

Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada

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Abstract: Diversity and productivity of stream food webs are related to habitat heterogeneity and efficiency of energy retention. We tested the hypothesis that experimental boulder placements in a second-order stream would increase diversity and abundance of macroinvertebrates by restoring detrital retention and habitat heterogeneity. Two relatively natural, upstream, reference reaches and a downstream treatment reach with a relatively straight channel and less woody debris were studied for 3 months before and 1.2 years after the placement of six boulder clusters in the treatment reach. Mean velocity and its coefficient of variation increased in the treatment reach (140 and 115%, respectively), whereas the reference reaches remained relatively unchanged after the placements. Enhanced particulate organic matter storage (550%) was accompanied by increased total macroinvertebrate abundance (280%) in the treatment reach, converging with those of the reference reaches almost 1 year after the treatment. Detritivorous taxa numerically dominated the macroinvertebrate community, the total densities of which were best predicted by the fine fraction of organic matter biomass at microhabitat scale. However, the effect of boulder clusters on taxonomic richness was negligible. Our findings suggest that boulder clusters can be used at least as a short-term means to restore macroinvertebrate productivity in detritus-based stream systems.

Résumé : Il existe une relation entre la diversité et la productivité des réseaux alimentaires en eau courante, d'une part, et l'hétérogénéité de l'habitat et l'efficacité de la rétention de l'énergie, d'autre part. Nous avons éprouvé l'hypothèse selon laquelle l'addition expérimentale de blocs de pierre dans un cours d'eau d'ordre 2 devrait augmenter la diversité et l'abondance des macroinvertébrés, en rétablissant la rétention du détritit et l'hétérogénéité de l'habitat. Nous avons étudié deux sections témoins en amont relativement naturelles et une section expérimentale en aval à chenal relativement droit et avec moins de débris ligneux durant les 3 mois qui ont précédé et durant 1,2 année qui a suivi l'addition de six amas de blocs de pierre dans la section expérimentale. La vitesse moyenne et son coefficient de variation ont augmenté dans la section expérimentale (respectivement de 140 % et de 115 %), alors que les conditions dans les sections témoins sont demeurées à peu près inchangées. L'accumulation accrue de matière organique particulaire (550 %) s'est accompagnée dans la section expérimentale d'une augmentation de l'abondance totale des macroinvertébrés (280 %) qui tendait à atteindre l'abondance observée dans les sections témoins presque 1 an après l'addition des blocs. En nombre, ce sont les taxons de détritivores qui dominaient dans la communauté de macroinvertébrés et leurs densités totales pouvaient être prédites le plus exactement par la fraction fine de la biomasse de la matière organique à l'échelle du microhabitat. Il n'y a eu qu'un effet négligeable des blocs de pierre sur la richesse taxonomique. Nos résultats laissent croire que des amas de blocs de pierre peuvent servir, au moins à court terme, à restaurer la productivité des macroinvertébrés dans les systèmes d'eau courante à base de détritit.

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Introduction

The cycling of energy and nutrients through the food web plays key roles in maintaining biological diversity and productivity in ecosystems (Polis et al. 1997). The physical structures of an ecosystem form a template for material cy-

cling by providing an array of physical environments that meet the requirements of various species and enable them to interact with each other through resource competition and consumption within the food web (Southwood 1988). In stream ecosystems, where the movement of solutes and particulates is largely governed by the unidirectional downstream dis-

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placement of water, the importance of physical structure is twofold: (i) it influences the residence time of materials controlling the rate and efficiency of energy flow and (ii) it affects habitat diversity.

Anthropogenic activities disrupt the integrity of stream ecosystems by either removing particular consumers or resources within a food web or altering the physical environment on which food web is founded, or both. As a consequence, shifts in temporal and spatial patterns of resources and consumer populations may result in lower productivity and diversity of stream systems. One of the major goals of restoration practices is to recover ecosystem-level processes such as energy flow and associated biological productivity and diversity from a disturbed to a predisturbance level (Palmer et al. 1997).

In low-order, forested streams, large woody debris (LWD) exerts a profound influence on geomorphic channel form and physical habitat structure. LWD controls the transport and storage of sediment influencing stream flow as well as the local geomorphology of a stream channel, as either debris jams or single pieces (Nakamura and Swanson 1993). LWD provides important fish habitat by creating pools and providing cover against predators and high flows (e.g., Bisson et al. 1987). Furthermore, in forested streams where the food web is limited by detritus biomass (Richardson 1991; Wallace et al. 1999), retention structures including LWD and associated depositional environments are regarded as major storage sites of particulate organic matter (POM) and thus a key component for stream productivity (Bilby and Likens 1980; Smock et al. 1989). Consequently the removal of LWD and channelisation can lead to decreased habitat heterogeneity and detritus retention, resulting in lower productivity and sometimes also lower diversity of fish and macroinvertebrate communities (e.g., Angermeier and Karr 1984; Haapala and Muotka 1998).

The placement of in-stream structures such as LWD, boulders, and their complexes has been used as a means to actively restore habitat heterogeneity and geomorphic channel form at a relatively small spatial scale, particularly focusing on fishes. A number of studies have demonstrated increased fish abundance and biomass after placements of in-stream structures (e.g., House and Boehne 1986; Crispin et al. 1993; Cederholm et al. 1997). Macroinvertebrate responses have increasingly received attention as a part of evaluation programs of restoration works that involve placement of in-stream structures (e.g., Friberg et al. 1998; Laasonen et al. 1998). The findings of these studies are somewhat confounded by having no prerestoration data or proper control sites because many restoration works in the early stages were conducted without monitoring programs and also the location and spatial size of treatment sites could not be always controlled by investigators. Manipulative experiments have examined the responses of POM storage and macroinvertebrates to in-stream structure in a more controlled environment (Dobson et al. 1995; Wallace et al. 1995). However, the foci of these studies were at relatively small scales such as habitat units or the microhabitat in which each structure was installed. Therefore, how in-stream structures influence ecosystem-level processes (i.e., POM retention and its influence on macroinvertebrates) at the stream reach (i.e., 10–100 m) has not been well understood despite restorations involving in-stream

structure placements having been done commonly at this scale (but see Muotka and Laasonen 2002).

Our objective in this study was to examine the effects of the placement of boulder clusters on ecosystem-level process, i.e., POM storage and the responses of macroinvertebrate community at a stream-reach scale. We tested the hypothesis that the placement of boulder clusters in a stream section in which habitat structure has been anthropogenically altered would increase habitat heterogeneity, POM storage, and thus abundance and diversity of macroinvertebrates. This hypothesis is based on previous studies suggesting seasonally food-limited macroinvertebrate communities in the detritus-based system in the study area (Richardson 1991) and a positive relationship between habitat heterogeneity and macroinvertebrate taxonomic diversity (e.g., Negishi et al. 2002). We use the terms detritus and POM interchangeably in this study.

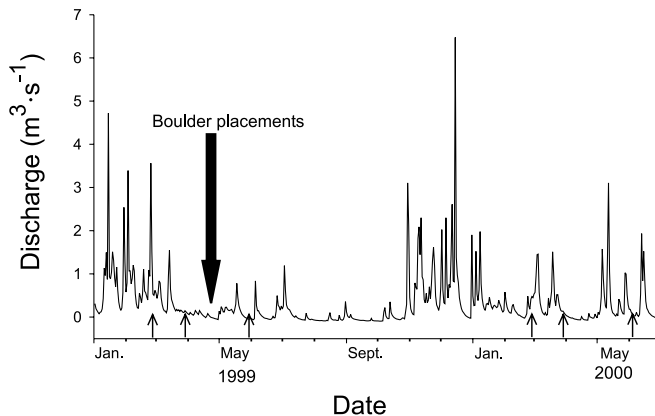
Materials and methods

Study site

This study was carried out from January 1999 to June 2000 within a 300-m segment 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 Range Mountains 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 *Tsuga heterophylla* (western hemlock), *Thuja plicata* (western red cedar), and *Pseudotsuga menziesii* (Douglas fir) are the dominant forest species. The riparian vegetation consisted predominantly of *Alnus rubra* (red alder), *Acer circinatum* (vine maple), and *Rubus spectabilis* (salmonberry). This creek is characterized by low and stable discharge in summer and higher and more-variable discharge in winter (Fig. 1). Minimum and maximum water temperatures of Spring Creek during the study period were 1.5 and 13.7°C, respectively. Stream water was characterized by high dissolved oxygen (near saturation), low suspended solids, and neutral to slightly acidic water. More-detailed hydrologic features and water chemistry of Spring Creek have been described elsewhere (Feller and Kimmins 1979). Spring Creek had an average gradient of 2.1% and variable wetted width of 2–5 m and bankful width of 4–8 m within the study segment. The stream channel is mostly characterized by pool–riffle sequences with substrate materials being dominated by cobble with occasional patches of sand and accumulation of organic detritus along the wetted channel margins as well as behind woody debris. The discharge of Spring Creek was calibrated from the discharge data of East Creek (continuously recorded by a V-notch weir), a tributary of Spring Creek that enters at the downstream end of the study segment. A discharge – water level relation was independently established for the study site by measurements at a range of water levels and corresponding discharges, and this was used to estimate mean daily discharge of Spring Creek.

Visual inspection revealed that one reach (hereafter referred as the treatment reach) of Spring Creek had a relatively straight channel and homogeneous habitat structure with fewer pieces of LWD (diameter greater than 10 cm,

Fig. 1. Estimated daily mean discharge of Spring Creek (British Columbia, Canada) during the study period. The upward arrows indicate the occasions of benthic sampling.



length longer than 1 m) compared with the adjacent reaches, partly because of the presence of a bridge at the downstream end of the reach (0.16 LWD pieces·m⁻¹, length 56.2 m, gradient 3.54%). Although there are no historical data on the channel form before the bridge construction, evidence of bank erosion and denudated alluvial deposits along the present channel suggest that degradation of the stream bed associated with bridge construction shifted a sinuous stream channel to a relatively straight one with increased channel gradient and less organic debris. As a result, the treatment reach had low amounts of longitudinal and cross-sectional morphological variation and thus few depositional habitats where slow flow generally accumulates food resource (POM). In addition to the treatment reach, two upstream reference reaches were selected: reference reach 2 was located 50 m upstream of the treatment reach (0.29 LWD pieces·m⁻¹, length 45.3 m, gradient 1.89%), and reference reach 1 was located 20 m upstream of reference reach 2 (0.40 LWD pieces·m⁻¹, length 40.0 m, gradient 1.08%). Reference reaches were chosen as representative of the stream channel with relatively natural condition of the riparian vegetation and had a visibly greater habitat heterogeneity with channel meanders, more abundant woody debris structures, and longitudinal variation of their channel morphology relative to the treatment reach. Reference reaches 1 and 2 were slightly different from each other in terms of habitat structure; pools with deep and slow flow dominated reference reach 1, whereas reference reach 2 was characterized by a wider channel profile and greater proportion of riffle habitats with shallow and fast flow. In January 1999, line transects were set over each reach with longitudinal intervals of 2 m and were marked using polyester threads. These transects were then marked at 1-m intervals to fix the sampling points at which benthic samples and physical habitat measurements were taken. The number of sampling points available varied depending on discharge and wetted channel width.

Placements of boulder clusters

It was intended first that boulder clusters would alter the flow environment and subsequently that channel morphology would be diversified through local scour and filling of substrate materials. Boulder clusters were placed as deflec-

tors so that slow-flow habitats downstream of the structures and fast-flow habitats on the narrowed side of stream channel would be formed. The longitudinal intervals of boulder clusters mimicked the occurrence interval of woody debris in the adjacent natural stream reaches, which was found to be approximately 6 m by survey. For the experimental manipulation, round boulders with long axes of 35–45 cm were collected from a quarry nearby in the Research Forest. Between 7 and 14 April 1999, a total of six boulder clusters were placed in the treatment reach. To minimize disturbance of stream banks and stream habitat, boulders were carried manually in a net. Each of the clusters consisted of three to seven boulders, depending on the bankfull channel width at the individual site. Boulder clusters were placed such that several boulders formed a diagonal line (45° angled downstream) in an alternating manner on either side of the stream; the upstream end was in contact with the stream bank. The boulders were placed on the streambed without extra excavation activities and thus were not buried or wedged tightly against each other. Although substantial flow still existed downstream of the clusters at the time of the placements, it was expected that inorganic and organic materials washed from upstream would eventually fill the spaces between the boulders making them deflect stream flow more efficiently, and channel morphology would adjust itself to the boulder clusters.

Benthic samples and measurements of physical variables

Benthic macroinvertebrates and POM were collected using a Surber sampler (WILDCO, Saginaw, Mich.; mesh size 300 µm; area 0.095 m²) in each reach on six occasions from 28 February 1999 until 3 June 2000 (Fig. 1). In 1999, benthic samples were collected on 28 February, 28 March, and 28 May. Sampling was repeated almost exactly a year later, on 26 February, 27 March, and 3 June in 2000. These three sampling occasions were referred to as February, March, and May, respectively, for convenience. Benthic samples were collected on a stratified random layout, at intervals of at least 1 month to allow a sufficient colonization period before subsequent samples. On each sampling occasion, 10 transects were randomly selected in each reach and one randomly chosen sampling point on each transect was sampled. When the same sampling point was chosen for consecutive sampling occasions, an adjacent patch similar to the sampled patch was substituted; this only occurred twice. Consequently, samples collected from different sampling occasions were assumed temporally independent.

Physical variables (i.e., current velocity, depth, and substrate coarseness) were measured along with the collection of benthic samples. Substrate coarseness was evaluated using a metal grid frame (30 × 30 cm) that consisted of nine subgrids (10 × 10 cm) placed on the streambed. The size of the dominant substrate material within each subgrid was visually estimated according to the following categories: 1–2 mm = sand; 2–64 mm = pebble; 64–264 mm = cobble; >264 mm = boulder and bedrock. These categories were then coded as follows: sand = 1; pebble = 2; cobble = 3; boulder = 4; bedrock = 5. These nine values within the subgrids were averaged to represent substrate coarseness of each sampling location. Velocity averaged over 30 s at 40%

depth from streambed was measured along with depth at the central point of the metal grid with a propeller-based flow meter (propeller diameter of 3.5 cm; model 2100, Swoffer Instruments, Inc., Seattle, Wash.). Samples were always collected starting from the downstream reach and sampling points within each reach to avoid downstream effects of sampling. Samples were preserved in 10% formalin in the field and taken back to the laboratory for processing. All materials retained on a 500- μm sieve were processed further. Macroinvertebrates were sorted, counted and identified to the lowest level possible, usually genus or species, based on Stewart and Stark (1993), Merritt and Cummins (1996), and Wiggins (1996). Particulate organic matter was separated from macroinvertebrates, divided into two different size fractions, i.e., fine particulate organic matter (FPOM, 500 μm – 1 mm) or coarse particulate organic matter (CPOM, >1 mm), dried for at least 24 h at 60°C, and subsequently ashed for at least 2 h at 550°C to obtain ash-free dry mass (AFDM).

Habitat characteristics

To examine differences in habitat characteristics between reaches as well as changes in habitat characteristics resulting from the placement of boulder clusters, physical variables (i.e., current velocity, depth, and substrate coarseness) were measured independent of benthic samples. These variables were measured across all of the sampling grid points available in each reach at similar discharges (Q) before and after the boulder placements. Substrate coarseness measurements were made on 25 January 1999 ($Q = 0.22 \text{ m}^3 \cdot \text{s}^{-1}$) and 10 January 2000 ($Q = 0.23 \text{ m}^3 \cdot \text{s}^{-1}$), whereas velocity and depth were simultaneously measured on 24 January 1999 ($Q = 0.35 \text{ m}^3 \cdot \text{s}^{-1}$) and 18 January 2000 ($Q = 0.35 \text{ m}^3 \cdot \text{s}^{-1}$).

Analyses

Ten benthic samples collected from each reach were not true, spatial replicates but subsamples; there was only one treatment reach. However, the presence of two reference sites and one treatment site before as well as after the treatment allowed inference of treatment effects (Underwood 1994). That is, the differences that were observed in connection with the placement of boulder clusters in the treatment reach but not in the reference reaches were attributable to the effects of treatment. To validate this argument, the following prediction was also to be examined: habitat structure and biological measures (i.e., POM biomass and macroinvertebrate) would remain relatively unchanged in the reference reaches during the study period. The two reference reaches were independently treated in the analyses as the differences between them were also of interest.

To examine the differences in habitat characteristics among the reaches and year (i.e., years 1999 and 2000), two-way analysis of variance (ANOVA) was used for physical variables with reach and year as main factors. A significant reach \times year interaction would suggest that the response variable changed over the boulder placements differentially among the reaches. Tukey's test was used for multiple comparisons: if a significant reach \times year interaction was detected, the means of six groups were compared; if the reach \times year interaction was insignificant, main factors were tested among groups.

The influence of boulder cluster placement on total POM biomass and macroinvertebrate abundance in the treatment reach was examined using asymmetrical ANOVAs, with reach and year as main factors and three sampling occasions nested within the year factor (Underwood 1994). Because there was no detectable change in channel morphology during the month between the boulder installation and the May sampling occasion in 1999, we assumed that there was no substantial effect on organic matter storage and macroinvertebrates at that stage. Therefore, sampling occasions in 1999 and 2000 were considered to represent the conditions of biological processes "before" and "after" the boulder cluster placement, respectively. In particular, two types of interactions were tested to detect the influence of boulder cluster placement: (1) an interaction between the mean biomass (or abundance) in the treatment reach and that in the reference reaches before (i.e., 1999) compared with after (i.e., 2000) the effects of boulder placements began; and (2) an interaction between occasions nested within the year (i.e., 1999) and the contrast of the treatment and reference reaches. Furthermore, two types of preplanned orthogonal contrasts were tested: (1) that the response variable measured on each sampling occasion of each year would be higher in the reference reaches than in the treatment reach, and (2) that the response variable measured in each reach on each sampling occasion would be higher in 2000 than in 1999.

To account for the mechanisms that caused reach-scale responses of macroinvertebrate abundance, relations between total macroinvertebrate abundance and each habitat variable (i.e., velocity, depth, substrate coarseness, and fine and coarse POM biomass) were examined at the scale of the Surber sample separately on each sampling occasion. The habitat variables that were found to have significant relations with total macroinvertebrate abundance using univariate regression analyses were further analyzed using stepwise multiple regression analysis.

The rarefaction technique (Krebs 1998) was used to estimate the expected total taxonomic diversity at the stream-reach scale accounting for the effects of sample sizes. The total number of taxa for 1000 individuals was estimated using ECOLOGICAL METHODOLOGY (Exeter Software, Setauket, N.Y.) for each reach on each occasion based on the total number of taxa and the number of individuals pooled from 10 samples.

Correlation-based principal component analysis (PCA) was used to examine (1) the differences in community structure among reaches on each sampling occasion, (2) the differences in community structure between years on each sampling occasion, and (3) the effects of placement of boulder clusters on community structure in the treatment reach. $\text{Log}_{10}(x + 1)$ -transformed abundances of the taxa that comprised greater than 1% of the total number of individuals sampled in this study were included. Principal components (PCs) 1 and 2 were then correlated with these taxa as well as habitat variables (i.e., velocity, depth, substrate coarseness, and fine and coarse POM biomass) to examine gradients of taxonomic composition for each axis in relation to habitat variables.

All statistical analyses were performed using SAS (Version 8.0; SAS Institute Inc., Cary, N.C.) unless mentioned otherwise, with the significance level $\alpha = 0.05$. To test for

Table 1. Summary of two-way ANOVAs to test the effects of year, reach, and their interactions on physical variables (i.e., current velocity, depth, and substrate coarseness).

Physical variable	Effects	df	MS	F	P
Velocity	Year (<i>Y</i>)	1	0.03	3.91	0.05
	Reach (<i>R</i>)	2	0.07	9.27	<0.0001
	<i>Y</i> × <i>R</i>	2	0.02	3.07	0.05
	Error	604			
Depth	Year	1	65.37	0.52	0.47
	Reach	2	5593.50	44.25	<0.0001
	<i>Y</i> × <i>R</i>	2	10.22	0.08	0.92
	Error	604			
Substrate coarseness	Year	1	0.11	0.56	0.46
	Reach	2	0.63	3.12	0.04
	<i>Y</i> × <i>R</i>	2	0.03	0.15	0.86
	Error	442			

Note: Bold type indicates statistical significance at $\alpha = 0.05$.

statistical assumptions of two-way and asymmetrical ANOVAs and univariate and multiple regressions, the data were first fitted to the complete general linear model for unbalanced ANOVA (PROC GLM, SAS Version 8.0; SAS Institute Inc.) and then residuals were compared for deviation from a normal distribution using the Shapiro–Wilks' test. $\text{Log}_{10}(x + 1)$ transformations were performed when needed to improve normality of the residual distribution before analysis.

Results

Habitat characteristics

Channel morphology did not change immediately after the placement of the boulder clusters. Stream discharge during the spring and summer of 1999 was relatively stable and low because of dry weather and there were few high flow events (Fig. 1). These high flow events did not result in detectable changes in channel morphology because there was insufficient hydraulic force to cause movement of bed materials. The flood that occurred on 14 December 1999, with the largest peak discharge ($6.5 \text{ m}^3 \cdot \text{s}^{-1}$) of the study period, caused detectable changes in channel morphology and habitat characteristics in the treatment reach. Inorganic and organic materials filled the spaces between the boulders, causing boulders to become imbricated, thereby creating fast-flow habitats on the opposite side of the channel by scouring out the streambed as well as forming a slow-flow habitat behind the clusters. During this event, the second boulder cluster from the upstream end failed when a log (diameter ~50 cm), against which the upstream boulder of the cluster rested, was moved downstream approximately 5 m, causing displacement of this boulder. After the flood event on 14 December, channel morphology did not detectably change again. The other five clusters remained intact throughout the study period. The measurements of substrate coarseness on 25 January 1999 and 10 January 2000 and depth and velocity on 24 January 1999 and 18 January 2000 were presumed representative of habitat structure before and after the treatment (placements of boulder clusters), as the high flow event that most significantly altered habitat structure occurred between these dates (i.e., 14 December 1999). The physical variables differed among reaches before treatment because of different channel morphology and gradients (Table 1; Fig. 2). Velocity and

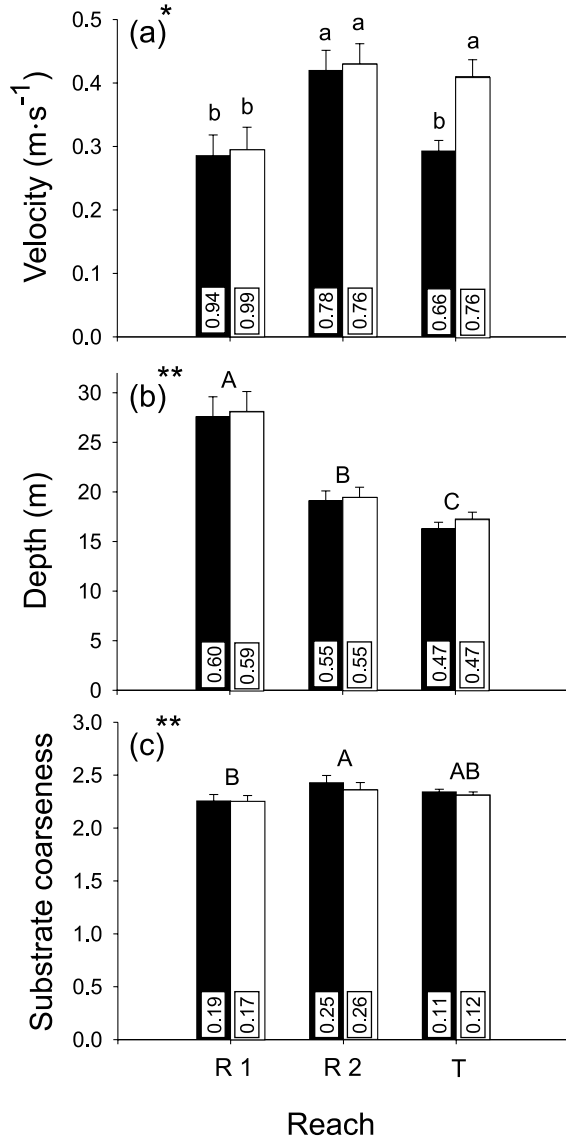
substrate coarseness were the highest in reference reach 2, followed by the treatment reach and then reference reach 1 (Fig. 2). Reference reach 1 and the treatment reach showed similar velocities, but the coefficient of variation was higher in reference reach 1 (Fig. 2). Depth was the highest in reference reach 1, followed by reference reach 2 and then the treatment reach. Overall, the treatment reach had the lowest variation in all three variables before boulder cluster placement. Depth and substrate coarseness remained at a similar level in all reaches after boulder cluster placement. However, velocity changed differentially among the reaches after boulder cluster placement, as shown by a significant reach × year interaction, with significant increase in the treatment reach (Table 1; Fig. 2). The increase of the coefficient of variation of velocity and substrate coarseness after boulder cluster placement was the highest in the treatment reach relative to the reference reaches, 15.2% for velocity and 9.1% for substrate coarseness, respectively. Nevertheless, the coefficient of variation of depth and substrate coarseness in the treatment reach was still the lowest among the three reaches after boulder cluster placement.

Total POM and macroinvertebrate abundance

Significant interactions were found both between the mean organic matter biomass in the treatment reach and that in the reference reaches before (i.e., 1999) compared with after (i.e., 2000) the effects of boulder cluster placement began and between occasions nested within year (i.e., 1999) and the contrast of the treatment and reference reaches (Table 2; Fig. 3). The proportion of FPOM to total POM biomass was in general low on all occasions, ranging between 3.5 and 10.8%. Preplanned contrasts indicated that POM biomass was lower in the treatment reach than in the reference reaches on the May sampling occasion in 1999 (Fig. 3). POM biomass was higher in 2000 than in 1999 in the treatment reach on the May sampling occasion.

Significant interactions were found both between the mean macroinvertebrate abundance in the treatment reach and that in the reference reaches before (i.e., 1999) compared with after (i.e., 2000) the effects of boulder cluster placement began and between occasions nested within year (i.e., 1999) and the contrast of the treatment and reference reaches (Table 2; Fig. 3). Preplanned contrasts showed that macro-

Fig. 2. Mean values (± 1 SE) of physical variables in each reach before and after the placements of boulder clusters: (a) current velocity, (b) depth, and (c) substrate coarseness. Solid and open bars denote "before" and "after" the placements, respectively; *, year \times reach interaction was significant (Tukey's multiple comparisons were conducted among six groups; different lower case letters denote significant differences); **, year \times reach interaction was not significant (Tukey's multiple comparison was conducted among reaches; different capital letters indicate significant difference). Numbers shown at the bottom of each bar denote coefficient of variation. R1, R2, and T refer to reference reaches 1 and 2 and the treatment reach, respectively.



invertebrates were more abundant in the reference reaches than in the treatment reach on the May sampling occasion in 1999 (Fig. 3). Total macroinvertebrate abundance was higher in 2000 than in 1999 in the treatment reach on the May sampling occasion.

Both FPOM and CPOM biomass were positively related to total macroinvertebrate abundance on three sampling occasions (Table 3). Substrate coarseness was also related to total macroinvertebrate abundance on March and May sam-

pling occasions, whereas velocity was related to total abundance only on the March sampling occasion. Stepwise multiple regression analyses revealed that total abundance was best explained by FPOM biomass for three sampling occasions: February, $y = 0.694x + 2.750$, $R^2 = 0.44$, $p < 0.0001$; March, $y = 0.801x + 2.826$, $R^2 = 0.44$, $p < 0.0001$; and May, $y = 1.042x + 2.928$, $R^2 = 0.72$, $p < 0.0001$. Although the homogeneity of slope test using analysis of covariance (ANCOVA), with total macroinvertebrates as the independent variable, reach as the main factor, and FPOM biomass as a covariate, approached significance ($p = 0.08$), the regression slope was highest on the May sampling occasion followed by March and February.

Number of taxa

The mean rarefied number of taxa for 1000 individuals was lowest in the treatment reach (T) only on the February sampling occasion before boulder cluster placement: R1 (49.5) > R2 (44.1) > T (42.3) in February; R2 (44.7) > T (41.0) > R1 (39.7) in March; and R2 (38.5) > T (37.8) > R1 (34.7) in May. Furthermore, the differences in the mean rarefied number of taxa between years were higher at least in one of the reference reaches than in the treatment reach, but without a consistent pattern in the direction of the changes. The percent changes of rarefied number of taxa among reaches from 1999 to 2000 were as follows: -5.6, -7.6, and -6.4 in February, +6.6, -0.5, and +3.1 in March, and +10.1, +2.2, and +2.0 in May for R1, R2, and T, respectively.

Community structures

PCs 1 and 2 together accounted for 51% of total variance in the data. Seventy taxa were found in this study and 19 taxa were included in the PCA (Table 4). PC 1 was positively correlated with the abundance of the numerically dominant taxa such as Chironominae, Orthocladinae, Tanytopodinae, and *Paraleptophlebia*, and thus this axis was highly correlated with the total abundance of macroinvertebrates ($r = 0.84$, $p < 0.0001$), whereas PC 2 was positively correlated with the abundance of the taxa such as *Baetis* spp., *Epeorus* sp., and *Rhyacophila banksi* but not correlated with the total abundance ($r = 0.04$, $p = 0.52$; Table 4). Habitat variables were significantly correlated with PC scores (Table 4). PC 1 was negatively correlated with velocity and substrate coarseness and positively correlated with organic matter biomass, and thus PC 1 can be interpreted as a gradient of the taxa that were found to be abundant in depositional habitat (depositional taxa). Depositional taxa except Tanytopodinae and Ceratopogonidae were considered as detritivores (Merritt and Cummins 1996). PC 2 was negatively correlated with depth and organic matter biomass and positively correlated with velocity, and thus PC 2 was interpreted as a gradient of the taxa that primarily resided in erosional habitat (erosional taxa).

Ordination plots of the PCA revealed dissimilarities of community structure among reaches as well as between years, particularly on the May sampling occasion (Fig. 4). On the February and March sampling occasions, there was a high degree of overlap of both PC 1 and PC 2 scores between years as well as among reaches, suggesting that the community structures were similar to each other. On the May sampling occasion, however, the treatment reach showed differences be-

Table 2. Summary of asymmetrical analyses of variance to detect the influence of boulder placements on total particulate organic matter (POM) biomass and macroinvertebrate abundance.

Effects	df	Total POM biomass			Total macroinvertebrate abundance		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Year (<i>Y</i>)	1	0.49			0.54		
Reach (<i>R</i>)	2						
Reference vs. treatment reaches (<i>T</i>)	1	2.93			<0.01		
Among reference reaches (<i>C</i>)	1	2.13			0.29		
Occasions nested within year (O_{year})	4	0.44			1.09		
$Y \times R$	2						
$Y \times T$	1	0.60	5.94	0.02	0.56	4.83	0.03
$Y \times C$	1	0.01	0.14	0.71	0.15	1.27	0.26
$O_{\text{year}} \times R$	4						
$O_{1999} \times R$	2						
$O_{1999} \times T$	1	0.83	8.15	0.01	0.60	5.15	0.03
$O_{1999} \times C$	1	0.32	3.12	0.08	0.10	0.90	0.35
$O_{2000} \times R$	2						
$O_{2000} \times T$	1	0.08	0.79	0.38	0.05	0.47	0.49
$O_{2000} \times C$	1	0.03	0.36	0.55	0.21	1.78	0.18
Error	166						

Note: Only relevant statistical hypotheses $Y \times T$, $Y \times C$, $O_{1999} \times T$, $O_{1999} \times C$, $O_{2000} \times T$, and $O_{2000} \times C$ are tested. Bold type indicates statistical significance at $\alpha = 0.05$.

tween years without an overlap with either PC 1 or PC 2 scores, whereas reference reach 2 was dissimilar between years in terms of the PC 2 score. Community structure in the treatment reach was dissimilar to that in reference reaches in 1999 but converged in 2000, at least in terms of the PC 1 score. The annual shift of community structure in the treatment reach, particularly obvious in May, involved the increase of the abundance of depositional taxa, which were numerically dominant and strongly correlated with total macroinvertebrate abundance. Although the shift of community structure in the treatment reach and reference reach 2 in May of 2000 also involved the increased abundance of erosional taxa, this had little influence on total macroinvertebrate abundance because of the lower abundance of erosional taxa relative to depositional taxa.

Discussion

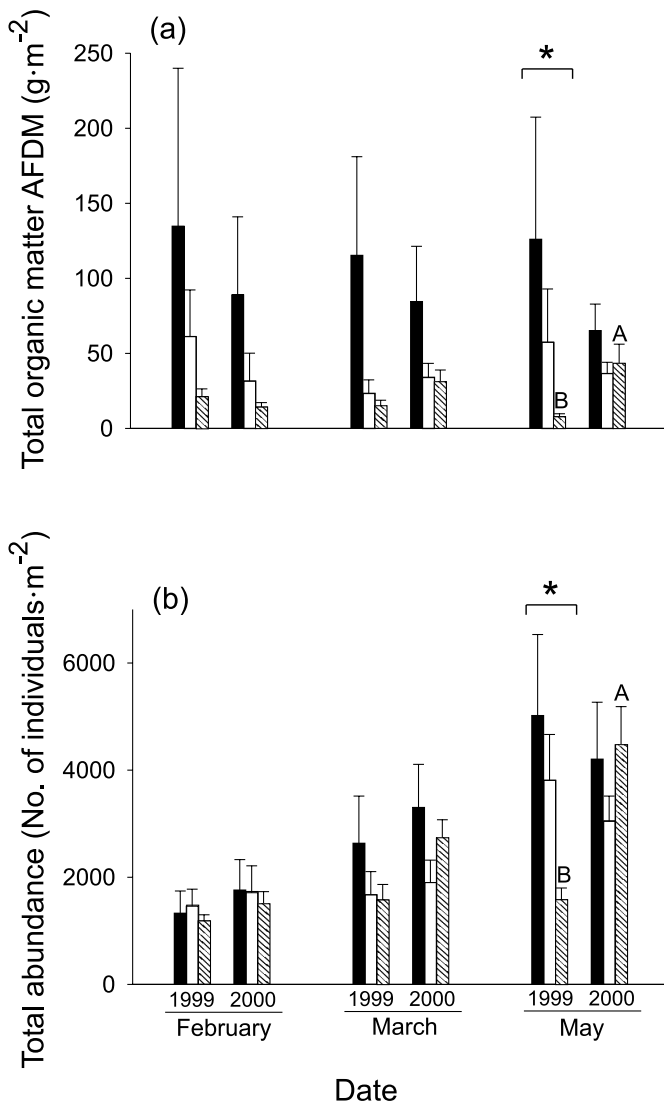
Boulder clusters increased habitat heterogeneity, at least in terms of velocity and substrate coarseness, resulting in increased benthic detritus storage and macroinvertebrate abundance and supporting the original predictions. However, the effects of the boulder clusters on the number of taxa appeared to be negligible. During the study period, habitat structures in the reference reaches remained almost unchanged, and the pattern of benthic detritus biomass and total macroinvertebrate abundance in the reference reaches were relatively consistent between the years. Therefore, we infer that the changes in the macroinvertebrate community and detritus storage observed in the treatment reach were caused by the placement of the boulder clusters.

As shown by similar mean values of depth and substrate coarseness before and after the boulder placements, overall change in channel morphology after the boulder cluster placement was slight. The formation of habitats with contrasting flow environments contributed to the increased heterogeneity

of velocity and substrate coarseness. A disproportionately larger area of fast-flow habitat was formed as boulder clusters concentrated flow compared with slow-flow habitats that were mostly formed behind the clusters. The increased proportion of pool area through scouring of stream beds after the placement of in-stream structures, e.g., woody debris and pieces of logs, has been widely reported (e.g., Crispin et al. 1993; Wallace et al. 1995; Hilderbrand et al. 1997). Furthermore, in some cases, mean channel velocity decreased after the placement (e.g., Wallace et al. 1995). The extent of the effects of in-stream structures on channel morphology varies depending on local substrate conditions and hydraulic characteristics such as local shear stress. Hilderbrand et al. (1997) reported that installation of log pieces in a high-gradient channel (3–6%) with coarse substrate dominated by large gravel, cobble, and numerous boulders resulted in little change in habitat structure, whereas in low-gradient streams (1%) that have sandy substrate, the installations caused substantial pool formation. This variability in channel response can be attributed to the differences in controlling factors in channel morphology among the sites. In Spring Creek, the predominant large substrate materials such as cobble and pebble probably limited the change in the channel morphology during the study period.

Despite the seemingly slight effects of the boulder clusters on channel morphology, macroinvertebrate habitat was greatly affected. The treatment reach originally lacked depositional habitat, and thus little detritus was stored before boulder cluster placement, particularly reflected in the May 1999 samples. After the placements of boulder clusters in May 2000, the treatment reach appeared to have stored detritus to a level similar to that in the reference reaches. There is in general a decreasing trend in mean value of detritus biomass in reference reaches from 1999 to 2000 on each of the sampling occasions, further supporting our hypothesis that reten-

Fig. 3. (a) Mean (+1 SE) total organic matter as ash-free dry mass (AFDM; $\text{g}\cdot\text{m}^{-2}$) and (b) mean (+1 SE) total macroinvertebrate abundances (number of individuals $\cdot\text{m}^{-2}$) in 1999 and 2000. Solid, open, and hatched bars represent reference reaches 1 and 2 and the treatment reach, respectively. Different letters above the bars indicate significant differences between years in each reach on each sampling occasion as results of pre-planned orthogonal contrast. Asterisks denote significant differences between the reference reaches and the treatment reach as results of pre-planned orthogonal contrasts.



tiveness and storage of detritus in the treatment reach increased as a result of the placement of boulder clusters. In natural streams, various geomorphic features such as woody debris, boulders, and shallow riffles can trap and store organic materials (e.g., Speaker et al. 1984). Artificially installed in-stream structures can also increase the storage and biomass of benthic detritus by directly trapping (Angermeier and Karr 1984; Dobson et al. 1995) or by indirectly facilitating deposition of materials behind the structures (Wallace et al. 1995; Lemly and Hilderbrand 2000). Although retention efficiency was not directly quantified in our study, it was

observed that the accumulations of fine detritus occurred behind the boulder clusters and larger particles of detritus were trapped on the upstream side of the clusters. The boulder clusters also might have increased the trapping efficiency of detritus within the substrate across the stream channel through increased substrate stability (Bilby 1984).

The increased detritus storage in the treatment reach resulted in increases of the numerically dominant detritivores and thus the total macroinvertebrate abundance, at least on the May sampling occasion. In forested streams in which primary productivity is limited, allochthonous input such as leaf litter derived from the surrounding terrestrial ecosystem serves as a primary energy source for stream communities (e.g., Cummins et al. 1989). Consequently, detritus biomass can limit productivity of a macroinvertebrate community (Richardson 1991; Wallace et al. 1999). As unidirectional flow displaces materials downstream unless trapped, channel structure and its retention efficiency can be a factor limiting productivity in detritus-based stream ecosystems (Cummins et al. 1989; Prochazka et al. 1991; Haapala and Muotka 1998). In our stream, placements of boulder clusters restored detritus-based energy flow from benthic detritus and detritus-feeding macroinvertebrates.

Improved retention efficiency and detritus storage following in-stream structure placement is a common finding (e.g., Dobson et al. 1995; Wallace et al. 1995; Muotka and Laasonen 2002). Depending on what factor limits community productivity, however, the consequences of in-stream structures on macroinvertebrate community can vary. In the studies of Hilderbrand et al. (1997) and Lemly and Hilderbrand (2000) conducted in streams of West Virginia, U.S.A., macroinvertebrate abundance did not increase at the stream-reach scale after log placement, although net biomass of benthic detritus increased within the channel. In their study, the total abundance of macroinvertebrates did not differ between riffles and pools, despite pools having a higher amount of benthic detritus, and hence the proportional change of habitat structure within a channel did not result in a net increase of macroinvertebrate abundance at the stream-reach scale. It is conceivable that the macroinvertebrate community was not limited by detritus food resources in their study streams. In Finnish streams, improved retention efficiency by in-stream structure placements did not result in the anticipated recovery of macroinvertebrate productivity because of the overriding importance of moss habitat in retention and productivity (Muotka and Laasonen 2002). In contrast, Wallace et al. (1995) found that macroinvertebrate abundance was higher in the depositional habitat that was created by the installations of log pieces compared with the pretreatment level in the stream of North Carolina, U.S.A. Dobson et al. (1995) also reported from mid-Wales that artificially created leaf-packs supported higher numbers of macroinvertebrates, in particular detritivores. Our finding is in general consistent with the last two studies in that productivity was increased by retention efficiency improved by in-stream structures.

Using artificial channels, Richardson (1991) experimentally demonstrated that certain shredder species were food-limited even in early summer (i.e., end of May) when May samples were collected in our study. Our findings from a natural stream in general support his finding, particularly on

Table 3. Results of univariate regression analysis using $\log_{10}(\text{total macroinvertebrate abundance} + 1)$ as the dependent variable and habitat variables as independent variables, separately shown for each sampling occasion.

Independent variables	Regression coefficient	Constant	r^2	F	P
February ($n = 60$)					
$\log_{10}(\text{fine POM biomass} + 1)$	0.694	2.750	0.443	46.160	<0.001
$\log_{10}(\text{coarse POM biomass} + 1)$	0.399	2.563	0.411	40.517	<0.001
$\log_{10}(\text{velocity} + 1)$	-0.675	3.153	0.025	1.458	0.232
$\log_{10}(\text{depth} + 1)$	-0.379	3.573	0.059	3.652	0.061
Substrate coarseness	-0.182	3.501	0.045	2.723	0.104
March ($n = 60$)					
$\log_{10}(\text{fine POM biomass} + 1)$	0.801	2.826	0.444	46.375	<0.001
$\log_{10}(\text{coarse POM biomass} + 1)$	0.400	2.707	0.333	29.011	<0.001
$\log_{10}(\text{velocity} + 1)$	-2.398	3.426	0.137	9.195	0.004
$\log_{10}(\text{depth} + 1)$	-0.136	3.382	0.008	0.441	0.510
Substrate coarseness	-0.189	3.696	0.150	10.198	0.002
May ($n = 60$)					
$\log_{10}(\text{fine POM biomass} + 1)$	1.042	2.928	0.725	152.744	<0.001
$\log_{10}(\text{coarse POM biomass} + 1)$	0.462	2.811	0.544	69.122	<0.001
$\log_{10}(\text{velocity} + 1)$	-1.010	3.515	0.046	2.779	0.101
$\log_{10}(\text{depth} + 1)$	-0.191	3.668	0.015	0.904	0.346
Substrate coarseness	-0.202	3.922	0.186	13.236	0.001

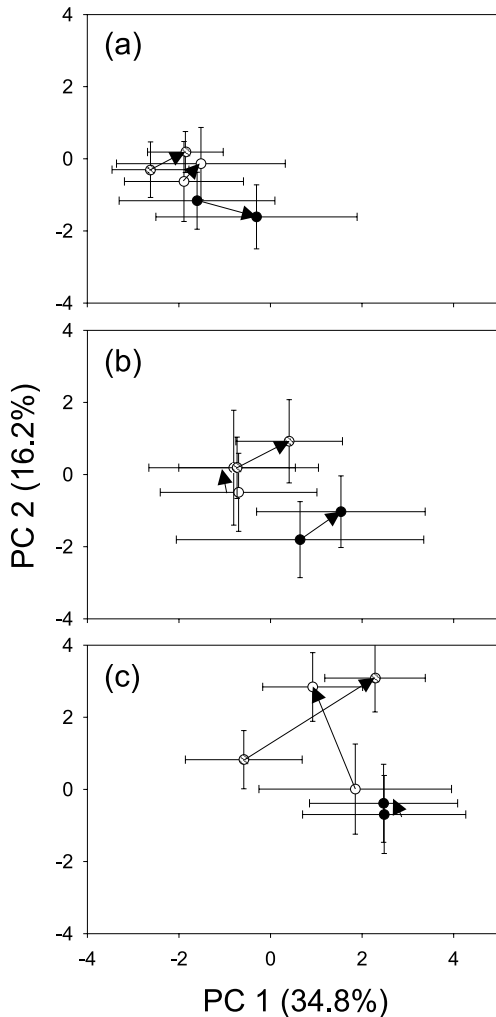
Note: POM, particulate organic matter. Bold type indicates statistical significance at $\alpha = 0.05$.

Table 4. Pearson's correlation coefficients between principal components (PCs) 1 and 2 and the abundances of the numerically dominant taxa and habitat variables.

	PC 1 ($p < 0.001$)	PC 2 ($p < 0.001$)
Taxa		
Chironominae (14%)	+0.83	
Orthocladiinae (11%)	+0.87	
Oligochaeta (8%)		
<i>Epeorus</i> (8%)		+0.63
Tanypodinae (7%)	+0.83	
<i>Paraleptophlebia</i> (7%)	+0.87	
<i>Baetis</i> spp. (6%)		+0.79
<i>Malenka</i> (5%)		
<i>Sweltsa</i> (5%)		
<i>Zaiteria</i> (4%)		
<i>Ameletus</i> (3%)	+0.69	
<i>Lepidostoma</i> spp. (3%)	+0.69	
<i>Cinygmula</i> (2%)		
<i>Despaxia augusta</i> (2%)	+0.73	
<i>Zapada cinctipes</i> (1%)		
<i>Rhyacophila banksi</i> (1%)		+0.68
<i>Heterlimnius</i> (1%)		
Ceratopogonidae (1%)	+0.70	
<i>Glossosoma</i> (1%)		
Habitat variables		
$\log_{10}(\text{velocity} + 1)$	-0.55	+0.46
$\log_{10}(\text{depth} + 1)$		-0.46
Substrate coarseness	-0.42	
$\log_{10}(\text{fine POM biomass} + 1)$	+0.66	-0.26
$\log_{10}(\text{coarse POM biomass} + 1)$	+0.72	-0.26

Note: For the abundance of numerically dominant taxa, only significant correlations (correlation coefficients >0.60) are shown for clarity. Numbers in parentheses denote relative abundance of each taxon based on all samples pooled. POM, particulate organic matter.

Fig. 4. Biplots of the principal components (PC) 1 and 2 based on the abundance of the taxa that comprised greater than 1% of total abundance based on all samples collected in this study. Means ($\pm 95\%$ confidence intervals) are shown for each sampling occasion. Solid, open, and hatched circles represent reference reaches 1 and 2 and the treatment reach, respectively. The directions of arrows denote the directional change from 1999 to 2000.



the May sampling occasion when organic matter biomass had strongest additive effects on and explained the highest variability of total macroinvertebrate abundance. Richardson (1991) tested food limitation by supplementation of CPOM, i.e., whole leaves of red alder and vine maple, whereas this study found the relationship between FPOM and macroinvertebrate productivity. A major difference between these two studies was that taxa such as *Despaxia augusta* and *Paraleptophlebia* were not found to be responsive to food supplementation in the former study, whereas those two taxa were among the numerically dominant and the ones most responsive to increased benthic detritus storage. One possible explanation is that these taxa have benefited from feeding on fine organic materials. Early summer is an important growing season for early instars of some detritivorous macroinvertebrates (Richardson 2001). During summer when leaf litter input is minimal, fine organic matter that mostly derives from autumn litter falls is still continuously

exported and transported owing to flash-out associated with occasional floods and gradual decomposition. Our finding emphasizes the importance of retentive structures even in spring and early summer as spatial and temporal distribution and availability of fine organic matter may bottleneck long-term macroinvertebrate productivity.

Habitat characteristics, organic matter biomass, and total abundance of macroinvertebrates remained relatively unchanged in reference reaches on each sampling occasion during the study period, enhancing the validity of our inferences. However, the abundance of erosional taxa increased in reference reach 2 as well as in the treatment reach on the May occasion in 2000, as shown in the results of the PCA. We suspect that this pattern was due to the differences in year-to-year variation of habitat-patch-specific community responses. After boulder placement, the treatment reach became more similar to reference reach 2 in terms of habitat structure as the areal extent of fast-flow habitat increased within the channel. In contrast, reference reach 1 was characterized more by slow-flow habitat. Different types of habitat patches can result in different responses of macroinvertebrates among seasons and years (e.g., Benke et al. 1984). Although what caused such an annual variation among reaches remains unknown, this pattern might have been caused by factors that are particularly influential to erosional taxa.

Contrary to our prediction, the placement of boulder clusters had no significant impact on taxonomic richness. The year-to-year variation in number of taxa was high even in the reference reaches, and the number of taxa was not necessarily lowest in the treatment reach even before the treatment. Similar patterns were observed when the Shannon-Weiner diversity index was calculated instead. Furthermore, 70 taxa that were identified in this study appeared in samples from all reaches at least on one sampling occasion. These patterns might be attributable to the proximity of our study reaches, which were separated by less than 50 m. Macroinvertebrates continuously disperse through drifting for a long distance (Townsend and Hildrew 1976), and thus sampling of individuals that were in the process of downstream drift searching for resources could have caused the variability as well as similarity of species richness among the reaches. Furthermore, even after boulder placement and increased habitat heterogeneity, the limited source of colonizers at the spatial scale examined in our study might have kept taxonomic richness in a similar level. Our findings at least suggest that community parameters such as species richness and diversity index themselves may not serve as meaningful endpoints to measure the status of ecosystem-level processes at the scale of our study.

Proper identification of limiting factors to a certain target species or processes is crucial for successful restoration practices (Palmer et al. 1997). In our study, macroinvertebrate community productivity was largely determined by the presence of fine detritus rich habitat patches. Therefore, lifting the limiting factor, that is, increased detritus storage within the channel, resulted in higher total macroinvertebrate abundance at the stream-reach scale. A variety of limiting habitats such as moss-covered habitat in Finnish streams (Muotka and Laasonen 2002) and snag habitat in sandy-bottomed streams of southeastern U.S.A. (Benke et al. 1984) has been found to exert important influences on macroinvertebrate

productivity and trophic dynamics. However, we stress that stream restoration involving in-stream structures should be planned in the context of large-scale natural processes that have produced such key habitat features rather than creation of such habitat patches as building blocks anticipating their net effects. Geomorphic characteristics of stream channels largely determine the distribution and form of physical habitat units within a stream channel (Brussock et al. 1985), geomorphic characteristics themselves being largely determined by larger-scale geology, watershed vegetation, lithology and flow regime, and local climate. Mere creation of habitat blocks without attention to large-scale processes can only provide short-term benefit and often is not feasible. In our case, for example, unless continuous supply of detritus and large organic debris that potentially could replace the function provided by boulder clusters in the future is maintained by appropriate management of upstream forested areas, there is little point in placing in-stream structures. Our findings suggest that the placement of boulder clusters can be used at least as a temporary remedy to restore productivity of macroinvertebrates in detritus-based stream systems. However, how these boulder structures will influence habitat characteristics and macroinvertebrate communities in the long run remains unknown.

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