BOREAL ENVIRONMENT RESEARCH 8: 19–30 ISSN 1239-6095
Helsinki 25 March 2003 © 2003

Distribution of benthic macroinvertebrates and leaf litter in relation to streambed retentivity: implications for headwater stream restoration

Antti Haapala[1], Timo Muotka[2] and Pekka Laasonen[2]

[1] *Kymijoen vesi ja ympäristö ry., Tapiontie 2, FIN-45160 Kouvola, Finland; Present address: North Savo Regional Environment Centre, P.O. Box 1049, FIN-70101 Kuopio, Finland (e-mail: antti.haapala@ymparisto.fi)*
[2] *Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland*

Haapala, A., Muotka, T. & Laasonen, P. 2003: Distribution of benthic macroinvertebrates and leaf litter in relation to streambed retentivity: implications for headwater stream restoration. *Boreal Env. Res.* 8: 19–30. ISSN 1239-6095

The distribution of leaf litter and benthic macroinvertebrates was studied in two boreal streams: a stream with a natural streambed (Merenoja), a channelized stream (Rutajoki), and the latter stream after its restoration. Leaf release experiments were performed to characterise the retentive structures of each stream. Benthic samples were collected from patches that retained artificial leaves (‘retention sites’) and from randomly located patches (‘random sites’). Retention sites contained significantly more benthic leaves than random sites in each stream, but the difference between patch types was most distinct in the channelized stream. Densities of shredders and other detritivores were distinctly higher in retention than in random sites in Rutajoki, both before and after restoration. In Merenoja, shredders were evenly distributed among the patch types. Restoration clearly increased the trapping efficiency of Rutajoki, but only slightly reduced the aggregation of detritivores to retentive stream patches. Our study highlights the importance of detritus aggregations for stream invertebrates, especially in channelized streams.

Introduction

The input of terrestrially-derived organic matter and its retention on the streambed are key processes shaping the invertebrate communities of woodland streams (e.g. Cummins *et al*. 1989). Exclusion of leaf litter input to a headwater stream can result in strong bottom-up effects propagating through detritivores to predatory invertebrates (Wallace *et al*. 1999). The elementary role of leaf retention to stream communities is previously documented in numerous studies

(Angermeier and Karr 1984, Smock *et al*. 1989, Dobson and Hildrew 1992). Streambed retention capacity to organic matter is greatly enhanced by debris dams (Bilby and Likens 1980, Smock *et al*. 1989), and addition of debris dams or other retentive structures to streambed has been suggested as a management tool for degraded headwater streams (e.g. Dobson *et al*. 1995, Riley and Fausch 1994, Sundbaum and Näslund 1998).

In headwater streams, leaves accumulating on retentive devices have a major influence on the abundance and distribution of detritivorous invertebrates (Prochazka *et al*. 1991, Dobson and Hildrew 1992). Richardson (1992) and Dobson *et al*. (1992) have shown that detritivores use leaf packs primarily as food rather than habitat. Predatory stoneflies also readily colonize leaf packs due mainly to the high densities of invertebrate prey they afford (Feminella and Stewart 1986, Malmqvist 1993).

Many streams and rivers throughout the world have been channelized for agricultural, flood protection or transportation purposes. Dredging of streams to facilitate log transport has been one of the major goals of channelization in Nordic countries and north-western Russia (Jutila 1992), as well as in the forested parts of northern USA and Canada (Sedell *et al*. 1991). Channelization results in homogenous stream channels with simplified flow patterns, longer spiralling distances and lower retention capacity (Petersen and Petersen 1991, Muotka and Laasonen 2002). Experiments manipulating leaf litter availability have shown that shredders in headwater streams may face seasonal food-limitation (Richardson 1991, Dobson and Hildrew 1992). Thus, detritivores in channelized streams might be severely food-limited, and their densities could be increased by enhancing the retention capacity of the streambed.

In this study, we tested whether the association of benthic macroinvertebrates with leaf accumulations varies between streams of contrasting retention properties, i.e. natural, channelized and restored streams. We hypothesized that in-stream habitat restoration should enhance the retentive capacity of a stream, and detritivores should be less dependent on the distribution of leaf packs after than before restoration. More specifically, we tested whether the abundances of detritivores and other invertebrates are higher in patches that retain leaves than in random patches of the same size, and whether differences among the patch types (retention vs. random) are more distinct in channelized than in restored and, especially, naturally retentive streams (*see* Dobson 1991).

Materials and methods

Study streams

This study was performed in two boreal streams, Merenoja and Rutajoki. They are woodland streams with contrasting rates of riparian litter input and retentive properties. Merenoja (66°N, 29°E) is a second-order stream in Oulanka National Park, northeastern Finland. The stream channel and its riparian zone have remained intact for at least 50 years. The stream has a relatively stable flow regime, with mean annual discharge of 0.40 $m^3 s^{-1}$ (range: 0.15–1.15 $m s^{-1}$). Merenoja is an oligotrophic (total P: 1–16 $\mu g l^{-1}$, total N: 112–726 $\mu g l^{-1}$), circumneutral (pH: 6.9–8.0) and mesohumic (water colour: 27–90 mg Pt l^{-1}) stream. The streambed is densely covered by aquatic vegetation, with the mosses *Fontinalis antipyretica* Hedw., *Hygroamblystegium fluviatile* (Hedw.) Loeske and *Brachythecium rivulare* Schimp. as the dominant species. Riparian vegetation is rather sparse, consisting of birch (*Betula pubescens* Ehrh., 50% of total cover), alder (*Alnus incana* L., 25%), Norway spruce (*Picea abies* L., 10%) and willows (*Salix* spp., 10%). The annual input of riparian CPOM (coarse particulate organic matter) is 62 g DM m^{-2}, of which 87% is deciduous leaf litter. The daily rate of litter fall reaches its maximum in September, when 65% of the annual litter input occurs within three weeks (T. Muotka, unpubl.).

Rutajoki (62°N, 26°E) is a third-order stream draining forested areas in central Finland. It is an oligotrophic (total P: 8–17 $\mu g l^{-1}$, total N: 330–610 $\mu g l^{-1}$), circumneutral (pH: 6.2–7.1) and mesohumic (water colour: 35–80 mg Pt l^{-1}) stream. It has a highly variable, yet predictable flow pattern: mean annual discharge is 1.22 $m^3 s^{-1}$, with a range of 0.40–4.61 $m^3 s^{-1}$. Peak flows, induced by spring snow melt, occur during a short period in mid-April through early May. During the summer months (June through late September), stream flow rarely exceeds 1.0 $m^3\ s^{-1}$ (Haapala and Muotka 1998). Aquatic vegetation is sparse, with *Fontinalis dalecarlica* Schimp. as the dominant species. The stream is bordered by dense riparian vegetation. The dominant species are birch (*Betula pendula* Roth, 75% of total cover), alder (15%), and willows (5%). The input of riparian CPOM is 310 g AFDM m^{-2} $year^{-1}$, 87% of which is deciduous leaf litter. The daily rate of litter fall reaches its maximum in late September, and 75% of litter input occurs within four weeks in September–October (Haapala and Muotka 1998).

Riffle sections of Rutajoki were channelized several times during the first half of the 20th century. Channelization involved removal of all major flow obstructions (large boulders, large woody debris, etc.) from the streambed, resulting in a simplified, almost debris-free channel. The stream was channelized primarily to facilitate log transport, which was ceased in the early 1950s. The stream was restored to its pre-channelization, near-natural state in October 1997. Restoration was mainly for fishery purposes, and it involved installation of boulders, boulder dams, flow deflectors and other in-stream structures (for structures commonly used for stream habitat enhancement in Finland, *see* Yrjänä 1998). Only stones were used for restoration, and no large woody debris was added to the streambed; thus, even after restoration, the stream channel contained few debris dams. Boulders were removed from the stream bank and placed into the channel bed using a bulldozer. Pebble-to-cobble sized stones were used to create nursery habitats for juvenile salmonids, and coarse gravel to create spawning grounds for adult fish.

Characterization of the stream habitat

To characterise the in-stream habitat structure, 20 cross-sectional transects were placed in 2.5-m intervals within each study section. In each transect, measurements of water depth, flow rate (at 0.6 × depth) and stone size (largest diameter) were made in 1-m intervals. We also estimated the percent cover of aquatic mosses in three regularly spaced 0.1 m^2 quadrats along each of the 20 transects. We measured streambed roughness using a bed profiler modified from that described by Young (1993) (length of plate: 1 m, height of pins: 50 cm, number of pins: 40). The profiler was placed tightly against the stream bottom, and the length of each pin below the plate was then measured. We made three successive profiles to obtain a 3-m long longitudinal transect; four such transects were made in each study stream. Mean roughness height (k) (*see* Young 1993) was used to calculate the relative bed roughness (k/D), an indicator of streambed complexity at a scale relevant to most benthic organisms (Davis and Barmuta 1989).

Description of leaf retention sites

We used leaf release experiments to locate and characterise the retentive structures present in each stream type. To facilitate the location of leaves on the streambed, we used strips of slowly-sinking plastic, cut to the approximate length of natural leaves. These are known to behave much like natural leaves during normal flows (Speaker *et al*. 1988), and we therefore performed the release experiments at base flow conditions in both streams (ca. 0.90 $m^3\ s^{-1}$ in Rutajoki, 0.40 $m^3\ s^{-1}$ in Merenoja). In Rutajoki, a similar experiment was conducted both before (October 1996) and after (November 1997) the stream was restored. In Merenoja, the experiment was conducted only once, in October 1996. We selected a 50-m long riffle section, representative of bed conditions in both streams, for the experiment. In Rutajoki, the same section was used on both occasions. A block net was stretched across the stream at the downstream end of the study reach. We then released 1000 plastic leaves (8 × 4 cm) on the water surface at the upstream end of the reach and, after three hours, we located and described all retention sites (i.e. sites that had trapped leaves) within the study section. Retentive structures were divided into: (i) boulders and other stones, (ii) woody debris (mainly twigs and small branches less than 2 cm in diameter), (iii) stream bank, (iv) aquatic vegetation, or (v) backwater or side-channel.

Benthic sampling

Immediately after the leaf release experiments, we collected samples of benthic macroinvertebrates in each stream. Our goal was to test whether patches that retained leaves also contained the greatest numbers of benthic invertebrates, especially detritivorous taxa. This was done by collecting benthic samples from patches that retained leaves (hereafter, retention sites) and from randomly selected patches (random sites), taking 25 samples from each patch type. Random samples were taken from five transects perpendicular to the flow, each containing four to six randomly positioned samples. Retention sites were selected randomly from the sites that had retained leaves in the release experiment. Both sets of samples were taken from the same 50-m long sample reach. A Surber sampler (20 × 20 cm, mesh size 0.25 mm) was used for all benthic sampling. All organic material and stones, if any, were removed to a depth of 10 cm, and included in the sample. Samples were preserved in 70% ethanol in the field, and macroinvertebrates and detritus were later sorted in the laboratory. Leaves and leaf fragments larger than 10 mm were oven dried at 60 °C for 24 h and weighed to obtain their dry masses. Macroinvertebrates were identified (mainly to species or genus level) and assigned to functional feeding groups according to Malmqvist *et al*. (1978) and Merritt and Cummins (1978). Chironomids were divided into three feeding groups: filterers (mainly *Rheotanytarsus* spp.), collector-gatherers (Orthocladiinae) and predators (Tanypodinae) (*see* Wiederholm 1983, Chauvet *et al*. 1993). In the graphical and statistical output, collector-gatherers and shredders will occasionally be presented as a collective group of 'detritivores', emphasizing the trophic role of these groups as detritus-feeding invertebrates.

Statistical analyses

We first tested for differences in the mass of benthic leaves and densities of macroinvertebrates in random vs. retention sites using independent sample t-tests, separately for each stream type. Next, we examined the distribution patterns of various groups of macroinvertebrates (total benthos, detritivores and *Nemoura* spp. stonefly nymphs) in each stream. For this, we used Morisita's index (I_δ; Elliott 1977), which is based on an analysis of the proportion of the total number of organisms found in each replicate sample. Its value ranges between $1 - [(n - 1)/\Sigma x - 1)]$ for maximum regularity and n when all individuals are in the same sample unit, indicating maximum aggregation (Σx = the sum of individuals found in all replicates, n = number of sample units). Values close to 1.0 indicate random distribution. The test criterion $I_\delta(\Sigma x - 1) + n - \Sigma x$, which is χ^2 distributed (Elliott 1977), was used to test whether the observed degree of aggregation was significantly higher than in a randomly distributed population. We chose this index because it is interpretable in a straightforward and biologically meaningful way, and because, unlike many other dispersion indices, it is relatively independent of population density (Hurlbert 1990, Downing 1991). Only the random site samples were included in the calculation of this index.

Finally, we used regression analysis to examine the relationships between leaf litter and animal densities in benthic samples (only random sites included). All variables were $\ln(x + 1)$-transformed to reduce skewness and heteroscedasticity of the data. Analysis of covariance was used to test for homogeneity of the regression slopes of the streams; lack of homogeneity would indicate differences in leaf litter–macroinvertebrate relationships among the streams. In case of a significant overall difference, t-tests were used to compare slopes between each pair of streams (Zar 1996).

Results

Habitat characteristics

As a result of restoration, streambed complexity of Rutajoki increased considerably, which was indicated by the high post-restoration bed roughness value. In fact, substratum became almost as heterogeneous in the restored as in the natural stream (Table 1). Other restoration-induced changes in habitat structure included widening of the stream channel, with lower water velocities and decreased moss cover after than before restoration.

Retention of artificial leaves

The natural stream, Merenoja, retained 76% of the 1000 leaves released, whereas the respective section of Rutajoki retained 25% before and 75% after its restoration. The most effective retentive feature in Merenoja was the stream bank, whereas cobbles and boulders trapped most leaves in the channelized Rutajoki, followed by woody debris (Table 2). After restoration, the role of woody debris became even more prominent in Rutajoki. Aquatic vegetation (mainly *Fontinalis* spp.) was an important retentive structure in Merenoja, but not in Rutajoki, where the average moss cover was low both before and after restoration (*see* Table 1).

Standing crop of leaf litter in random vs. retention sites

The biomass of leaf detritus was distinctly higher in retention sites than in random sites in all streams (Fig. 1). The difference between the patch types was least abrupt in the natural stream, whereas it was greatest in Rutajoki before restoration: here, the leaf biomass was 28 times higher in the retention than in random sites. After restoration, the standing crop of leaf CPOM was overall considerably higher (Fig. 1), with retention sites supporting roughly an order of magnitude more leaf biomass than the random sites. This difference between the sample types, albeit smaller than before restoration, was still significant.

Invertebrate densities in random vs. retention sites

Total macroinvertebrate densities tended to be higher in retention than in random sites in all streams, although the difference was not significant for Merenoja. In Rutajoki, densities in retention sites were roughly twice as high as in random sites, both before and after restoration (Fig. 2A). Highest macroinvertebrate densities, exceeding 500 individuals 0.04 m^{-2}, were found in retention sites of Rutajoki after restoration.

In Rutajoki, both before and after restoration, densities of detritivores were significantly higher in retention sites, whereas in Merenoja the difference between the patch types was non-significant (Fig. 2B). Shredder densities differed significantly between the patch types in Rutajoki, both before and after restoration, but not in Merenoja, which supported the highest overall densities of shredders (Fig. 2C). Densi-

Table 1. Physical characteristics of the study streams. Relative bed roughness is expressed as *k*/*D* (substrate roughness/depth; *see* Davis and Barmuta 1989).

	Depth (m)	Width (m)	Flow rate ($m\ s^{-1}$)	Relative bed roughness (cm)	Stone size (%)	Moss cover (%)	Canopy cover	Litter input (g AFDM $m^{-2}\ y^{-1}$)
Merenoja	0.26	4.5	0.31	0.44	36	60	35	62
Rutajoki channelized	0.35	5.0	0.62	0.11	34	10	60	310
Rutajoki restored	0.38	5.9	0.31	0.39	38	3	64	–

– = no data available

Table 2. Percentages of leaves retained by various habitat features in the study streams.

	Woody debris	Stones	Stream bank	Backwater	Aquatic vegetation
Merenoja	18.5	19.7	41.3	0	20.4
Rutajoki, channelized	43.6	49.5	6.9	0	0
Rutajoki, restored	52.6	39.8	7.0	0.6	0

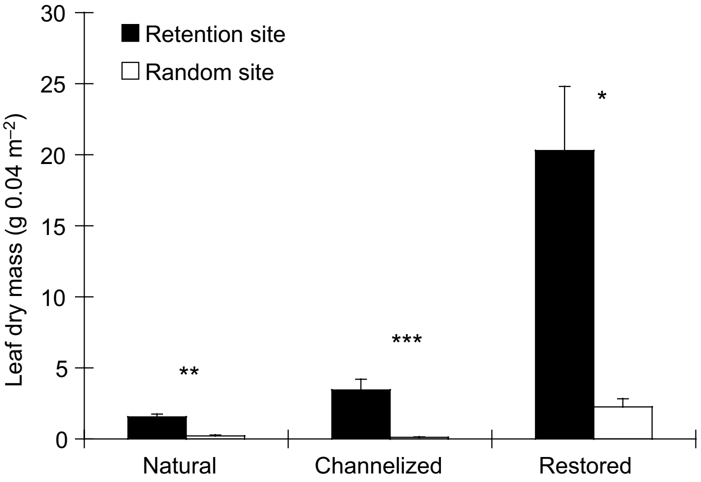

Fig. 1. Average dry weights of the leaf CPOM in Merenoja (natural stream), and in Rutajoki before (channelized stream) and after (restored stream) stream habitat restoration. $N = 25$ for both types of samples in each stream. Error bars represent one standard error of the mean. Asterisks indicate significant differences between the retention and random sites for each stream (Student's *t*-test, $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$).

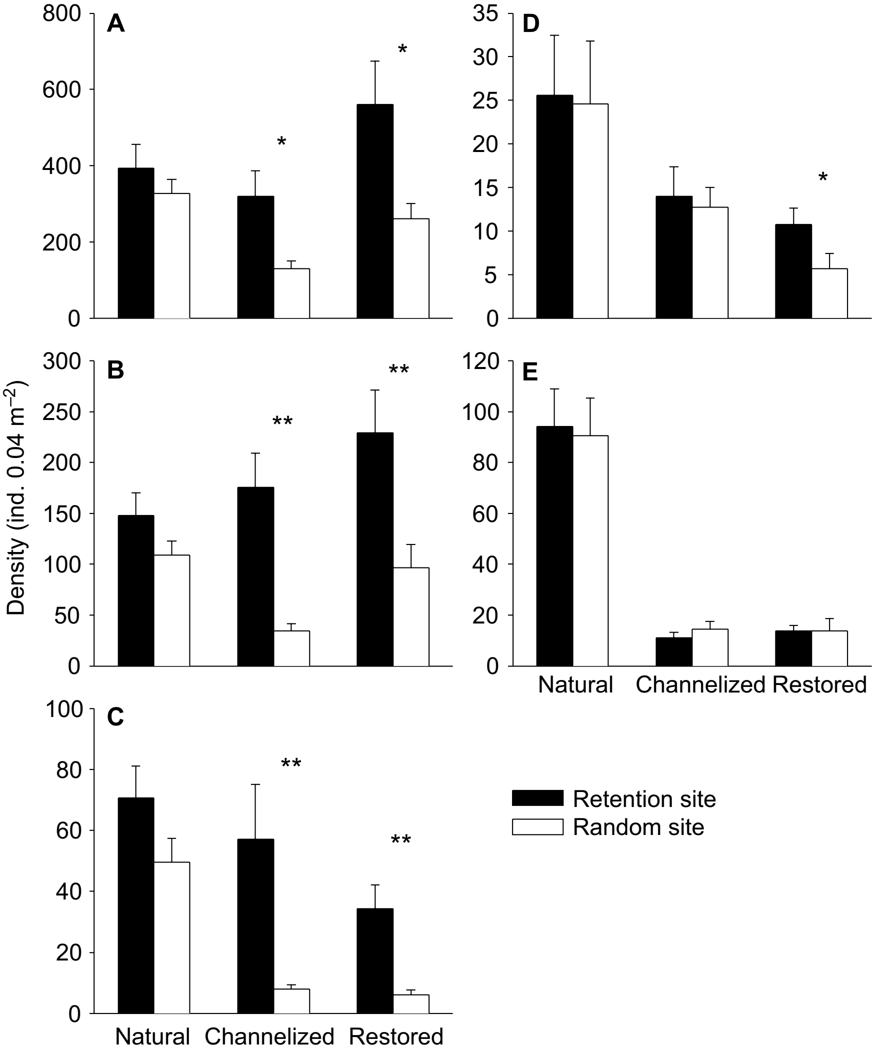

Fig. 2. Mean densities of (**A**) total macroinvertebrates, (**B**) detritivores, and (**C**) shredders, (**D**) predators and (**E**) scrapers in the natural, channelized and restored stream. $N = 25$ for both types of samples in each stream. Error bars represent one standard error of the mean. Asterisks indicate significant differences between the retention (black bars) and random sites (open bars) for each stream.

ties of predatory (Fig. 2D) and algae-scraping (Fig. 2E; mainly *Baetis* spp. mayfly nymphs in both streams) invertebrates differed little among the patch types in any of the streams, the only exception being higher densities of predators in retention sites in Rutajoki after restoration.

The chironomid subfamily Orthocladiinae was the numerically dominant detritivore in both streams, accounting for 80%–92% of the group in Rutajoki and 31% in Merenoja. Densities of Orthocladiinae were significantly higher in retention than in random sites in Rutajoki, but not in Merenoja (Fig. 3A). Nemouridae stoneflies (mainly *Nemoura cinerea* (Retzius) in Rutajoki, and *N. cinerea*, *Protonemura intricata* (Ris) and *Amphinemura borealis* (Morton) in Merenoja) were the dominant shredders in Merenoja, and in Rutajoki before restoration. After restoration, limnephilid caddis larvae (mainly *Potamophylax cingulatus* (Stephens)) were about as abundant as *Nemoura* in Rutajoki. Differences between retention and random sites in densities of these two shredder taxa were significant in all comparisons (Fig. 3B and C).

Distribution patterns of benthic invertebrates

Both the total benthos and detritivores, as well as *Nemoura* spp. stoneflies, exhibited a strongly aggregated distribution pattern in all streams (Table 3). In all cases, the χ^2 distributed test criterion for Morisita's index (*see* Elliott 1977) indicated a significantly ($P < 0.001$) more aggregated distribution pattern than expected for a randomly distributed population. Interestingly, however, total invertebrates tended to be most aggregated in the channelized, and least so in the natural stream. *Nemoura* stoneflies were an exception to this pattern, being least aggregated in Rutajoki after restoration.

Table 3. Distribution patterns of total invertebrates, detritivores and *Nemoura* spp. stonefly nymphs in the study streams, as indicated by Morisita's index of dispersion. The index equals one for a randomly distributed population and values greater than one indicate contiguous distribution.

	Stream type		
	Natural	Channelized	Restored
Total invertebrates	1.43	2.40	2.06
Detritivores	1.43	2.79	2.13
Nemoura spp.	5.32	6.38	4.28

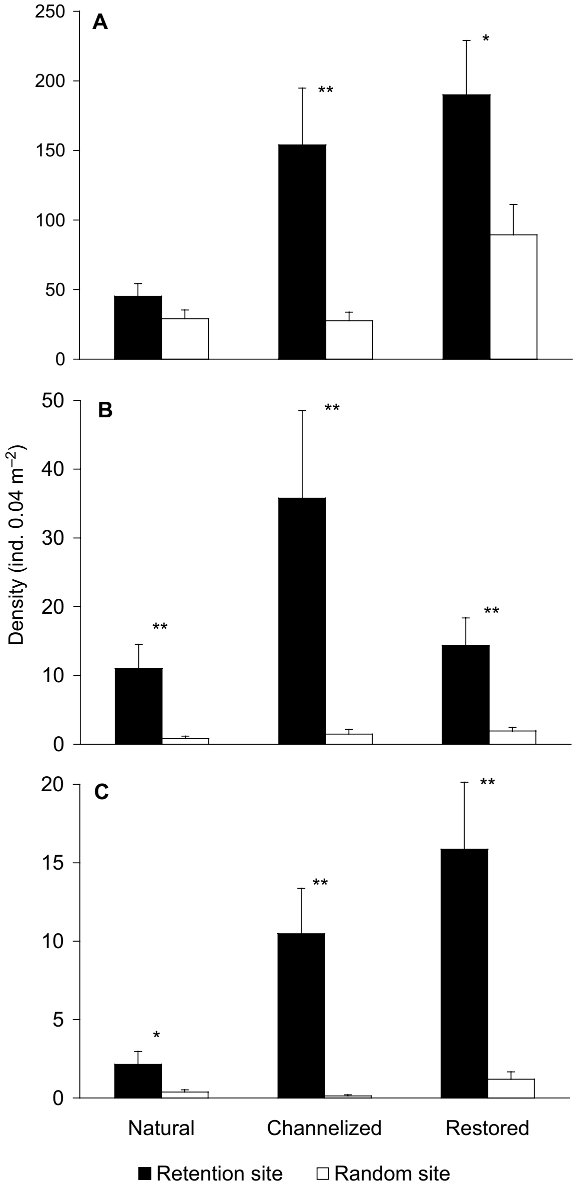

Fig. 3. Mean densities of (**A**) Orthocladiinae midge larvae (**B**) *Nemoura* spp. stonefly nymphs and (**C**) Limnephilidae caddis larvae in the natural, channelized and restored stream. Error bars, number of samples and symbols as in Fig. 2.

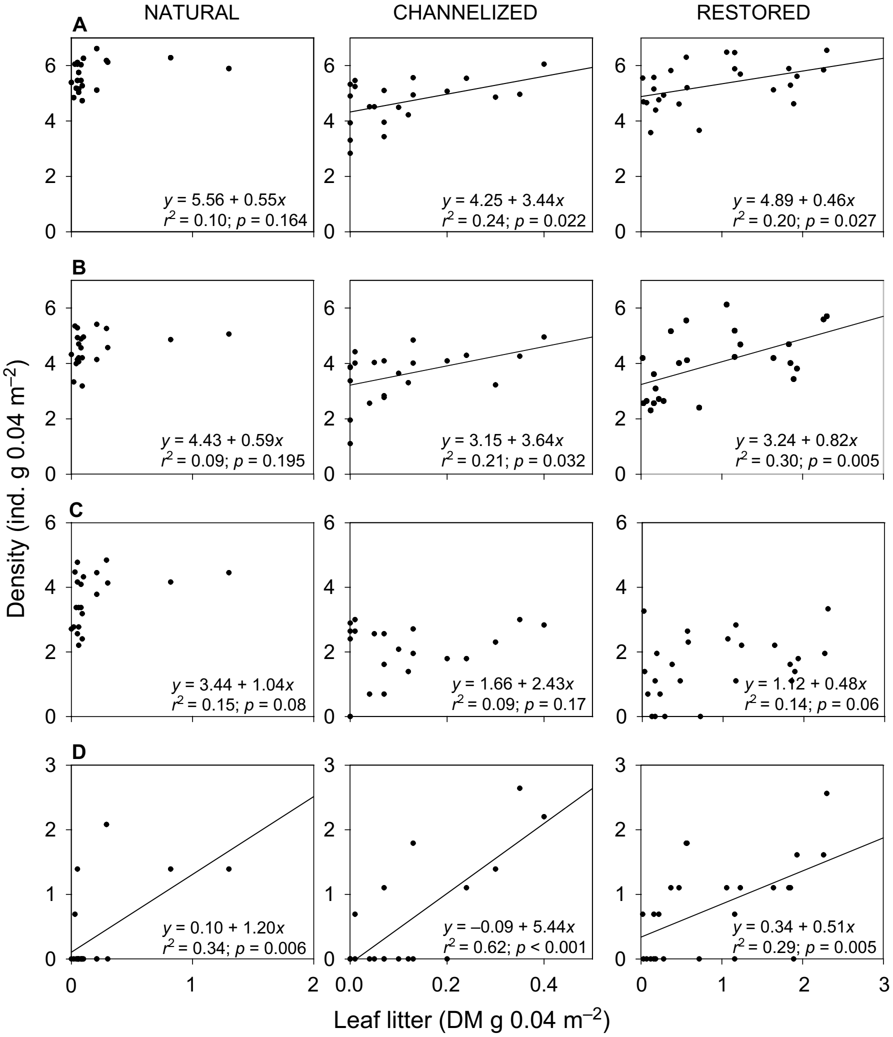

Fig. 4. Relationship between leaf litter and densities of (**A**) total macroinvertebrates, (**B**) detritivores, (**C**) shredders, and (**D**) *Nemoura* spp. stonefly nymphs in the study streams. Regression lines are drawn only when there is a significant fit among the two variables.

Associations between leaf detritus and benthic animals: regression analysis

Dry mass of leaf CPOM was a relatively good predictor of both total and detritivorous macroinvertebrate densities in Rutajoki, both before and after restoration. By contrast, the relationships between leaf dry mass and densities of all macroinvertebrates, and of detritivores, were non-significant for the stream Merenoja (Fig. 4A and B).

The relationship between leaf CPOM and shredder density was non-significant for all streams (Fig. 4C). However, the dominant shredder taxon, *Nemoura* spp., displayed a linear positive relationship to the amount of benthic leaves in all streams (Fig. 4D). In pre-restoration samples from Rutajoki, leaf mass accounted for as much as 62% of variation in nemourid density. Analysis of covariance indicated significant differences among the slopes of the regression lines for the three streams ($F_{2,69} = 11.92$; $P < 0.001$). The slope for the channelized Rutajoki was significantly steeper than that for Merenoja ($t = 5.48$; $P < 0.001$) and Rutajoki after restoration ($t_{1,46} = 6.37$; $P < 0.001$). By contrast, slopes for Merenoja and Rutajoki after restoration did not differ ($t_{1,46} = 0.84$, $P = 0.42$). Shredders other than nemourids were not correlated with the leaf CPOM. For example, leaf litter accounted for only 6%–14% of variation in densities of limnephilid caddis larvae in the study streams.

Discussion

Overall, our results coincide well with those of Dobson and Hildrew (1992) for four southern English streams with contrasting retentivity. Numbers of shredding invertebrates were higher in the stream Merenoja, whereas association of detritivores with leaf packs was more distinct in the less retentive Rutajoki. In poorly retentive streams, shredders are strongly dependent on few, sparsely distributed leaf packs, while in more retentive streams the amount of leaves is not the prime determinant of shredder distribution (Dobson 1991). Restoration of Rutajoki did not reduce the dependence of detritivores on leaf packs: after restoration, densities of most detritivorous taxa were still higher in retentive than in random patches, although less distinctly so. This relatively minor change occurred regardless of the fact that the retentive capacity of the stream was clearly enhanced by restoration. These observations have two important implications.

First, the lack of aggregation by most detritivores to retentive patches in Merenoja suggests that these invertebrates may be less limited by the number of leaf-packs in natural than in channelized or recently restored streams. There was, however, taxon-specific variation in this regard: nemourid stoneflies and limnephilid caddis larvae were strongly associated with retentive structures in all study streams. It is also important to notice that our experiments were conducted in late autumn when the amount of leaves on the streambed reaches its annual maximum, and any food limitation is probably least likely to occur then. It is quite possible that detritivores are seasonally food-limited even in natural woodland streams, but any food shortage should not occur until late spring when the stock of benthic leaves becomes rapidly exhausted (Richardson 1991, *see* also Malmqvist and Oberle 1995, Haapala and Muotka 1998).

Second, the unexpectedly slight change in the distribution of detritivores after restoration may relate to the fact that post-restoration samples were taken only one month after restoration. The recovery period may have been too short for invertebrates to respond to alterations in habitat structure and resource distribution. However, we do not consider this a likely explanation, because stream biota is known to be highly responsive to resource alterations. For example, Dobson and Hildrew (1992) reported that shredding invertebrates responded very rapidly (within a few months) to increased resource availability in three low order streams in southern England. It thus seems likely that the enhancement of streambed retentivity did not release detritivores from potential resource limitation in Rutajoki, as indicated by the strongly aggregated distribution of detritivores even after restoration. Clearly, restoration did increase the trapping efficiency of the streambed, and it is quite possible that, in the long run, the increased resource availability caused by restoration might translate to higher densities of detritivores. However, any demographic responses due to increased fecundity would not be observable until next autumn (*see* Dobson and Hildrew 1992).

The most important retentive feature in Rutajoki after restoration was small woody debris, i.e. branches of alder and birch that dropped from the overhanging canopy during storms and became trapped among the stony enhancement structures. It may thus appear that the mere use of stones for stream habitat enhancement does not adequately increase the retentive capacity of channelized woodland streams, but that additional enhancement structures, especially woody debris, are needed for effective management of these streams (*see* also Maridet *et al*. 1995). It must be emphasized that the main goal of restoration of Rutajoki was to enhance its trout production, and responses by other stream biota were given little consideration when the project was planned. Since retentivity to organic matter inputs is a key factor regulating headwater stream ecosystems, any habitat modification that alters the retentive characteristics of the streambed may have far-reaching effects on the trophic structure of the community, including fish. Thus, we wish to reiterate Dobson *et al*.'s (1995) plea for the use of small retention devices to enhance the retentive capacity and invertebrate production of headwater streams. Another option might be to use moss transplants, since aquatic mosses are known to be important retentive structures in many boreal forest streams (e.g. Vuori and Joensuu 1996, Muotka and Laasonen 2002). Our study suggests that, with proper design, stream restoration practices enhancing bed retentivity may indeed have strong bottom-up effects on populations of detritivorous invertebrates. These impacts may then propagate further up in lotic food webs (*see* Wallace *et al.* 1999), with a potential of increasing the production of stream fishes.

Highly retentive patches are good microhabitats for benthic invertebrates, due to the combined effects of food availability and shelter from floods and predation. Lancaster and Hildrew (1993, *see* also Winterbottom *et al.* 1997) have shown that some microhabitats may function as hydraulic refugia where environmental conditions remain essentially unaltered even during peak discharges. Macroinvertebrates accumulate in these patches during floods, and use them as centers for recolonization after disturbance. Lancaster and Hildrew (1993) showed also that although these patches contain high abundance of leaves at all discharges, many invertebrates colonize them only during floods. Nevertheless, Dobson *et al.* (1992) measured hydraulic conditions near leaf-trapping obstacles and found only slight evidence of reduced shear stress. They concluded that detritivores exploit leaf litter primarily as food rather than habitat (*see* also Richardson 1992). While our study was not designed to test the importance of leaf packs as food vs. microhabitat, it does provide indirect support to Dobson *et al.*'s (1992) and Richardson's (1992) views. Highly retentive patches contained more detritivores than did random patches, especially in Rutajoki, whereas densities of other invertebrates differed little (predators) or not at all (scrapers) among the two patch types. It thus appears that detritivores aggregate to retentive patches primarily for the food (i.e. leaves) they afford, whereas their role as microhabitat is probably less important. It must be noted, however, that our experiments were conducted at base flow conditions, and at higher flows retentive patches could well serve as flow refugia to invertebrates (*see* Winterbottom *et al.* 1997).

Somewhat surprisingly, we found that although the retention efficiencies of the natural and the restored stream were almost equal (76% and 75%, respectively), the amount of benthic leaf litter was an order of magnitude higher in both random and retention sites in the restored stream. Even the channelized stream with its poor retention efficiency (25%) contained as much leaf litter as did the natural stream. Since leaf input and standing crop of benthic CPOM are often positively correlated (Cummins *et al.* 1989, Stewart and Davies 1990, Grubbs and Cummins 1996), this unexpected result was probably caused by notably different rates of riparian litter input in the two streams. Input was five fold higher in Rutajoki, and the higher retention capacity of the natural stream did not fully offset this difference. Merenoja is bordered by a much sparser canopy than Rutajoki, and the riparian trees in this northern boreal stream are smaller than those in Rutajoki (*see* also Malmqvist and Oberle 1995). It thus appears that factors limiting populations of detritivorous invertebrates are different in natural and channelized woodland streams. Pristine forest streams in northern areas appear to be limited more by litter input than by streambed retentivity, whereas the opposite may be true for channelized streams. It must be borne in mind, however, that the streams compared in this study differ in many respects other than streambed restoration. Many of these factors (e.g. stream size, land use history, litter input, moss cover) potentially affect the availability of detritus to benthic consumers, making any conclusions based on these data tentative. These ideas should therefore be treated as hypotheses awaiting rigorous experimental testing, not as broad generalizations.

Acknowledgements: Funding for this study was provided by the Academy of Finland (grant SA/35586 to TM). We thank Niina Kautto, Kai Korsu, Heikki Mykrä, Martti Niskanen and Mikko Paavilainen for their assistance in the field and laboratory. David Wilson provided helpful comments on a previous version of the manuscript. This is a contribution from the Finnish National Graduate School on Environmental Ecology, Ecotoxicology and Ecotechnology.

References

Angermeier P.L. & Karr J.R. 1984. Relationship between woody debris and fish habitat in a small warmwater stream. *Trans. Am. Fish. Soc.* 113: 716–726.

Bilby R.E. & Likens G.E. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61: 1107–1113.

Chauvet E., Giani N. & Gessner M.O. 1993. Breakdown and invertebrate colonization of leaf litter in two contrasting streams: significance of Oligochaetes in a large river. *Can. J. Fish. aquat. Sci.* 50: 488–494.

Cummins K.W., Wilzbach M.A., Gates D.M., Perry J.B. & Taliaferro W.B. 1989. Shredders and riparian vegetation. *Bioscience* 39: 24–30.

Davis J.A. & Barmuta L.A. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwat. Biol.* 21: 271–282.

Dobson M. 1991. An assessment of mesh bags and plastic leaf traps as tools for studying macroinvertebrate assemblages in natural leaf packs. *Hydrobiologia* 222: 19–28.

Dobson M. & Hildrew A.G. 1992. A test of resource limitation among shredding detritivores in low order streams in southern England. *J. Anim. Ecol.* 61: 69–78.

Dobson M., Hildrew A.G., Ibbotson A. & Garthwaite J. 1992. Enhancing litter retention in streams: do altered hydraulics and habitat area confound field experiments? *Freshwat. Biol.* 28: 71–79.

Dobson M., Hildrew A.G., Orton S. & Ormerod S.J. 1995. Increasing litter retention in moorland streams: ecological and management aspects of a field experiment. *Freshwat. Biol.* 33: 325–337.

Downing J.A. 1991. Biological heterogeneity in aquatic ecosystems. In: Kolasa J. & Pickett S.T.A. (eds.), *Ecological heterogeneity,* Springer-Verlag, New York, pp. 160–180.

Elliott J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwater Biological Association, Scientific Publication* 25.

Feminella J.W. & Stewart K.W. 1986. Diet and predation by three leaf-associated stoneflies (Plecoptera) in an Arkansas mountain stream. *Freshwat. Biol.* 16: 521–538.

Grubbs S.A. & Cummins K.W. 1996. Linkages between riparian forest composition and shredder voltinism. *Arch. Hydrobiol.* 137: 39–58.

Haapala A. & Muotka T. 1998. Seasonal dynamics of detritus and associated macroinvertebrates in a channelized boreal stream. *Arch. Hydrobiol.* 142: 171–189.

Hurlbert S.H. 1990. Spatial distribution of the montane unicorn. *Oikos* 58: 257–271.

Jutila E. 1992. Restoration of salmonid rivers in Finland. In: Boon P.J., Calow P. & Petts G.E. (eds.), *River conservation and management.* Wiley & Sons Ltd, Chichester, pp. 353–362.

Lancaster J.L. & Hildrew A.G. 1993. Flow refugia and the microdistribution of lotic invertebrates. *J. N. am. Benthol. Soc.* 12: 385–393.

Malmqvist B. 1993. Interactions in stream leaf packs: effects of a stonefly predator on detritivores and organic matter processing. *Oikos* 66: 454–462.

Malmqvist B. & Oberle D. 1995. Macroinvertebrate effects of leaf pack decomposition in a lake outlet stream in Northern Sweden. *Nord. J. Freshw. Res.* 70: 12–20.

Malmqvist B., Nilsson L.M. & Svensson B.S. 1978. Dynamics of detritus in a small stream in southern Sweden and its influence on the distribution of the bottom animal communities. *Oikos* 31: 3–16.

Maridet L., Wasson J.G., Philippe, J.M. & Amoros C. 1995. Benthic organic matter dynamics in three streams: riparian vegetation or bed morphology control? *Arch. Hydrobiol.* 132: 415–425.

Merritt R.W. & Cummins K.W. (eds.) 1978. *An introduction to the aquatic insects of North America.* Kendall/Hunt, Dubuque, Iowa.

Muotka T. & Laasonen P. 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. *J. Appl. Ecol.* 39: 145–156.

Petersen L.B.M. & Petersen R.C. 1991. Short term retention properties of channelized and natural streams. *Verh. int. Ver. Limnol.* 24: 1756–1759.

Prochazka K., Stewart B.A. & Davies B.R. 1991. Leaf litter retention and its implications for shredder distribution in two headwater streams. *Arch. Hydrobiol.* 120: 315–325.

Richardson J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 73: 873–887.

Richardson J.S. 1992. Food, microhabitat or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwat. Biol.* 27: 169–176.

Riley S.C. & Fausch K.D. 1994. Trout population response to habitat enhancement in six northern Colorado streams. *Can. J. Fish. Aquat. Sci.* 52: 34–53.

Sedell J.R., Leone F.N. & Duval W.S. 1991. Water transportation and storage of logs. In: Meehan W.R. (ed.), Influences of forest and rangeland management on salmonid fishes and their habitats. *Am. Fish. Soc. Spec. Publ.* 19: 325–368.

Smock L.A., Metzler G.M. & Gladden J.E. 1989: Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* 70: 764–775.

Speaker R.W., Luchessa K.J., Franklin J.F. & Gregory S.V. 1988. The use of plastic strips to measure leaf retention by riparian vegetation in a coastal Oregon streams. *Am. Midl. Nat.* 120: 22–31.

Stewart B.A. & Davies B.R. 1990. Allochthonous input and retention in a small mountain stream, South Africa. *Hydrobiologia* 202: 135–146.

Sundbaum K. & Näslund I. 1998. Effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. *Can. J. Zool.* 76: 56–61.

Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. 1999. Multiple levels of a forest stream linked to terrestrial litter inputs. *Ecol. Monographs* 277: 102–104.

Wiederholm T. 1983. *Chironomidae of the Holarctic region. Keys and diagnoses.* Part 1. Larvae. *Entomologica Scandinavica.* Supplement, 19. Borgströms Tryckeri AB, Motala.

Winterbottom J.H., Orton S.E. & Hildrew A.G. 1997.

Field experiments on the mobility of benthic invertebrates in a southern English stream. *Freshwat. Biol.* 38: 37–47.

Vuori K.-M. & Joensuu I. 1996. Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: do buffer zones protect lotic biodiversity? *Biol. Conserv.* 77: 87–95.

Young W.J. 1993. Field techniques for the classification of near-bed flow regimes. *Freshwat. Biol.* 29: 337–383.

Yrjänä T. 1998. Efforts for instream fish habitat restoration within the river Iijoki, Finland — goals, methods and test results. In: Waal L., Large A.R.G. & Wade M. (eds.), *Rehabilitation of rivers*, John Wiley, Chichester, pp. 239–250.

Zar J.H. 1996. *Biostatistical analysis*. Third edition. Prentice Hall, New Jersey. 662 pp.

Received 20 August 2001, accepted 15 May 2002