macroinvertebrate colonization during spates is greater within hydraulically sheltered refugium patches relative to patches exposed to stream flow, and (2) spate-induced colonization rates of coarse detritus feeding macroinvertebrates (shredders) into refugium patches is disproportionately greater

with higher flood resource availability. To examine real world complexity and processes of the system, field experiments were carried out during natural spates by sampling organisms within at least 2 days before and 1 day after the events.

Materials and methods

STUDY SITE

This study was carried out between September 1999 and May 2000 in a 180-m reach of Spring Creek, a second order stream that flows through the University of British Columbia's Malcolm Knapp Research Forest. The Research Forest is located in the Coast Mountain Range approximately 60 km east of Vancouver (122°34′W, 49°16′N). The watershed of Spring Creek lies in the Coastal Western Hemlock biogeoclimatic zone, and the conifers western hemlock *Tsuga heterophylla*, western red cedar *Thuja plicata* and Douglas-fir *Pseudotsuga menziesii* were the dominant forest species. The riparian vegetation consisted predominantly of red alder *Alnus rubra*, vine maple *Acer circinatum* and salmonberry *Rubus spectabilis*. Minimum and maximum water temperatures of Spring Creek during the study period were 1·5 °C and 13·7 °C, respectively. Stream water was characterized by high dissolved oxygen (near saturation), low suspended solids, and neutral to slightly acidic water. Low and stable discharge in summer and higher and more variable discharge in winter typically feature the hydrograph of Spring Creek (Feller & Kimmins 1979). The study reach had a gradient of approximately 1·7% and variable wetted width ranging between 3 and 5 m under low flow conditions and bankfull width of 4–8 m. Repeated series of pool, riffle and glide habitat constituted the stream channel with gravel-sized substrate materials dominant (2–65 mm) and with the occasional occurrence of large woody debris (0·21 pieces m^{-1}). Mean organic matter standing stock within channels typically was in the range of 3–55 g m^{-2} with coarse leaf litter occasionally comprising up to 20% of the total mass (Richardson 1992a; Negishi & Richardson 2003); patchy leaf litter accumulation of *c*.100 g m^{-2} were common during autumn along channel margins and other geomorphic roughness elements (unpublished data, J.N. Negishi). The discharge of the study reach was calibrated from the flow data of continuously gauged East Creek that enters Spring Creek at the upstream end of the study reach. A discharge water level relationship ($R^2 = 0.88$, $P < 0.001$) that was independently established for Spring Creek was used to estimate mean daily discharge of Spring Creek based on the calibration curve with East Creek discharge ($R^2 = 0.84$, $P < 0.001$).

EXPERIMENTAL APPROACH

Cylinder-shaped colonization cages were used as experimental units. The sides and top of the cage were made with plastic mesh (mesh size 1·5 cm) to a height of 15 cm, and attached to a round, flat plastic base (surface area 415 cm^2). This mesh size retained or excluded very coarse organic matter, but smaller particles of organic matter (< 1·5 cm) and most macroinvertebrates could move in and out of the experimental cages. It was practically impossible to control the rates of food resource accumulation during spates independent of hydraulic environments without influencing macroinvertebrate colonization. We instead controlled available food resource quality by adding either artificial or natural leaf packs within colonization cages. Forty cages were assigned to three factors (i.e. food resource, refugium and spate) with two levels of each with five replicates for a total of eight factorial combinations.

FOOD RESOURCE FACTOR

The cages were provided with either natural or artificial leaf packs. For the natural leaf treatment, we used recently fallen red alder leaves (within a few days) collected from the nearby riparian forest floor in September 1999 after air-drying them for at least 2 weeks. Red alder is a common riparian species that naturally provides a large amount of leaf litter into the stream in this area. Artificial leaves were pieces of heavy polyester that were cut into one of four different representative sizes of red alder leaves and passed through a flame to seal the edges to keep them from fraying. Each natural leaf pack was made by grouping 10 (± 0·25) g of alder (air-dried weight) leaves, whereas artificial leaf packs consisted of randomly chosen artificial leaves that provided a similar surface area to that of 10 g of alder leaves.

REFUGIUM FACTOR

The cages were either sheltered from (sheltered treatment) or exposed to (exposed treatment) stream current. A single concrete block ($40 \times 19 \times 19$ cm) was placed approximately 7 cm upstream of each 'refugium' cage having its longest axis positioned perpendicular to the flow direction so as to maximize the sheltering effects. The blocks were anchored by driving steel bars 30 cm deep into the streambed through two vertical holes ($12 \times 12 \times 19$ cm) followed by filling those holes with substrate materials. The bottom part of the concrete blocks was buried approximately 3 cm deep to ensure no flow emerged from underneath the blocks.

SPATE FACTOR

We collected cages either before or after a spate. This treatment was achieved with three spates, and these repetitions are hereafter referred to as trial 1, 2 and 3, respectively. Pre-spate samples were collected within 2 days before the onset of a spate (i.e. initial increase of discharge) with the aid of regional weather forecasts. To capture any spate-induced distributional shifts of
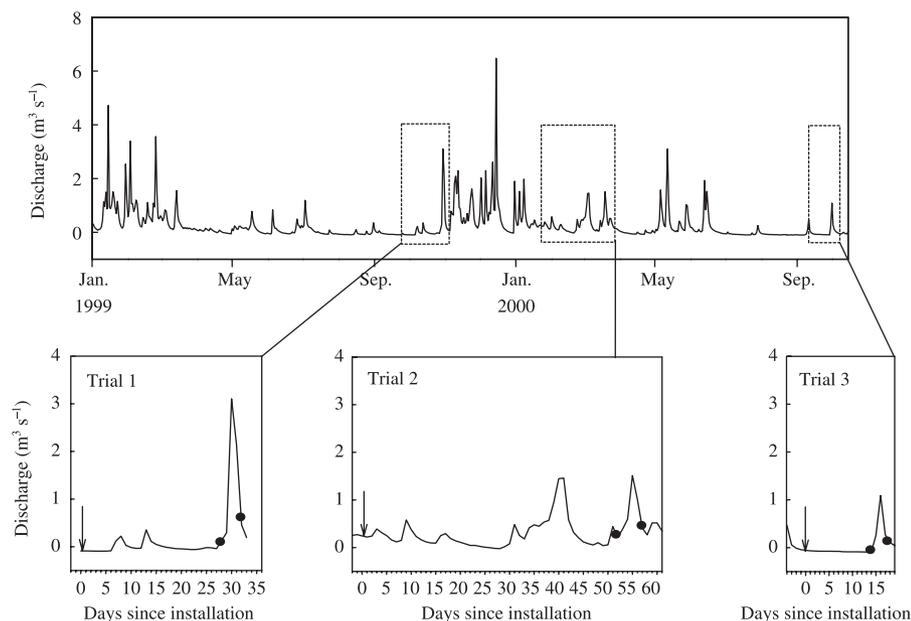
Fig. 1. Estimated daily mean discharge of Spring Creek during the study period. Arrows indicate the timing of the cage installations; dots indicate the timing of pre- and post-spate sampling in each trial.

detritus and macroinvertebrates, post-spate sampling was carried out as soon as possible after the peak discharge of the spate and flow conditions allowed sampling; in 2 days for trial 1 and in 1 day for trials 2 and 3. The cages were installed at least 2 weeks before the treatment spates to allow conditioning of leaf materials and macroinvertebrate colonization.

The three sampled spates were within the range of commonly occurring flow fluctuations (Fig. 1). The peak discharge of the spate in trial 1 ($3 \cdot 1$ m^3 s^{-1}) was the highest among the three spates; the peak discharges of the two other spates were less than half that of the trial 1 spate ($1 \cdot 5$ m^3 s^{-1} for trial 2 and $1 \cdot 1$ m^3 s^{-1} for trial 3). Discharge for pre-spate sampling was similarly low for the autumn spates ($0 \cdot 12$ m^3 s^{-1} for trial 1 and $0 \cdot 13$ m^3 s^{-1} for trial 3) and higher for the winter spate ($0 \cdot 26$ m^3 s^{-1} for trial 2); ratios of maximum to pre-spate discharge for each treatment spate were therefore $25 \cdot 5$, $3 \cdot 9$ and $8 \cdot 5$ for trials 1, 2 and 3, respectively. Cages for trials 1, 2 and 3 were installed on 30 September 1999, 23 January 2000 and 12 September 2000, respectively. The durations of colonization periods (i.e. the period from the installations until the pre-spate sampling occasion) were 27, 52 and 14 days for the first, second and third spates, respectively (Fig. 1). The first spate was intense and several post-spate samples were lost. Exposed cages were severely damaged (seven of 10 exposed cages were lost: four natural leaf treatment and three artificial leaf treatment) and several refugium cages were also destroyed owing to the rollover of concrete blocks (three natural leaf treatments were lost). In subsequent trials, the anchoring for the concrete blocks and colonization cages were reinforced to prevent further losses. One cage with natural leaf, refugium and pre-spate treatment in trial 1, and one cage with artificial leaf, refugium,

and pre-spate treatment in trial 2 were excluded from the analyses because site selection was not appropriate (dewatered before the treatment spate).

CAGE INSTALLATIONS

The 180-m study reach was divided into five sections (i.e. block effect) to control for differences of benthic community owing to potential longitudinal differences in local gradient and characteristics of riparian vegetation. All eight types of treatments were arranged within each of the five sections. To control for the substrate characteristics, the colonization cages were filled *in situ* with similar substrate materials (diameter 3–10 cm) that were collected from Spring Creek and rinsed to remove all macroinvertebrates but not the biofilm on the substrate surface. These cages were then embedded in the streambed along the wetted margin of the stream channel (approximately 10 cm deep) in glide habitats (transition areas between pools and riffles) such that substrates within the cages were flush with the surrounding materials. Cages were separated by at least $1 \cdot 5$ m from each other, and refugium and exposed cages were arranged alternately to avoid confounding treatments by affecting flow conditions. Food resource and spate treatments were randomly assigned within this constraint. All cages were fixed with metal pins (15 cm long) driven through their upstream ends into the streambed. Leaf packs were prepared at the site by soaking leaves in stream water for 2 h, subsequently packed into 1 cm mesh plastic bags (10×10 cm), and placed over the substrate materials within the cages. All the installations were carried out under low flow conditions to prevent the cages from falling dry during the colonization periods. Concrete blocks and cages were taken out

of the stream at the end of each trial, cleaned and reinstalled for the following trials. Thus each trial was assumed to be independent. We cleared the cages and concrete blocks of debris during colonization periods: every 3 days for trials 1 and 3; every 5–7 days for trial 2.

CURRENT VELOCITY MEASUREMENTS

We used flow velocity measured at 0·4-depth from the streambed as a hydraulic measure for the refugium treatments. Before cage installation during pre-spate sampling and after the cage retrieval at the post-spate sampling, current velocity was measured at the locations of both sides and the upstream side of the cages using a propeller-based flow meter (propeller diameter 3·5 cm; model 2100, Swoffer Instruments). These three values were averaged to obtain a 0·4-depth velocity for each cage. Although we did not have continuous measurements of flow velocity, our measurements for the post-spate occasion with flow rate still being elevated above the pre-spate occasion would likely provide conservative estimates of the effects of concrete blocks as refugium treatments. When either cages or concrete blocks were found dislodged at the post-spate sampling occasion, they were reinstalled in the original locations followed by velocity measurements as described above.

CAGE RETRIEVALS AND SAMPLE PROCESSING

A net (mesh size 250 μm) was held immediately downstream of each cage, and the cages were quickly lifted out of water. Leaf packs were carefully removed from the cages first and stored separately, and the contents (cage sediment) were transferred to a bucket. Organic matter and macroinvertebrates were elutriated and separated from cage sediment. These samples were immediately taken back to the laboratory where all macroinvertebrates and organic matter were washed out of the leaf packs within 6 h. Alder leaves that originated from the 'natural leaf' treatment were thoroughly identified and separated. Organic matter (excluding the experimentally added leaves) and macroinvertebrates from cage sediment and leaf pack were then pooled for each corresponding cage and were preserved in 5% formalin until further processing. Only macroinvertebrates and organic matter that were retained on a 500-μm sieve were further examined. Organic matter was separated into coarse (CPOM, > 1 mm) and fine (FPOM, 500 μm^{-1} mm) sizes. Macroinvertebrates were identified to the lowest level possible, usually genus or species, based on Stewart & Stark (1993), Merritt & Cummins (1996), and Wiggins (1996), and counted. Organic matter was oven-dried for at least 24 h at 60 °C and subsequently ashed for 2 h at 550 °C to obtain ash-free dry mass (AFDM).

STATISTICAL ANALYSES

Three-way ANOVA was used to test the effects of three main factors, their interactions and block effect on flow velocity. Two-way ANOVA was used to test the effects of two main factors (food resource and spate), their interactions and block effect on the other response variables separately for exposed and sheltered cages. The response variables were, total organic matter biomass, total FPOM biomass, total abundance of macroinvertebrates, and abundance of numerically dominant taxa. Macroinvertebrate abundance was the number of individuals within each cage, whereas the total organic matter biomass referred to the biomass of organic material (> 500 μm) that accumulated within the cages excluding the biomass of alder leaves used for natural leaf packs. These analyses were carried out separately for each of the three trials. For the exposed cages of trial 1, however, response variables were tested by one-way ANOVA with spate as a main factor because mean estimation was meaningless for the food resource factor with the treatment of 'natural leaf and exposed cage' having no replicates after the spate due to sample loss. To test for statistical assumptions of ANOVAs, the data were first fitted to the complete general linear model for unbalanced ANOVA (PROC GLM, SAS Version 8·0), and residuals were compared for deviation from a normal distribution using the Shapiro–Wilks test. The dependent variables were $\log_{10}(x + 1)$-transformed to improve normality of residual distributions wherever appropriate. Statistical significance level α was set at 0·05.

The following statistical hypotheses in the ANOVAs were of particular interest. For current velocity, the refugium × spate interaction was tested to examine whether 'sheltered' cages provided hydraulically benign environments relative to the 'exposed' cages during the spates. The current velocity for the 'exposed' cages was predicted to be elevated on the post-spate occasion relative to the pre-spate one, while current velocity for the 'sheltered' cages was expected to remain at a similarly low level on both occasions. For organic matter and macroinvertebrates, the spate effect was first tested to examine whether microdistributional shifts of organic matter and macroinvertebrates occurred during a spate. Organic matter biomass and macroinvertebrate abundance were predicted to increase in the 'sheltered' cages after spates, whereas 'exposed' cages remain stable or reduced. Furthermore, for macroinvertebrates, the spate and food resource interaction was tested to examine whether spate-induced colonization rate was greater for the cages with higher food resource value. Macroinvertebrates (especially shredders) were predicted to show greater colonization rates when provided with the higher food resource value.

One potential artefact of food resource treatments is the trapping efficiency of drifting and depositing matter that is in general greater for natural leaves relative to polyester ones (see Richardson 1992b). This could confound our interpretation of spate × food resource interaction because greater colonization rates of macroinvertebrates within the cages provided with natural leaves could be caused by higher trapping efficiency rather than food resource effects. To check this possibility,

when we found significant interactions between spate × food resource, two-way ANOVAS were repeated including fine organic matter biomass as a covariate. Persistence of significant interactions between spate × food resource with the inclusion of the covariate would suggest preferential colonization was not caused at least by the artefact related to trapping efficiency.

Results

CURRENT VELOCITY

The current velocity at the colonization cages was greater at the post-spate occasion than pre-spate sampling for all three trials (Table 1 and Fig. 2). Furthermore, the difference of flow velocity between post- and pre-spate occasions was disproportionately greater for exposed cages relative to sheltered cages as shown by significant spate × refugia interactions. The food resource factor did not significantly affect any other factors tested.

ORGANIC MATTER

The responses of organic matter biomass within cages varied among the three trial spates (Table 2 and Fig. 3). No responses were observed in trial 2, whereas signifi-

cant spate-induced responses were observed in trials 1 and 3. In trial 1, organic matter accumulated into refugium cages; exposed cages did not show a significant spate effect. In trial 3, both exposed and refugium cages accumulated organic matter during spates. In all cases, excluding the exposed cages in trial 1, response of total organic matter was not affected by the food resource treatments (i.e. insignificant spate × food resource interaction, Table 2). However, fine organic matter showed a significant interaction between spate × food resource for the exposed cages in trial 3.

MACROINVERTEBRATES

Responses to the spates of total macroinvertebrate abundance within refugium cages varied among the trials (Table 2 and Fig. 3). In all three trials, the total abundance of macroinvertebrates was significantly higher in the cages provided with natural leaf packs. After the spates, abundance of macroinvertebrates significantly increased in sheltered cages in both trial 1 and 3, and also in exposed cage in the trial 3. No significant response of total macroinvertebrate abundance was observed in trial 2.

The identity and relative abundance of numerically dominant taxa differed slightly between the three trials due to seasonal effects and perhaps the varying lengths

Table 1. Summary of three-way ANOVAS to examine the effects of food resource, refugium, spate and their interactions on flow velocity measured at 0·4-depth

Effects	Trial 1			Trial 2			Trial 3		
	d.f.	MS	*F*	d.f.	MS	*F*	d.f.	MS	*F*
Food	1	< 0·01	0·04	1	< 0·01	0·01	1	< 0·01	3·60
Refugium	1	1·46	101·61***	1	0·17	179·48***	1	0·15	537·53***
Spate	1	1·90	132·34***	1	0·06	64·95***	1	0·06	215·29***
Block	4	0·01	0·92	4	< 0·01	0·63	4	< 0·01	2·18
F × R	1	< 0·01	0·01	1	< 0·01	1·00	1	< 0·01	1·06
F × S	1	0·01	0·99	1	< 0·01	0·11	1	< 0·01	0·05
R × S	1	0·99	69·07***	1	0·06	64·16***	1	0·04	156·86***
F × R × S	1	< 0·01	0·23	1	< 0·01	2·53	1	< 0·01	0·15
Error	25			28			28		

Asterisks indicate significant differences: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.
F, R and S denote food resource, refugium and spate effects, respectively.
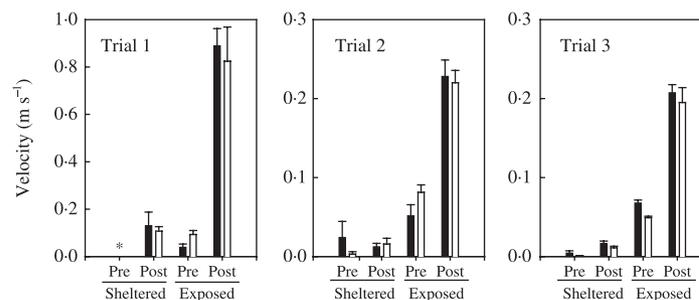
Fig. 2. Mean (+1 SE) of velocity (m s^{-1}) measured at 0·4-depth beside the cages. Filled and open bars denote natural and artificial leaf treatment, respectively. Pre and post refer to 'pre' and 'post' spate sampling occasions, respectively. Note that scales of *y*-axis differ among the trials. Asterisk indicates that flow velocity was below the detection limit of the flow meter.
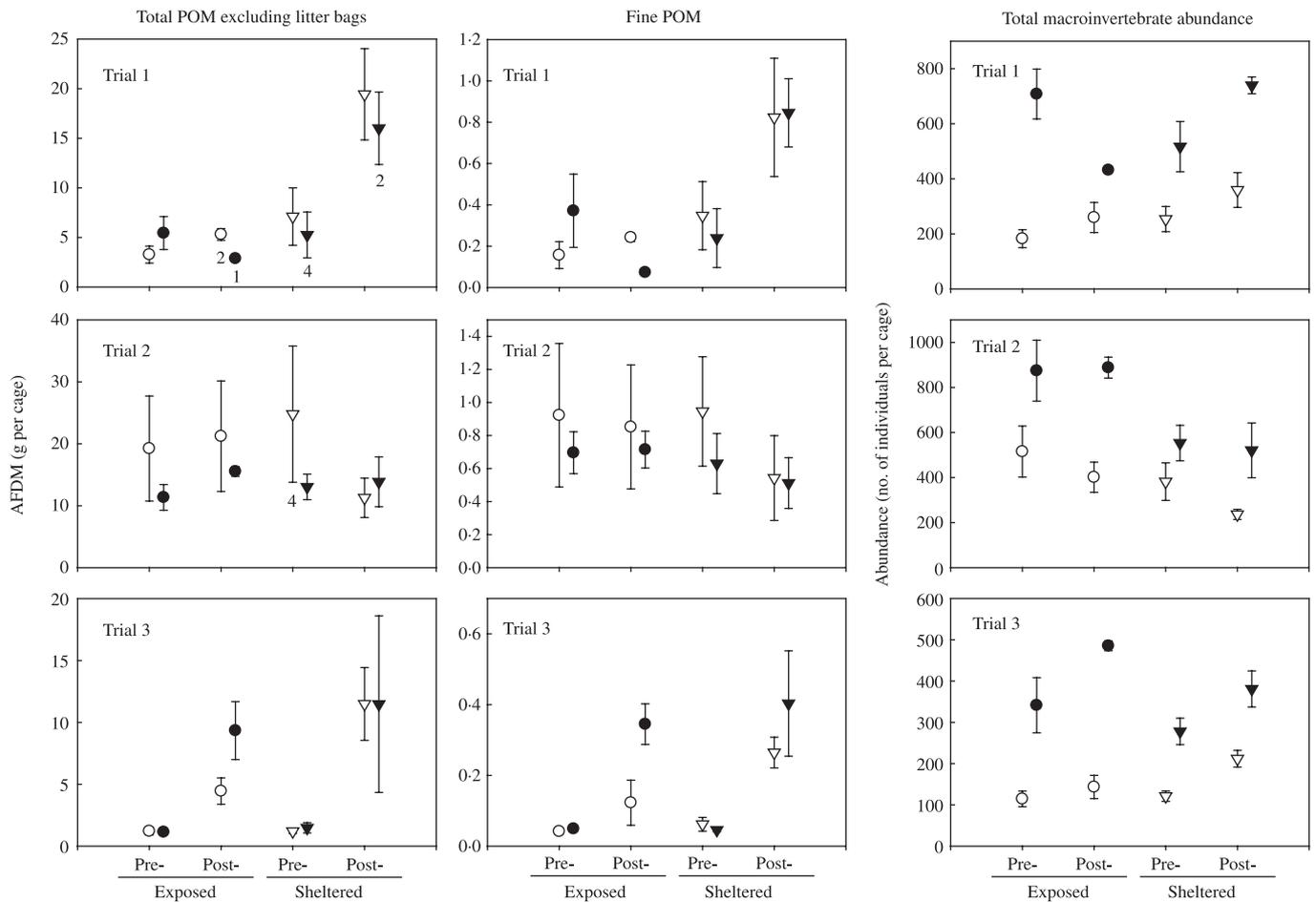
Fig. 3. Mean (+1 SE) of total organic matter biomass (g AFDM per cage) excluding alder leaves used for natural leaf treatment, fine organic matter biomass, and total abundance of macroinvertebrates within a cage (415 cm²) including individuals found in the leaf bags. Filled and open circles denote natural and artificial leaf treatment, respectively. Numbers below bars for the total organic matter biomass indicates numbers of replicates left after damaged and dewatered cages were excluded; bars without any numbers denote treatments with five replicates; these replicates also apply to the other data presented in Figs 3 and 4. Note that scales of *y*-axis differ among the trials.

Table 2. Summary of two-way ANOVAs to examine the effect of food resources (F), spate (S) and their interactions on total particulate organic matter, fine particulate organic matter and total macroinvertebrate abundance

| | | Trial 1 | | | | Trial 2 | | | | Trial 3 | | | |
| | | Exposed | | Sheltered | | Exposed | | Sheltered | | Exposed | | Sheltered | |
	Effects	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS
TPOM	S	1	12	1	231*	1	0·06	1	201	1	163**	1	2***
	F	NA	NA	1	104	1	0·02	1	105	1	29	1	0·01
	S × F	NA	NA	1	49	1	< 0·001	1	257	1	31	1	0·04
	B	4	12	4	122	4	0·09	4	83·2	4	5	4	0·11
	Error	7	5	8	24	12	0·06	11	224	12	10	12	0·05
FPOM	S	1	0·02	1	0·03*	1	< 0·001	1	0·34	1	0·02**	1	0·39**
	F	NA	NA	1	0·01	1	0·001	1	0·15	1	0·008*	1	0·02
	S × F	NA	NA	1	0·001	1	< 0·001	1	0·1	1	0·007*	1	0·03
	B	4	0·09	4	0·03	4	0·020	4	0·14	4	< 0·001	4	0·05
	Error	7	0·07	8	0·006	12	0·02	11	0·34	12	0·001	12	0·02
Total abundance	S	1	0·52	1	38 568*	1	12 600	1	39 605	1	37 325*	1	46 754**
	F	NA	NA	1	233 523***	1	893 799**	1	259 464*	1	404 417***	1	132 682***
	S × F	NA	NA	1	38	1	20 352	1	15 905	1	16 589	1	186
	B	4	0·20	4	41 697*	4	42 995	4	55 816	4	2194	4	9219
	Error	7	20	8	7130	12	48583	11	28 767	12	8880	12	2767

Asterisks indicate significant differences: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
B indicates block effect.
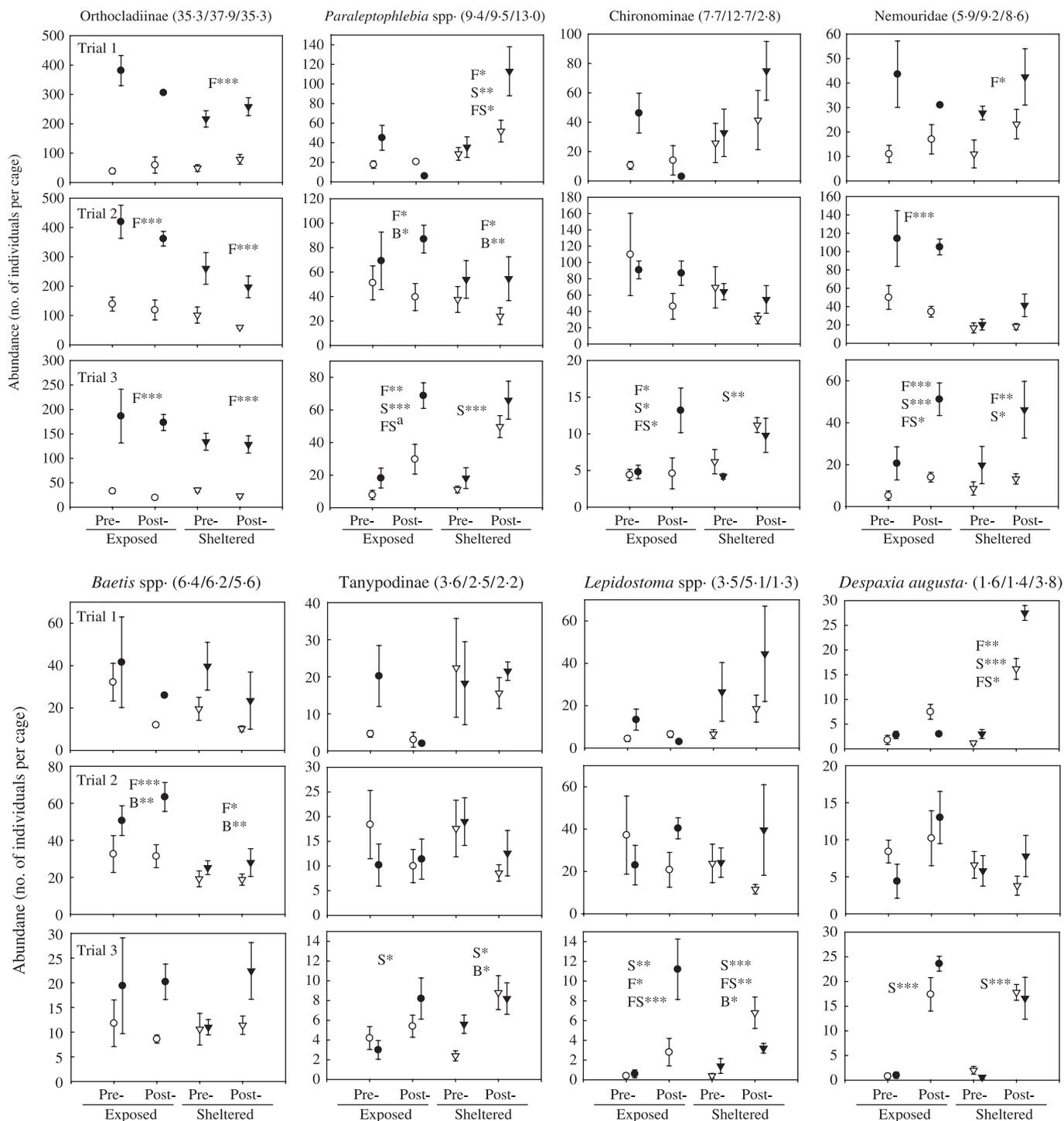
Fig. 4. Mean (+1 SE) of total abundance of the numerically dominant taxa within a cage (415 cm²) including the individuals found in the leaf bags. Filled and open circles denote natural and artificial leaf treatment, respectively. Pre and post refer to 'pre' and 'post' spate sampling occasions, respectively. Note that scales of *y*-axis differ among the trials. Percentages shown in parentheses beside taxon names indicate relative abundance of the numerically dominant taxa for trials 1, 2 and 3. Alphabetical letters denote results of statistical analyses; B, F, S and FS indicate block, food resource, spate and food resource × spate interaction, respectively. Asterisks are the significance levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. [a]The interaction between spate and food resource was nearly significant ($P = 0.06$).

of the colonization periods preceding each spate (Fig. 4). To compare the responses of numerically dominant taxa within each trial and among the three trials, the taxa that comprised at least 3% of the total abundance for at least one of the three trials, and > 1% in all three trials were selected. For example, *Capnia* spp. was

excluded from further analyses owing to low relative abundance (< 1% in trial 2). Although *Zapada cinctipes* (Banks) was not common in trial 2, an exception was made and this taxon was included together with *Malenka* spp. in trial 2 as Nemouridae, as these two taxa share similar morphology and food. Consequently,

eight macroinvertebrate taxa that comprised 73% (trial 1), 84% (trial 2) and 73% (trial 3) of the total abundance were further examined.

Significant, spate-induced responses at the taxon level only appeared in trials 1 and 3 (Fig. 4). In trial 1, *Paraleptophlebia* spp. and *Despaxia augusta* (Banks) abundance increased in sheltered cages and the colonization rate was disproportionately greater (200% and 170%, respectively) for the cages provided with natural leaves relative to the cages with artificial leaves. In trial 3, these two taxa colonized into both the exposed and sheltered cages; only *Paraleptophlebia* spp.'s preferential colonization into food-enriched, exposed cages was nearly significant (spate × food resource interaction; $P = 0.06$). In trial 3, Tanypodinae, Chironominae, Nemouridae and *Lepidostoma* spp. also colonized both sheltered and exposed cages; the latter three taxa showed significant spate × food resource interactions of our interest in the exposed cages. Orthocladiinae and Baetis did not show any flow-induced responses.

The spate × food resource interactions for *Paraleptophlebia* spp., Chironominae and *Lepidostoma* spp. in trial 3 became insignificant with fine organic matter as a covariate; $P = 0.76$, $P = 0.26$ and $P = 0.12$, respectively. This suggests that differential colonization rates between the cages with a different level of food resource quality was independent of potential difference in retention efficiency of leaf types only for *Paraleptophlebia* spp. and *D. augusta* in trial 1 and Nemouridae in trial 3.

Discussion

The important roles of physical disturbance associated with flow fluctuation relative to biotic factors (e.g. predator–prey interactions) have been highlighted in structuring lotic communities (e.g. Townsend 1989). Empirical studies on the effects of frequency and magnitude of physical disturbance on local community are common (e.g. Death 1996 and literature cited therein; Biggs *et al*. 1999). In contrast, few studies have examined feedback effects of flow disturbance on spatial distribution of stream community across heterogeneous stream patch landscapes (e.g. Lancaster & Hildrew 1993a; Robertson *et al*. 1995; Palmer *et al*. 1996; Matthaei, Arbuckle & Townsend 2000; Negishi *et al*. 2002), conceivably due to technical difficulty in observing the rapid redistribution of community over relatively unpredictable events. The hydraulically benign flow environment we experimentally created with concrete blocks in this study could correspond to natural refugia behind woody debris and boulders during high flow events. Our findings provided results consistent with the hypothesis that microdistributional shifts of certain detritivorous macroinvertebrates among disturbed and sheltered patches during spates were mediated not only by hydraulic controls but also by food resource quality available within sheltered patches. However, such responses were not consistently observed for all three

events. Unfortunately several lost samples during the largest event urges caution in interpretation of our results relative to the hypotheses. Nevertheless, the observed variable responses of macroinvertebrates related to food resource among spates was reasonably explained by interactions between seasonally preconditioned distribution of organisms and resources prior to events and spate characteristics.

Despite the variable durations of colonization periods, the presence of natural leaves consistently resulted in higher macroinvertebrate colonization rates relative to the artificial leaf treatment. This pattern is consistent with previous findings on the strong effects of organic matter biomass on macroinvertebrate productivity and colonization, particularly in food-limited environments (Richardson 1991; Wallace *et al*. 1999; Negishi & Richardson 2003). Richardson (1992b) demonstrated that macroinvertebrates colonized leaf materials primarily as a food resource, rather than simply as a microhabitat (see also Dobson & Hildrew 1992). Different colonization rates of artificial and natural leaf packs by nonshredder animals were due to a differential accumulation rate of fine organic matter between the leaf types. In our study, the potential difference of leaf types in trapping efficiency of organic matter and organisms was only significant for the exposed cages in trial 3. In trials 1 and 2 at least therefore we attributed the high total macroinvertebrate abundance in the natural leaf treatment with the numerically dominant detritivorous taxa such as Orthocladiinae, *Paraleptophlebia* spp. and Nemouridae (Merritt & Cummins 1996) to the direct effects of experimentally provided alder leaves.

The three trials resulted in different responses of macroinvertebrates and organic matter biomass. The spate-induced accumulation of macroinvertebrates and organic matter were minimal in trial 2 while the responses that occurred in trials 1 and 3 differed somewhat from each other among the numerically dominant taxa of macroinvertebrates. Interpretations of these results need to be made carefully in the context of the different spate characteristics (i.e. the antecedent conditions and magnitude) and environmental conditions at the time of the sampling. Movements of organic matter can be assumed to be passive and entirely under hydraulic controls. Thus, the negligible spate-induced shifts of organic matter and macroinvertebrates in trial 2 suggest that there was a minimal effect of the spate on spatial distributions of macroinvertebrates and organic matter across the stream. The standing crop of organic matter within a channel is related to the timing of leaf input and its retention is inversely related to discharge (King *et al*. 1987; Richardson 1992a; Snaddon, Stewart & Davies 1992; Wallace *et al*. 1995). In February and March, organic matter input from allochthonous sources is fairly low except the input of needles (Richardson 1992a). Furthermore, the spate in trial 2 was preceded by variable discharge and the occurrence of spates of a similar magnitude, possibly having led to loss or

redistribution of easily transportable organic matter and associated macroinvertebrates (Irvine 1985; Cuffney & Wallace 1989). In contrast, trials 1 and 3 coincided with the timing of high allochthonous input to the stream (Richardson 1992a) and both the treatment spates occurred after a period of relatively low and stable flows. Consequently, the stable antecedent flow and high supply of organic litter may have formed spate-prone detritus patches in certain areas of the channel. One such type of resource patches was riffles where entrapped leaf packs and accumulations of fine organic matter that were heavily colonized by macroinvertebrates at low flow were washed out during the spates (personal observations, J.N. Negishi).

Trials 1 and 3 were both conducted at a similar time of year (i.e. early autumn) and with similar antecedent flow characteristics (i.e. low and stable flow). However, the two spates differed in their magnitude, i.e. the much higher peak discharge and peak : base flow ratio in trial 1 relative to that in trial 3. Our results from trial 1 are in general agreement with the previous studies on hydraulic refugium functions; community-level accumulation into hydraulically benign patches was observed with variable responses at the taxon level (e.g. Winterbottom *et al.* 1997). In contrast to our prediction, however, similarly high macroinvertebrate and organic matter accumulation rates were observed also in the exposed patches in trial 3 despite the observation that concrete blocks seem to have moderated hydraulic environment of the refugium treatment. These seemingly contradicting patterns might be explained by the magnitude of disturbance and scale-dependent function of refugia (Sedell *et al.* 1990). One possibility is that the location of the cages (i.e. at the edges of the wetted stream channel) provided hydraulically benign environments relative to the channel centres in trial 3 (see Negishi *et al.* 2002) regardless of our refugium treatment types, whereas the entire channel including the channel edges was disturbed by the larger spate in trial 1.

Among the eight taxa whose responses were carefully examined, only *Paraleptophlebia* spp. and *D. augusta* responded significantly to both spates. The variable species-specific response was related to the characteristics and seasonal context of each flood and is consistent with prior studies (e.g. Lancaster & Hildrew 1993b; Palmer *et al.* 1996). Besides morphological traits favourable for high mobility such as swimming (in particular *Paraleptophlebia* spp.) and crawling (both taxa), their primary diet of coarse detritus and its spatial and temporal dynamics may account for the sensitivity of these two taxa to high flow events. In the environment where resource availability is highly patchy and fluctuate considerably both at temporal and spatial scales, consumers with efficient resource tracking may have competitive advantages within community over other less mobile detritus feeding animals (Rowe & Richardson 2001). For example, Ledger *et al.* (2002) showed that macroinvertebrate mobility, i.e. the colonization rate, was related to their diet, being consistent with the

hypotheses on the positive relationships between the degree of patchiness of organisms' food resource and their mobility. High flow events in early winter with a subsequent period of progressively reduced litter input and continuously variable flow, which typically characterize autumn to winter transition of season in the study area, results in detritus-rich patches being confined to hydraulically benign depositional areas. Thus, locating and settling in hydraulically sheltered environments with high organic matter loads is likely to have two important positive feedback effects to populations of these organisms: lower spate-induced mortality of individuals, and greater efficiency of food acquisition and thus productivity. Earlier field observations have reported that Leptophlebiidae species were abundant in riffle leaf packs during summer periods (Lehmkuhl & Anderson 1972; Miller & Golladay 1996) but shifted their distribution into more depositional habitat after the disturbance. To efficiently track and exploit food resources whose patchy distribution changes seasonally, shredding *Paraleptophlebia* spp. and *D. augusta* may have adaptive traits of high mobility. The shredder Nemouridae showed food resource preference only in the smaller autumn spate (trial 3) but no responses in trial 1. Intriguingly, such a response was only observed in the exposed cages, the reason for which remains unclear.

The influence of organic matter biomass on the abundance or accumulation of macroinvertebrates on hydraulically sheltered refugia has been refuted as macroinvertebrate food resources were not considered limiting and the taxa examined were not necessarily detritivores (Lancaster & Hildrew 1993b; Winterbottom *et al.* 1997). In our study system, the detrital food resource has been found strongly limiting macroinvertebrate productivity (Richardson 1991; Negishi & Richardson 2003), and experimental manipulation of detritus resource availability resulted in rapid responses in the spatial distribution of shredding macroinvertebrates (Rowe & Richardson 2001). Thus preferential colonization by two detritivorous taxa in the refugium habitat with higher food resource only during large storms may reflect the intensification of foraging effort of mobile shredding organisms in trial 1 relative to trial 3. Similar behavioural adaptation in response to changes in available food resource level has been reported for various organisms including terrestrial and aquatic insects (Kohler 1984; Rowe & Richardson 2001). How then, did these two species preferentially accumulate in flow refugia provided with high food value? In order to identify the food resource value of flow refugia, these individuals had to colonize patches in the first place. Given that the probability of reaching flow refugia is independent of leaf types, it is likely that individuals elected to stay or leave based on the habitat quality available in the flow refugia. Individual organisms probably left flow refugia to seek other patches even during high flow events if food resource value was not adequate, suggesting that colonization by these taxa

occurred rather quickly over the spates. However, the absence of such food resource-value effects on refugium colonization in trial 3 suggest that their pursuits of high quality food resources within refugia may be the consequence of trade-offs between the benefits and risks of foraging resources via movements across patches based on degree of resource scarcity within a system.

Previous disturbance theory and related empirical studies have emphasized that resistance to and recovery from disturbance depends on the timing of these events relative to life history and successional stages of affected organisms (e.g. White 1979; Sousa 1980; Harvey 1987; Peterson & Stevenson 1992; Robinson, Rushforth & Burgherr 2000). Moreover, several lines of evidence suggest that disturbance affects distribution of organisms not only by directly influencing fitness of individuals but also by altering food resource distribution and thus mediating a gradient of consumer populations across landscapes (Ehrlich *et al.* 1980; Waide 1991). Nevertheless, how the preconditioning of ecosystems prior to disturbance in terms of consumer and resource distributions affect responses during disturbance and post-disturbance recovery have not been articulated or empirically examined. In our system, distribution and abundance of detritus food resource within the channel is under strong control of interplays between timing and magnitude of riparian litter input and flow rate. For detritivores, food resource patches may spatially expand across stream channels owing to low flow rate and high litter input particularly in early autumn, potentially reducing resource competition and increasing productivity. In turn, however, colonizers to the expanded habitat areas (e.g. leaf packs in riffles) may face the risk of being susceptible to subsequent spate disturbance with perhaps higher mortality. Thus spates potentially result in varying consequences in consumer responses dependent on preconditioning of the system involving detritus food resource and flow dynamics. In an evolutionary sense, mobile detritus feeders such as *Paraleptophlebia* spp. and *D. augusta* with the capability of preferentially colonizing refugium patches with higher food quality may be favoured with enhanced productivity under local environmental variability. Our study suggests that timing of disturbance events may indirectly influence macroinvertebrate detritivores through variably affecting the spatial distribution and availability of food resources as well as quality of hydraulically sheltered refugium patches, which is crucial for long-term population maintenance.

Acknowledgements

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