

Pekka Laasonen

The Effects of Stream Habitat
Restoration on Benthic Communities
in Boreal Headwater Streams



UNIVERSITY OF JYVÄSKYLÄ

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ABSTRACT

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Diss.

The changes in stream benthic communities after restoration of channelized rivers was studied in northern headwater streams. More specifically, this thesis concentrates on the effects of restoration on short and long term changes in macroinvertebrate communities, habitat characteristics and coarse particulate organic matter (CPOM) retention in headwater streams.

Restoration clearly increased the stream bed roughness and heterogeneity of the flow regime but not enough to mimic natural rivers effectively. Rivers were still, after restoration, characterized by too fast flows and deep waters. The CPOM retention capacity increases but not enough to reach the level of natural rivers. The restoration process detached mosses from large areas of the stream bed, and the full recovery of mosses was observed to last over a decade.

As an immediate response to restoration disturbance, all abundant taxa were evenly reduced, thus leaving the structure of the benthic community essentially unchanged. The short-term recovery of stream macroinvertebrates after restoration was rapid, showing the great resilience of the stream biota. The long-term effects on macroinvertebrate communities were minor, even so small that they were hard to detect. The macroinvertebrate richness of natural rivers was not reached. The increased retention capacity of CPOM did not remove the resource limitation of detritus-feeding invertebrates.

The results of the restoration were not a great success ecologically. The restoration may have been the first step to the right direction by increasing the heterogeneity of the stream bed and the flow regime, but the macroinvertebrate richness and CPOM retention capacity of natural rivers were still not reached. I suggest that the following three key factors, (i) the loss of mosses, (ii) the absence of debris dams and (iii) insufficient heterogeneity of the stream bottom, which slow down the recovery process considerably, be given adequate consideration in order to restore our channelized rivers more effectively.

Key words: Aquatic mosses; benthic macroinvertebrates; boreal headwater streams; organic matter retention; stream habitat restoration.

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LIST OF ORIGINAL PUBLICATIONS

- I Tikkanen, P., Laasonen, P., Muotka, T., Huhta, A. & Kuusela, K. 1994. Short-term recovery of benthos following disturbance from stream habitat rehabilitation. *Hydrobiologia* 273: 121-130
- II Laasonen, P., Muotka, T. & Kivijärvi, I. 1998. Recovery of macroinvertebrate communities from stream habitat restoration. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 8: 101-113.
- III Haapala, A., Muotka, T. & Laasonen P. 2000. Distribution of benthic macroinvertebrates and leaf litter in relation to stream bed retentivity: implications for headwater stream management. Manuscript, submitted.
- IV Laasonen, P. & Muotka, T. 2000. Enhanced leaf retention as a mechanism of recovery in restored headwater streams. Manuscript, submitted.

In addition, the thesis Introduction contains previously unpublished material.

RESPONSIBILITIES OF PEKKA LAASONEN IN THE ARTICLES OF THIS THESIS

- I I participated in the study design and writing of the manuscript, and did most of the field and laboratory work and data analysis.
- II I was responsible for all phases of the study. I also wrote the first draft of the manuscript, which was then completed together with Timo Muotka.
- III All authors participated in the design of the study. I collected the field material, identified the invertebrates and analysed the data with Antti Haapala. I also participated in writing of the manuscript.
- IV I was responsible for all phases of the study. I also wrote the first draft of the manuscript, which was then completed together with Timo Muotka

1 INTRODUCTION

The restoration of rivers and streams has gained increasing general interest during the last two decades. Despite the great amount of literature describing local restoration projects, there is a general lack of scientific documentation that could help to identify ecological effects of restoration. Most studies that concern restoration projects and stream biota are focused on fish population responses or habitat hydraulics (e.g. Newbury & Gaboury 1993, Rabeni & Jacobsen 1993, Huusko & Yrjänä 1997). There are fewer publications concerning other biota like macroinvertebrates (but see Smith et al. 1990, Friberg et al. 1994, 1998, Görtz 1999) or plants (Biggs et al. 1998, Baattrup-Pedersen et al. 2000). In particular, monitoring biological processes in restored streams in order to determine the ultimate effects of river restoration requires more studies over longer time periods.

Most restoration projects have been carried out in lowland rivers, which have been dredged for agricultural, flood protection or transportation purposes. The applicability of the results from these studies to boreal woodland streams is, however, questionable. In Finland, there have been a few studies addressing the effect of restoration on fish populations (e. g. Huusko & Yrjänä 1997) but other stream organisms or biological processes have not been observed to this extent. Furthermore, the connection between the stream and its riparian vegetation, which must be taken into account in woodland rivers, has received little attention. This thesis aims to reduce these discrepancies by concentrating on short and long term changes in macroinvertebrate communities, habitat characteristics and coarse particulate organic matter (CPOM) retention in restored headwater streams in northern boreal areas.

The restoration process is a severe disturbance causing great damage to the stream biota. While the stream biota may have evolved adaptations to regularly occurring natural disturbances (Resh et al. 1988), unpredictable disturbances may have a devastating effect on both the individual taxa and the stream community as a whole. On the other hand, recovery of the stream biota to pre-disturbance levels is usually fast, i. e. stream communities have low resistance but high resilience (Fisher 1983, Lake 1990). This has been documented

both in experimental studies manipulating restricted areas of stream bottom (Reice 1985, 1991, Boulton et al. 1988, Doeg et al. 1989, Lake et al. 1989, Matthaei et al. 1999) and in 'natural experiments', whereby the recovery of the stream community following a major disturbance event has been monitored (Hoopes 1974, Fisher et al. 1982, Giller et al. 1991, Lamberti et al. 1991). However, the rate of the recovery is dependent on the severity of the disturbance and its areal extent, availability and characteristics of potential colonists, heterogeneity of the disturbed area, and timing of the disturbance (Sousa 1984).

In spite of the usually fast recovery of macroinvertebrate communities after disturbance, restoration may have permanent effects which will change the structure of the stream communities in the long run. Restoration causes changes in stream geomorphology, moss/plant cover and leaf litter retention properties. The slow adaptation of river organisms to these new abiotic conditions is the ultimate result of restoration.

A possible change in a stream's retention efficiency after restoration is one of the most important permanent effects of stream habitat restoration. Most streams draining forested lowlands are characterized by a strong link between the riparian vegetation and stream habitat. The input of terrestrially-derived organic material and its retention to the stream bed are among the key processes shaping the invertebrate communities of woodland streams (e. g. Cummins et al. 1989). Allochthonous material entering the stream is utilized by a wide array of lotic organisms from bacteria and fungi to detritivorous invertebrates. 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. 1997, 1999). Species composition and cover of the riparian vegetation are not, however, the sole determinants of the amount of benthic organic material. The elementary role of leaf retention to stream communities has been documented in numerous studies (Angermeier & Karr 1984, Smock et al. 1989, Dobson & Hildrew 1992). Stream bed retentiveness is greatly enhanced by debris dams (Bilby & Likens 1980, Smock et al. 1989, Ehrman & Lamberti 1992, Wallace et al. 1995), and the addition of debris dams or other retentive structures to stream bed has been suggested as a management tool for acidified upland streams (Dobson et al. 1995).

Globally, a large number of streams and rivers have been channelized for agricultural, flood protection or transportation purposes. The dredging of streams to facilitate log transport has been one of the major goals of channelization in Nordic countries (Jutila 1992). By the 1950's, 13 000 km of streams were dredged in Finland for floating timber. Most rapids were dredged and the largest meanders were realigned. All this work was done using a bulldozer which pushed the material from the river to the embankments surrounding the channel. Channelization resulted in homogenous stream channels with simplified flow patterns, longer spiralling distances, lower bed retentiveness and weakening of the aquatic-terrestrial linkage (Petersen & Petersen 1991, Quinn et al. 1992).

The water transport of timber ceased in the 1970's, and extensive restoration programs have thereafter been launched to rehabilitate these streams to

their original, pre-channelization condition. Restoration mainly aims at providing a better habitat for important game fish such as brown trout. The restoration process is carried out mainly with an excavator, which places the boulders back to the river while moving slowly down the river channel. The material needed for the construction of various restoration structures is readily available along the stream edges and, in most places, the only thing needed is the dismantling of the embankments. The main structures used in habitat restoration are boulder dams, boulder groups, deflectors, cobble ridges and excavations (Yrjänä 1998). A single boulder dam is created by setting large boulders across the river and by filling up the dam with cobbles and rubbles. A current deflector is constructed from boulders in the same way as dams but the deflectors are not as wide as the channel. Deflectors increase water velocities and make channels deeper by creating erosion areas and gravel-trapping pools. Single large boulders (0.5-1.5 m) or boulder groups are placed in the bottom to stabilize the stream bed, to facilitate the formation of ice cover and to increase the number of feeding and cover areas for large fish. In many cases, excavations are made behind the boulders. Cobble ridges are constructed from the former embankment lining the dredged rivers. Furthermore, cobble-to-pebble sized stones are used to create nursery habitats for juvenile trout (Yrjänä 1998).

The main goal of this thesis is to examine changes in the stream biota and the biological processes in headwater streams induced by stream habitat restoration. I was particularly interested in (i) the changes in the stream habitat structure, (ii) the immediate responses of macroinvertebrates to restoration-caused disturbance, (iii) the long term changes in the stream biota, including macroinvertebrates and aquatic mosses, (iv) the changes in the connection between the riparian vegetation, stream retention capacity and benthic macroinvertebrates.

2 MATERIALS AND METHODS

2.1 Study areas

The studies contained 25 rivers in the northern and eastern parts of Finland (63° - 66° N, 27° - 30° E), except (III), which was partly conducted in Central Finland (62° N, 26° E). All these rivers run through lowland areas dominated by coniferous forests (mainly pine (*Pinus sylvestris* L.), spruce (*Picea abies* L.) and birch (*Betula* spp. L.)). The riparian zones along the rivers are dominated by birch, alder (*Populus tremula* L.), European aspen (*Alnus incana* L.) and willows (*Salix* spp.). Forestry practices have taken place in the drainage areas of these rivers during the last century. Channelized rivers were dredged in the 1950's and the first restoration projects started at the end of the 1970's. Rivers can be classified to Group 3 of Nordic rivers, i. e. boreal forest streams (Petersen et al. 1995). They are 2nd or 3rd order streams with circumneutral, oligotrophic and often slightly humic water. In the wintertime (November to April) the streams are ice covered and their hydrology is characterized by a spring flood induced by snowmelt in May and by a secondary flood in September – early October.

2.2 Responses of benthic macroinvertebrates to stream restoration

2.2.1 Short-term responses

The short-term recovery of benthic macroinvertebrates after disturbance from stream habitat restoration was studied in the River Livojoki, northern Finland. Specifically, we were interested in finding out whether the restoration procedure reduces invertebrate densities and how soon they recover to the original level. The 50-m long sample reach was first sampled 15 days before restoration. The same locality was sampled again on days 2, 4, 7, 15 and 30 after the river had been restored. The control site, 1.5 km upstream, was sampled 5 days befo-

re and 10 and 30 days after the onset of the restoration. Individual stones were used as sampling units, and 30 randomly selected stones per date and location were sampled. The samples were preserved on site in 70 % alcohol, and the invertebrates were later sorted in the laboratory. The animals were identified to the lowest practical taxonomic unit. The surface areas of the stones were estimated according to Graham et al. (1988).

Physical habitat characteristics, including water depth, velocity and bed roughness, were measured along several transects at the restored site both before and after restoration. Moss cover and particle size were determined from 50 quadrates of 0.25 m² in size. The reference site was sampled in a similar way simultaneously with the 'after' samples from the restored site. To quantify the roughness of the stream bed, we used a contour-plotting device slightly modified from Statzner et al. (1988). Froude number, Reynolds number, shear velocity and roughness Reynolds number were calculated from the measured variables (see e.g. Davis & Barmuta 1989).

Detrended correspondence analyses (DCA, Hill 1979) were run on log-transformed ($\ln(x+1)$) densities of taxa comprising at least 5 % of the total fauna. Chironomids, which were not identified to species level, were excluded from the DCA.

2.2.2 Long-term responses

Macroinvertebrate communities and habitat characteristics in streams with differing recovery periods (from 0 to 16 years) from restoration were compared with those in channelized and near-pristine streams. Macroinvertebrate samples were collected on two occasions, June and October, using the kick-sampling method (net frame 25 x 25 cm, mesh size 0.25 mm). Four 1-min samples were taken from each site. The samples were preserved on site in 70 % alcohol, and the invertebrates were later sorted in the laboratory. The animals were identified to the lowest feasible taxonomic level. Simuliids and chironomids were identified only to the family level and these two groups were excluded from all analyses, except the calculation of total benthic densities and densities of detritivores (simuliids included). Taxa were assigned to functional feeding groups according to Merritt & Cummins (1984) and Malmqvist & Brönmark (1985)

Several habitat characteristics were measured at each site. Water depth (D), current velocity (at 0.6 x depth) and substrate size were measured at 30 or more random points along evenly spaced transects perpendicular to the flow. Percentage cover of moss was estimated from the same transects using a quadrate of 0.25m². Stream bed roughness was quantified using a contour-plotting device similar to that of Statzner et al. (1988). Relative bed roughness (Davis & Barmuta 1989) was again used to indicate substrate heterogeneity.

The amount of leaf litter on the stream bed was quantified by collecting all leaf material from 8 randomly placed quadrates, each 0.1 m². The samples were placed in plastic bags and transferred to the laboratory where leaves and leaf fragments were sorted from all other material, dried at 60°C for 24 h and

weighed to obtain their dry weight per 0.1 m². These samples were collected only in October, one to two weeks after the peak leaf fall.

The differences in macroinvertebrate numbers (log-transformed) and in the amount of benthic leaf litter among the stream groups were tested by one-way ANOVA, followed by pairwise comparisons using Tukey's test with $\alpha = 0.05$. The patterns in macroinvertebrate assemblage structure among the stream groups were assessed with species-rank curves and an ordination method, Canonical Correspondence Analysis (CCA). The species counts were log transformed ($\ln+1$) before entering the analysis. The significance of the first ordination axis was tested by a Monte Carlo permutation method where the actual ordination is compared with a null model derived from random permutations of species with respect to habitat variables (Ter Braak 1988).

2.3 Distribution of benthic macroinvertebrates and leaf litter in relation to stream bed retentivity

The relationship between the distribution of leaf litter and benthic macroinvertebrates was studied in two boreal woodland streams. We tested whether the association of benthic invertebrates with leaf accumulations varies between streams of contrasting retention properties, i.e. natural, channelized and restored streams. To characterize the habitat structure in each stream, 20 cross-sectional transects were placed in 2.5-m intervals within each study section. In each transect, water depth (D), flow rate (0.6 x depth) and stone size (largest diameter) were measured in 1-m intervals, and moss cover (%) in three 0.1 m² quadrates. The stream bed roughness was measured using a bed profiler modified from that described by Young (1993).

A leaf release experiment using artificial leaves (plastic strips) was used to locate and characterize the retentive structures present in each stream. Plastic leaves of the approximate length of natural leaves are known to behave much like natural leaves (Speaker et al. 1988). In Rutajoki, the leaf release experiment was done both before (October 1996) and after restoration (November 1997), in the natural stream Merenoja the experiment was conducted only once, in October 1996. A block net was stretched at the end of a 50-m long riffle section. One thousand plastic leaves (8 x 4 cm) were released on the water surface at the upstream end of the reach and, after three hours, all retention sites (i. e. sites that had trapped leaves) within the study section were located and described. 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, and (v) backwater or side channel.

Immediately after the leaf release experiment, benthic macroinvertebrate samples were collected in each stream. These samples were collected both from patches that retained artificial leaves (retention sites) and from randomly selected patches (random sites), 25 samples for each patch type. Both sets of sam-

ples were taken from the same 50-m long sample reach. A modified Surber sampler (20 x 20 cm, mesh size 0.25 mm) was used for all benthic sampling. The 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. Chironomids were divided into three feeding groups: filterers (mainly *Rheotanytarsus* spp.), collector-gatherers (Orthoclaudiinae) and predators (Tanypodinae) (see Wiederholm 1983, Chauvet et al. 1993).

The differences in the mass of benthic leaves and the densities of macroinvertebrates in random vs. retention sites were tested using independent sample t-tests, separately for each stream type. Morisita's index was used to examine the distribution patterns of various macroinvertebrate groups in each stream. Regression analysis was used to examine the relationships between leaf litter and animal densities in the benthic samples.

2.4 Enhanced leaf retention as a mechanism of recovery in restored headwater streams

The changes in retention characteristics induced by the restoration were tested in natural, channelized and restored headwater streams. Specifically, we addressed the following questions: does the restoration enhance a stream's retentive capacity; is the state of a natural stream achieved; and do benthic invertebrates respond to changes in retention capacity? To assess whether restoration achieved the goal of enhancing streambed heterogeneity, we again used the contour plotting device (Young 1993) to quantify streambed roughness. The distances from permanent reference marks on the stream banks were used to certify that measurements before and after restoration were made at the same positions.

To examine the changes, if any, in the retention capacity of a stream after restoration, we performed a set of leaf release experiments. The experiments before and after restoration were conducted three years apart (September to early October 1993 and 1996, respectively), at closely corresponding stream discharges. We used red-and-yellow plastic strips (8x4 cm) as artificial leaves in our experiments. In each experiment, 2000 leaves were released at the upstream end of a 50-m study section. The downstream end of the section was blocked with a wire screen. Three hours after the release, we counted the number of leaves that had arrived at the screen and searched the entire reach for leaves that had been retained within the 50-m section. It has been noted previously that the number of leaves in transport stabilizes within 2-3 h of the release (Speaker et al. 1984, Petersen & Petersen 1991). For each leaf found, we noted the distance travelled. We also recorded the retaining object (stone, small

woody debris, moss, other aquatic vegetation, backwater, stream edge) for each leaf. At each retention point, we measured water depth, current velocity (at $0.6 \times$ depth) and substrate size (if stone). The same habitat characteristics were also measured for the whole study reach in transects perpendicular to the flow, positioned in 3-m intervals. For each transect, depth, water velocity, moss cover, substrate size and presence/absence of wood were recorded at 0.5-m intervals.

The effect of discharge on leaf retention was measured in one randomly selected stream for each stream group. In each of these streams, we conducted a leaf release experiment with 2000 artificial leaves on four discharges, using the methods described above. The discharges for conducting the experiments were selected to represent the flow regime of each stream. In this experiment, only the number of leaves travelling through the study section was recorded.

The macroinvertebrate samples were collected by kick-sampling (net frame 25×25 cm, mesh size 0.25 mm), and four 1-min samples were taken from each site. The samples were taken 1-2 weeks before and again three years after the restoration. The post-restoration samples were collected at the same time of the year as the pre-samples three years earlier (September to early October). Similar samples were also collected from the four natural streams, both in September 1993 and 1996. The animals were identified to species or genus, and they were assigned to functional feeding groups.

Leaf transport was fit to the negative exponential model of $L_d = L_0 e^{-kd}$ where L_0 is the number of leaves released into the reach and L_d is the number of leaves in transport at distance d from the release point. The slope, $-k$, is the instantaneous leaf retention rate and $1/k$ is the average distance a leaf travels in the stream before being retained (Speaker et al. 1984). The differences between (i) the channelized and restored streams and between (ii) the restored and natural streams were tested by using a priori comparisons. The variables examined were retention efficiency, retention coefficient and densities (log-transformed) of macroinvertebrate feeding groups.

3 RESULTS AND DISCUSSION

3.1 Short-term responses

It is well known that the intensity of disturbance is hard to measure. Nevertheless, it has been suggested that substratum movement could be used as an indicator of natural disturbance in streams (Cobb et al. 1992, Poff 1992). At our study site, barren substrate amounted to less than 5 % of the stream bed and the restoration process was thus probably only a moderate disturbance to benthic invertebrates. Except for the scouring effect of the moving bulldozer, the old substrate was essentially kept intact. Some large boulders were transferred from the adjacent river banks, and barren substrate was also created by digging excavations. There was only a slight increase in the roughness and mean particle size of the stream bed, but a remarkable decrease in the moss cover, which may in the long run decrease the densities of some benthic animals (e. g. Brusven et al. 1990). The changes in the flow patterns were only minor, but a trend towards slightly more turbulent, hydraulically rougher conditions was evident.

The direct effects of restoration on macroinvertebrate densities were confounded by the seasonality of benthic populations. The restoration disturbance reduced all abundant taxa evenly, thus leaving the structure of benthic community essentially unchanged. The DCA and species rank analyses showed little changes in the macroinvertebrate community. Most species-level changes and community patterns reflected seasonal life history events. However, the disturbance of the restoration was still evident because there was a slight decrease in the numbers of most benthic insects. Although the high resilience of stream communities is generally acknowledged (e.g. Fisher 1983, Lake 1990), the recovery at our study site was exceptionally fast. The recovery to pre-disturbance densities occurred within less than a week. In experimental studies (Reice 1985, Robinson & Minshall 1986, Boulton et al. 1988, Doeg et al. 1989), the recolonization of disturbed reaches by macroinvertebrates has taken from a few days to approximately two months, depending mainly on the areal extent of the disturbance. In natural disturbances (e.g. Fisher et al. 1982, Minshall et al. 1983, Lamberti et al. 1991), the recovery rate has varied from months to several years. I

suggest two reasons for the rapid recovery at our study site; (i) restoration left some areas of the stream bed intact and these patches were used as refuges by invertebrate colonists (the "hydraulic refuge" hypothesis of Townsend 1989); (ii) the timing of the disturbance in relation to the life histories of the species ensured a rich pool of colonists.

3.2 Recovery of macroinvertebrate communities from stream habitat restoration a comparative approach

The aim of restoration is to increase the habitat heterogeneity of channelized streams by rearranging their substrate. In the streams studied here, this goal was clearly achieved. Water depth and current velocity were generally lower, and the relative bed roughness higher in the restored than the dredged channels, yet not reaching the roughness of the natural streams. Cummins et al. (1989) and Dobson et al. (1995) showed that channels with greater stream bed roughness retain leaf litter more effectively, and often support higher numbers of shredders and other detritivores. In southern Sweden, Petersen & Petersen (1991) also showed that channelized streams are only half as retentive as natural streams. In our restored streams, the standing stock of leaf litter was lower than in natural streams but in most cases higher than in channelized streams. The amount of leaf litter retained on the stream bed was closely related to relative bed roughness. CCA- analysis of the autumn invertebrate data could be attributed to among-site variation in habitat hydraulics, moss cover and leaf litter. Dredged channels with high velocities and low bed profiles, and natural streams with high retention efficiency were the end points of this gradient.

Since increasing stream bed heterogeneity is an essential part of stream habitat restoration, this should, once the immediate disturbance effect has diminished, reinforce the build-up of high shredder numbers in restored channels. However, data from this study supports this contention only partly. Numbers of shredders, as well as all invertebrates, were higher in streams restored a few years ago than in recently (a month ago) restored streams, but only comparable to, or even slightly lower, than those in the channelized streams. The highest numbers were found in the natural streams. There was a tendency toward higher abundance of shredders with a longer recovery period, but the streams restored 8 and 16 years ago still contained relatively sparse shredder populations.

The reason why the numbers of invertebrates in the restored streams were not higher than those in the channelized streams is most likely the dramatic loss of mosses induced by the restoration process. Mosses serve multiple purposes in headwater streams: they provide shelter from predators and shear forces of flow, an attachment site for periphyton and, perhaps most importantly, they are effective accumulators of fine detritus, thus affording a plentiful food supply for many collector-gathering invertebrates (Suren & Winterbourn 1992, Vuori &

Muotka 1999). It has been repeatedly documented that there is a positive relationship between moss biomass and macroinvertebrate diversity (e. g. Englund 1991, Suren 1991, Vuori & Joensuu 1996). In this study, moss cover was very low in recently restored streams. During the first few years after the restoration, the tendency for higher macroinvertebrate abundance with a longer recovery period was paralleled by a relatively rapid re-establishment of stream mosses. In contrast to a rapid recovery during the first years after the restoration, the older restorations, i. e. streams restored 8 or 16 years ago, did not fit the trend of gradually increasing densities of macroinvertebrates. The explanation for this relates to the much less radical restoration practices used in the 1970's. The results from this study thus suggest that mosses may play a key role in the recovery of macroinvertebrate assemblages in restored streams. In fact, due to their potentially important contribution to the retentive capacity of a stream, their role in the recovery of stream ecosystem processes may be even more far-reaching.

3.3 Distribution of benthic macroinvertebrates and leaf litter in relation to stream bed retentivity: implications for headwater stream management

The natural stream Merenoja retained 76 % of the leaves released to the experimental section, whereas the stream Rutajoki retained 25 % before and 75 % after its restoration. In the natural stream, the most effective retentive structure was the stream bank. Cobbles and boulders trapped the most leaves in the channelized stream, and twigs and branches in the restored stream. The retention sites contained significantly more leaves than the random sites in each stream. The difference between the patch types was most distinct in the channelized stream before its restoration. After the restoration, the standing crop of the leaf CPOM was overall considerably higher.

Total macroinvertebrate densities were higher in the retention than random sites in all streams, although the difference was not significant for the stream Merenoja. The highest densities (c. 500 individuals per 0.04 m²) were found in the retention sites of the stream Rutajoki after the restoration. The densities of leaf shredding-insects and other detritivores were distinctly higher in the retention than the random sites in Rutajoki, both before and after the restoration, but not in Merenoja which, however, supported the highest overall shredder densities. The densities of predatory and algae-scraping invertebrates differed little among the patch types in any of the streams, the only exception being higher densities of predators in the retention sites in the river Rutajoki after the restoration. In both rivers some shredder taxa (nemourid stoneflies, limnephilid caddis larvae) were significantly more abundant in the retention than the random sites. According to Morisita's index, total benthos and detritivores exhibited a strongly aggregated distribution pattern in all streams. In-

vertebrates and their resources (benthic leaves) tended to be most aggregated in the channelized, and least so in the natural stream. Nemouridae stoneflies were an exception to this pattern, being least aggregated in the river Rutajoki after the restoration.

The regression analysis showed that the dry mass of the leaf CPOM was a good predictor of total, as well as detritivorous macroinvertebrate density in the River Rutajoki, both before and after the restoration. In contrast, the relationship was non-significant in Merenoja. The relationship between the leaf CPOM and shredder density was non-significant for all streams. However, the dominant shredder taxon, *Nemoura* spp., displayed a strong positive relationship to the amount of benthic leaves in all streams. The analysis of covariance indicated significant differences among the slopes of the regression lines between Rutajoki and Merenoja. The slope in the channelized stream Rutajoki was significantly steeper than that in Merenoja and Rutajoki after the restoration. Shredders other than nemourids did not correlate with the leaf CPOM.

On the whole, our results coincide well with those of Dobson & Hildrew (1992) for four southern English streams with contrasting retentivity. The number of shredding invertebrates was higher in the stream Merenoja, whereas the association of detritivores with leaf packs was more distinct in the less retentive stream 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). However, the restoration of the river Rutajoki did not reduce the dependence of detritivores on leaf packs. After the restoration, the densities of most detritivorous taxa were still higher in the retentive than the random patches, although the difference between the patch types was usually less distinct than. This relatively minor change occurred regardless of the fact that the retentive capacity of the stream was clearly enhanced by the restoration.

These observations have two important implications. First, invertebrates seemed to be less food-limited in the natural stream than in the channelized or recently restored streams. Second, the enhancement of the streambed retentivity did not release detritivores from resource limitation in the stream Rutajoki. Still, it is quite possible that detritivores are seasonally food-limited even in natural woodland streams, but food shortage in these streams should not occur until late spring when the stock of benthic leaves becomes exhausted (Richardson 1991, Malmqvist & Oberle 1995, Haapala & Muotka 1998). In the long run, the increased resource availability caused by restoration might translate into higher densities of detritivores. However, the short-term response suggests that the density and effectiveness of the retentive structures used in the restoration may have been too low.

3.4 Enhanced leaf retention as a mechanism of recovery in restored headwater streams

The leaf release experiments conducted in this study indicated that restoration clearly enhanced a stream's retention capacity but not enough to reach the level of natural streams. Compared to most previous studies (e.g. Petersen & Petersen 1991), our channelized streams showed extremely poor retentivity, which was clearly related to their highly simplified bed structure. The leaf transport curves generally conformed well to the negative exponential loss model, although a linear model produced nearly as good a fit for all the channelized and most restored streams. In the natural streams, retention sites were patchily distributed, whereas in the channelized rivers the leaves were retained evenly along the study reach. A highly patchy distribution of retentive structures, and hence organic matter, is typical of streams with debris dams, and this has been reported to result in extreme patchiness of the community and ecosystem-level functions in these streams (Smock et al. 1989). Debris dams were overall very rare in our study streams but were to some extent compensated by cobble ridges and dense moss tufts.

Mosses and stones were the most effective retentive structures in the channelized and natural rivers, but in restored rivers the role of mosses was negligible. Adding stones to the river bed in the restoration process increased bed heterogeneity but at the same time decreased the moss cover. In spite of quite intense restoration measures, the heterogeneity of natural rivers remained a distant goal. The restoration structures used in Finland do not seem to effectively mimic the physical complexity of naturally retentive stream habitats.

It is well known that increasing stream discharge reduces the retention efficiency of a stream to allochthonous inputs (Speaker et al. 1988, Jones & Smock 1991, Snaddon et al. 1992). We found that while the retention capacity of a natural stream was clearly reduced by increasing discharge, the reduction was only minor in a channelized stream. Similarly, Webster et al. (1987) observed that discharge had little effect on the retention of fine particulate matter on smooth surfaces, but increased discharge greatly reduced retention on more complex (artificial turf, gravel) substrates. While the secondary peak in the flow regime of boreal streams typically occurs during or immediately after the leaf fall (Hyvärinen 1985, Haapala & Muotka 1998), increasing discharge can equalize the amount of CPOM retained on the river bed in different types of rivers. This is further accentuated by the lack of debris dams in the natural streams of our study area. Stones are effective in leaf retention only at low discharges, whereas the role of debris dams generally increases with rising discharge (Smock et al. 1989, Jones & Smock 1991, Raikow et al. 1995).

Many studies have shown the connection between CPOM retention and detritivorous invertebrates (e. g. Wallace 1995, 1999). Therefore we expected shredder abundance to increase after restoration, but the only invertebrate feeding group which increased significantly was algae-scraping invertebrates.

We believe that the dramatic reduction of moss cover in large areas of the stream bed created new bare substrate which was effectively colonized by periphytic algae. The increasing heterogeneity of the stream bottom compensates to some degree the loss of mosses, but the retention capacity did not increase enough to raise the abundance of shredding invertebrates. Thus, stream habitat restoration seems to induce a shift towards autochthonous resource base for the benthic invertebrate community.

In this study, large canopy-forming moss species (e. g. *Fontinalis* spp., *Hygrohypnum* spp.) were especially effective in leaf retention. In other studies, aquatic macrophytes have been shown to have a central role in organic matter retention (Speaker et al. 1988, Angradi 1991) and massive loss of macrophytes during restoration has been reported to slow down the community recovery after stream restoration (Biggs et al. 1998, Friberg et al. 1998). Especially because the colonization and growth rates of aquatic bryophytes are poorly known and can last even decades, I underline the importance of causing as little damage as possible to mosses during the restoration practices

3.5 Habitat characteristics in channelized, restored and natural streams: does restoration create unnatural habitats?

I used principal components analysis (PCA) to summarize the habitat characteristics of channelized, natural and restored streams. Five streams from the earlier studies (I, II, IV) were selected for each stream group and the following habitat attributes were used in the analysis: depth (D), current velocity, bed roughness (k), relative roughness (k/D), particle size and moss cover. I then used the site scores from the PCA-analysis to test for differences along the first two axes (PCA1, PCA2) between each of the stream groups using one-way ANOVA. Furthermore, I used data from study IV to produce histograms showing the frequency distributions of some habitat characteristics for the three stream types.

TABLE 1 Summary of Principal Component Analysis on habitat characteristics in channelized, restored and natural streams. Loadings with an absolute value greater than 0.70 are shown in bold.

	PCA-Axis		
	I	II	III
Eigenvalue	2.26	1.16	1.12
% variance explained	37.7	27.9	18.9
Cumulative %	37.7	65.6	84.4
Roughness	0.844	0.404	-0.125
Relative roughness (k/D)	0.834	-0.394	0.203
Particle size	0.786	0.317	-0.237
Moss cover	0.329	0.149	-0.825
Depth	-0.115	0.933	-0.249
Current	-0.338	0.600	0.525

The first ordination axis of the PCA analysis separated the stream groups along a gradient of bed roughness, current velocity and water depth (Table 1). The end points of this gradient were natural rivers (NA) with high bed profiles and shallow water, and dredged channels (CH) with high current velocity and deep water (Fig. 1A). Restored rivers with increased bed roughness positioned in the middle section of the first axis, indicating that they still have too fast flows and deep waters to mimic effectively natural rivers. The stream groups were significantly separated along the first ordination axis (1-way ANOVA: $F_{3,16} = 7.334$, $p = 0.003$), with the dredged channels differing significantly from the natural streams (Tukey's test, $p = 0.002$), and from the streams restored eight to nine years ago ($p = 0.032$). The third ordination axis was primarily attributable to moss cover (Table 1, Fig. 1B). The rivers restored three years (RE3) before sampling (average moss cover 25%) were situated farthest from the natural rivers (moss cover 75%). The oldest restored streams showed that the full recovery of the moss cover takes at least a decade. ANOVA showed a significant overall difference along the third axis ($F_{3,16} = 3.936$), $p = 0.027$), with significant pairwise differences between the natural streams (NA) and streams restored three years earlier (RE3) (Tukey's test, $p = 0.025$), and between the dredged channels (CH) and RE3-streams ($p = 0.05$).

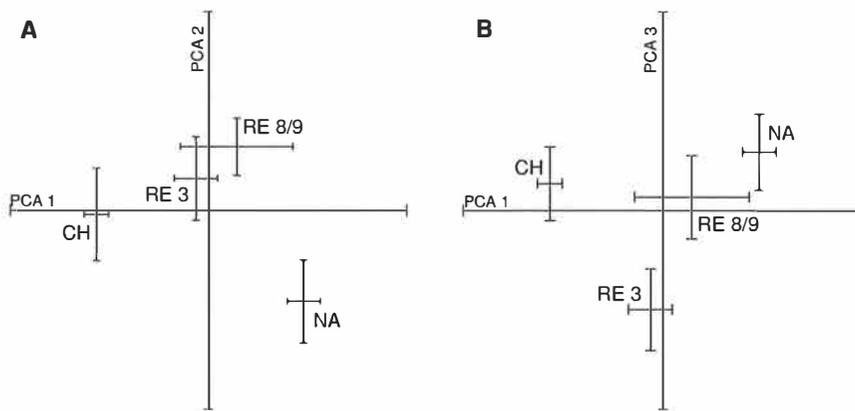


FIGURE 1 PCA of habitat characteristics in channelized (CH), three (RE3), eight-to-nine (RE 8/9) years ago restored, and natural streams. Vertical and horizontal lines represent ± 1 SE, $n = 5$.

During the restoration process mosses were detached from large areas of the stream bed (Fig. 2). The intensive restoration practices used in the river Kosterjoki decreased the moss cover from 42 % to 5 %. Only a few untouched moss patches occurred on the river bed after the restoration. Before the restoration, river Kosterjoki was characterized by fairly homogenous, simplified flow patterns (Fig. 2). The flow was fast and only a few slow-current sites occurred along the stream banks. Boulder dams and excavations altered the previously

homogenous channel to one characterized by more variable flow patterns with effective pool/riffle alternation. The river Kosterjoki is a fine example of how a restoration project may succeed in changing the habitat characteristics of a stream to mimic the hydraulic regime of a natural river quite effectively. Nevertheless, the almost total loss of mosses and the lack of any debris will slow down the recovery process for an unknown, but certainly long period of time.

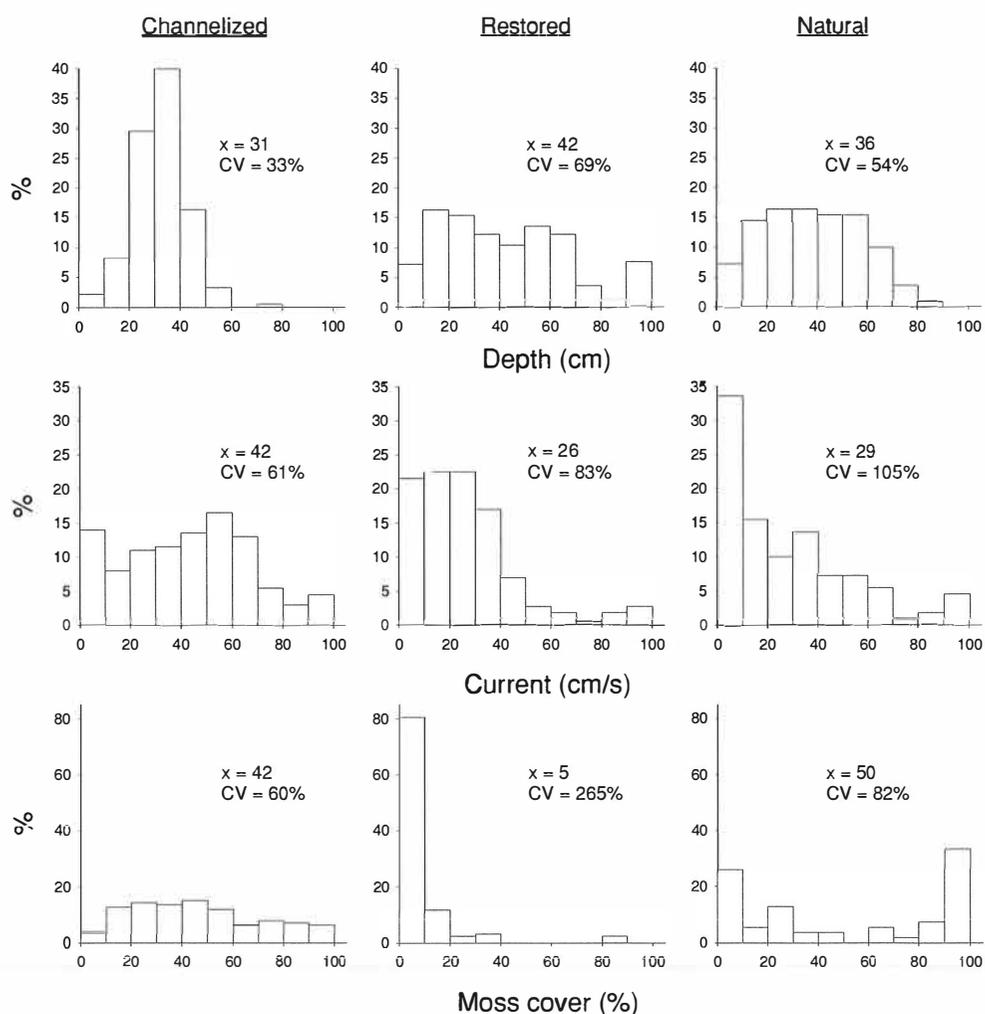


FIGURE 2 Frequency distributions of selected habitat characteristics in a channelized (Kosterjoki), restored (Kosterjoki) and natural (Merenoja) stream.

4 CONCLUSIONS AND RECOMMENDATIONS

In recent river restoration projects (see e.g. Dahm et al. 1995, Muhar et al. 1995) user-oriented, one-sided goals are beginning to be replaced by goals favouring the comprehensive protection of the river ecosystems. Many older projects with narrow aims, such as the enhancement of individual species or groups of species, were usually carried out for the purpose of increasing sport fisheries. According to Muhar et al. (1995) such projects cannot be classified as restoration projects at all but rather as 'restructuring' projects limited to morphological improvements of the riverbed. In comprehensive restoration projects the goal is to improve the ecological health of the whole river, including the drainage area. Restoration programs potentially use natural rivers as a reference. However, as pointed out by Osborne et al. (1993), pristine conditions (or if not available, quasi-pristine conditions) should only serve as a point of reference and not as a goal of stream restoration, because a truly pristine state is unattainable in catchments where humans have modified the land use and cover. However, Higgs (1997) strongly emphasized ecological fidelity as the goal of restoration: (i) a restored ecosystem must strongly resemble the structure and composition of the so-called natural ecosystem, (ii) the functional success of the restored ecosystem must align ecologically with the system it is designed to reproduce, (iii) the restored ecosystem must hold up over a significant period of time, significant being defined relative to the type of ecosystem.

In Finland streams are restored mainly for fishery purposes, and therefore we should pose the following question: how well has the one-goal restoration practice succeeded in the goals of ecological restoration? Has this process succeeded in improving biological processes and the habitats for the other biota but fishes? As shown in this study, the short-term recovery of stream macroinvertebrates was rapid, showing the great resilience of the stream biota. The long-term effects in macroinvertebrate communities were minor, even so small that they were hard to detect. The restoration enhanced the retention capacity of the streams, but not enough to remove the resource limitation of detritus-feeding invertebrates. In the light of these results the restoration was not a great success ecologically. It may have been the first step to the right direction by in-

creasing the heterogeneity of the stream bed and the flow regime, but the macroinvertebrate species richness and CPOM retention capacity of natural rivers were still not reached. There are two key factors to this lack of success: the loss of mosses and the absence of debris dams, which may both considerably slow down, or even hinder, the recovery process.

Many studies have documented the positive relationship between moss biomass and macroinvertebrate diversity (e.g. Englund 1991, Suren 1991, Vuori and Joensuu 1996). It has been noted that mosses are effective accumulators of fine detritus, thus affording a plentiful food supply for many collector-gathering invertebrates (Suren and Winterbourn 1992). In this study, mosses also turned out to be effective in leaf litter retention, so after a gradual recovery of mosses the retention capacity for CPOM inputs should also increase. The final outcome of restoration for macroinvertebrate communities cannot be seen until the full recovery of the stream mosses has taken place.

It has been frequently shown that the manipulation of debris dams alters dramatically the retention characteristics of a stream, thereby also regulating abundances of benthic organisms, especially detritivorous invertebrates (e.g. Bilby & Likens 1980, Smock et al. 1989, Trotter 1990, Wallace et al. 1995, 1999). Debris dams played an unimportant role in our studies and occurred rarely in both channelized and restored rivers. Even in natural rivers they were very rare. Debris dams are mostly composed of large woody debris (LWD). In Finland, nearly all forests have been occasionally cut during the last hundred years and, until very recently, no buffer strips were left to protect the rivers. Thus, the natural formation of debris dams has been prohibited by excessive human activities in the catchment area. As ecosystem restoration is becoming increasingly important, there is now clearly an opportunity to "jump over" a whole century in debris dam formation simply by setting large logs on the river bed (see Wallace et al. 1995).

The dredging of streams for log floating in Finland took place during more than 40 years. Since the cessation of log transport, these streams have stabilized to new conditions, characterized, for example, by a relatively high moss cover. After the restoration, it will probably take decades for the rehabilitated rivers to reach a new "natural state". Before initiating a restoration project, we should always consider whether it is really useful to "restore" a stream with reasonably natural habitat conditions and a relatively rich biota. In Finland, tens of millions of marks have been spent in restoration projects, without any close inquiry to stream ecology. As Osborne (1993) summarized in the 1st Lowland Streams Restoration congress: "our present understanding of restoration is as much an art-form as it is a science with much to be learned from failed and successful projects". Thus I emphasize the importance of carefully studying the stream geomorphology, hydraulics, biota and biological processes in future restoration projects in Finland. I also suggest re-thinking the goals of the restoration, because streams in Finland are mostly rehabilitated for fishery purposes. Not only will the biodiversity of the stream biota decrease but even the biodiversity of our stream types may decrease if all the rivers are restored in the same, trout-favouring, way. Obviously, even relatively slight changes in resto-

ration practices could mitigate the succession towards more natural streams, which could ultimately benefit even stream fishes and fisheries.

Finally, I summarize the recommendations of how to improve Finnish restoration practices: (i) the recovery of mosses should be facilitated by reducing damage to mosses during restoration and by leaving intact patches to the stream bottom; (ii) formation of debris dams should be aided by adding large woody debris, especially logs, in the river bed; (iii) the heterogeneity of the stream bottom and the flow regime should be increased more effectively by increasing the bottom roughness and dismantling all the embankments; (iv) in order to secure distinctive and unique rivers, restoration measures used should vary among streams, following the individual characteristics and geomorphological features of each river to be restored.

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YHTEENVETO

Koskikunnostuksen vaikutukset jokien pohjaeläimistöön

Tukin uiton loppumisen myötä uittoa varten tehtyjä rakenteita on alettu purkaa ja perattuja koskia kivetä. Kunnostuksen vaikutuksia jokien ekologiaan ei kuitenkaan ole juuri tutkittu muuten kuin kalaston osalta. Tämä väitöskirja keskittyy tarkastelemaan kunnostuksen vaikutuksia joen habitaatin rakenteisiin, pohjaeläimistöön ja biologisiin prosesseihin. Erityisesti tarkasteltiin kunnostuksen aiheuttamia muutoksia joen pohjan habitaattirakenteissa ja jokien kyvyssä pidättää orgaanista ainesta sekä pohjaeläinyhteisöjen lyhyt- ja pitkäaikaisvasteita kunnostuksen aiheuttamaan häiriöön ja muuttuneeseen elinympäristöön.

Lyhytaikaisvasteita tutkittiin vertailemalla ennen ja jälkeen kunnostuksen otettuja pohjaeläinnäytteitä kunnostamattoman, peratun jokiuoman näytteisiin. Kunnostuksen pitkäaikaisvaikutuksista saatiin tietoa vertailemalla 0-16 vuotta sitten kunnostettujen, kanavoitujen ja luonnontilaisten jokien pohjaeläinyhteisöjä ja pohjan habitaattirakenteita. Jokien orgaanisen aineksen pidättämiskykyä ennen ja jälkeen kunnostuksen verrattiin lehtien kellutuskokeen avulla.

Kunnostus muuttaa merkittävästi joen habitaattirakennetta. Kanavoitu, pohjarakenteeltaan ja virtaamaltaan homogeeninen, rännimäinen virta muuttuu parhaimmillaan monipuoliseksi jokiympäristöksi, jossa syvänteet ja koskikivikot vuorottelevat. Tutkimuksissa havaittiin kunnostuksen selvästi monipuolistavan joen pohjarakenteita ja virtaamamalleja. Myös pohjaeläimistölle tärkeän ravintolähteen, orgaanisen aineksen, pidättyminen parani merkittävästi kunnostuksen yhteydessä. Kuitenkin sekä pohjan heterogeenisyys että lehtien pidättämiskyky jäivät alhaisemmiksi kuin vertailujokina olleissa luonnontilaisissa uomissa. Pohjasammalisto vaurioitui pahoin kunnostuksen yhteydessä. Sammaliston palautumisen rajusta kunnostuksesta havaittiin kestävän yli vuosikymmenen.

Pohjaeläimistö palautui nopeasti, noin kahdessa viikossa, kevyen keski-kesällä toteutetun kunnostusprojektin jälkeen. Pitkäaikaisseurannoissa kunnostuksen ei havaittu aiheuttavan muutoksia pohjaeläimistön yhteisörakenteisiin. Pohjaeläimistön pilkkojayhteisöt eivät odotetusti runsastuneet, eikä niiden resurssirajoitteisuus poistunut. Kunnostettujen jokien pohjaeläintiheydet eivät saavuttaneet luonnontilaisten jokien tiheyksiä, vaan jäivät perattujen, kunnostamattomien jokien tasolle.

Miksi kunnostus ei sitten merkittävästi paranna pohjaeläimistön olosuhteita, ja miksi eläimistö ei saavuta luonnontilaisten jokien tiheyksiä? Tähän vaikuttaa pääasiassa sammaliston hidas palautuminen, pidättävien puupatojen puuttuminen ja pohjan riittämätön heterogeenisyys. Tulevissa kunnostustöissä ehdotankin seuraavien seikkojen parempaa huomioimista: (i) sammaliston palautumisen nopeuttamiseksi sammaliston tuhoutumista on vähennettävä ja koskemattomia sammallaikkuja jätettävä jokeen; (ii) puupatojen kehittymistä on autettava asettamalla suuria tukkeja jokeen; (iii) pohjan ja virtauksen heterogeenisyyttä on kasvatettava enemmän lisäämällä pohjan karkeutta ja purka-

malla kaikki perkauksen yhteydessä syntyneet virtaamaa kanavoivat rakenteet; (iv) jotta jokien tunnusomaiset ja ainutlaatuiset piirteet pystyttäisiin säilyttämään, kunnostustapoja pitäisi vaihdella enemmän kunkin joen ominaispiirteiden ja geomorfologisten piirteiden mukaan.

REFERENCES

- Angermeier, P.D. & Karr, J.R. 1984. Relationship between woody debris and fish habitat in small warmwater streams. *Trans. Am Fish. Soc* 113: 716-726.
- Angradi, T. R. 1991. Transport of coarse particulate organic matter in an Idaho river, USA. *Hydrobiologia* 211: 171-183.
- Baatrup-Pedersen, A., Riis, T., Hansen, N. O. & Friberg, N. 2000. Restoration of a Danish headwater stream: short-term changes in plant species abundance and composition. *Aquat Conserv* 10: 13-23.
- Biggs, J., Corfield, A., Grön, P., Hansen, H.O., Walker, D., Whitfield, M. & Williams, P. 1998. Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, V-Short-term impacts on the conservation value of aquatic macroinvertebrate and macrophyte assemblages. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 8: 241-255.
- Bilby, R. E. & Likens, G.E. 1980. Importance of debris dams in the structure and function of stream ecosystems. *Ecology* 61: 1107-1113.
- Boulton, A. J., Spangaro, G. M. & Lake, P. S. 1988. Macroinvertebrate distribution and recolonization on stones subjected to varying degrees of disturbance: an experimental approach. *Arch. Hydrobiol.* 113: 551-576.
- Brusven, M. A., Meehan, W. R. & Biggam, R. C. 1990. The role of aquatic moss on community composition and drift of fish-food organism. *Hydrobiologia* 196: 39-50.
- 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.
- Cobb, D. G., Galloway, T. D. & Flannagan, J. F. 1992. Effects of discharge and substrate stability on density and species composition of stream insects. *Can. J. Fish. Aquat. Sci.* 49: 1788-1795.
- Cummins, K. W., Wilzbach, M. A., Gates, D. M., Perry, J. B. & Taliaferro, W. B. 1989. Shredders and riparian vegetation. *BioScience* 39: 24-30
- Dahm, C.N., Cummins, K.W., Valett, H.M. & Coleman, R.I.. 1995. An ecosystem view of the restoration of the Kissimmee River. *Restor. Ecol.* 3: 225-238.
- Davis, J. A. & Barmuta, L. A. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater 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? *Freshwater 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. *Freshwater Biol.* 33: 325-337.
- Doeg, T. J., Lake, P. S. & Marchant, R. 1989. Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River Victoria. *Aust. J. Ecol.* 14: 207-220.
- Ehrman, T.P. & Lamberti, G.A. 1992. Hydraulic and particulate matter retention in a 3rd-order Indiana stream. *J. N. Am. Benthol. Soc.* 11: 341-349.
- Englund, G. 1991. Effect of disturbance on stream moss and invertebrate community structure. *J. N. Am. Benthol. Soc.* 10: 143-153.
- Fisher, S. G. 1983. Succession in streams. In: J. R. Barnes & G. W. Minshall (eds), *Stream Ecology: Application and Testing of General Ecological Theory*: 7-27. Plenum Press, New York.
- Fisher, S. G., Gray, N. B., Grimm, N. B. & Busch, D. E. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecol. Monogr.* 52: 93-110.
- Friberg, N., Kronvang, B., Svendsen, L.M. & Hansen, H.O. 1994. Restoration of a channelized reach of the River Gelså, Denmark: effects on the macroinvertebrate community. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 4: 289-296.
- Friberg, N., Kronvang, B., Hansen, H.O. & Svendsen, L.M. 1998. Long-term, habitat-specific response of a macroinvertebrate community to river restoration. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 8: 87-99.
- Giller, P.S., Sangpradub, N. & Twomey, N. 1991. Catastrophic flooding and macroinvertebrate community structure. *Verh. int. Ver. Limnol.* 24: 1724-1729.
- Görtz, P. 1998. Effects of stream restoration on the macroinvertebrate community in the River Esrom, Denmark. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 8: 115-130.
- Graham, A. A., McCaughan, D. J. & McKee, F. S. 1988. Measurement of surface area of stones. *Hydrobiologia* 157: 85-87.
- Haapala, A. & Muotka, T. 1998. Seasonal dynamics of detritus and associated macroinvertebrates in a channelized boreal stream. *Arch. Hydrobiol.* 142: 171-189.
- Higgs, E.S. 1997. What is good ecological restoration? *Conservation Biology* 11: 338-348.
- Hill, M. O. 1979. Decorana - A FORTRAN Program for Detrended Correspondence analysis and reciprocal averaging. *Ecology and Systematics*, Cornell University, Ithaca, New York.
- Hoopes, R.L. 1974. Flooding, as the result of Hurricane Agnes, and its effect on a macrobenthic community in an infertile headwater stream in central Pennsylvania. *Limnol Oceanogr.* 19: 853-857.
- Huusko, A. & Yrjänä, T. 1997. Effects of instream enhancement structures on brown trout, *Salmo trutta* L., habitat availability in a channelized boreal river: a PHABSIM approach. *Fish. Manage. Ecol.* 4: 453-466.
- Hyvärinen, V. 1985. River discharge in Finland. *Publ. Water Res. Inst.* 59: 3-23.

- Jones, J. B. & Smock, L. A. 1991. Transport and retention of particulate organic matter in two low-gradient headwater streams. *J. N. Am. Benthol. Soc.* 10: 115-126.
- Jutila, E. 1992. Restoration of salmonid rivers in Finland. In: P.J. Boon, P. Calow & G.E. Petts (eds), *River Conservation and Management*: 353-365. Wiley & Sons, London.
- Lake, P. S. 1990. Disturbing hard and soft bottom communities: A comparison of marine and freshwater environments. *Aust. J. Ecol.* 15: 477-488.
- Lake, P.S., Doeg, T.J. & Marchant, R. 1989. Effects of multiple disturbance on macroinvertebrate communities in the Acheron River, Victoria. *Aust. J. Ecol.* 14: 507-514.
- Lamberti, G.A., Gregory, S.V., Ashkenas, L.V., Wildman, R.C. & Moore, K.S. 1991. Stream ecosystem recovery following a catastrophic flow. *Can. J. Fish. Aquat. Sci.* 48: 196-208.
- Malmqvist, B. & Brönmark, C. 1985. Reversed trends in the benthic community structure in two confluent streams; one spring-fed, the other lake-fed. *Hydrobiologia* 124: 65-71.
- Malmqvist, B. & Oberle, D. 1995. Macroinvertebrate effects on leaf pack decomposition in a lake outlet stream in Northern Sweden. *Nordic J. Freshwat. Res.* 70: 12-20.
- Matthaei, C. D., Peacock, K. A. & Townsend, C. R. 1999. Patchy surface stone movement during disturbance in a New Zealand stream and its potential significance for the fauna. *Limnol. Oceanogr.* 44: 1091-1102.
- Merritt, R.W. & Cummins, K.W. 1984. *An Introduction to the Aquatic Insects of North America*, 2nd ed. Kendall/Hunt.
- Minshall, G. W., Andrews, D. A. & Manuel-Faler, C. Y. 1983. Application of island biogeographic theory to streams: macroinvertebrate recolonization of the Teton River, Idaho. In: J. R. Barnes & G. W. Minshall (eds), *Stream Ecology: Application and Testing of General Ecological Theory*: 279-297 Plenum Press, New York.
- Muhar, S., Schmutz, S. & Jungwirth, M. 1995. River restoration concepts – goals and perspectives. *Hydrobiologia* 303: 183-194.
- Newbury, R. & Gaboury, M. 1993. 'Exploration and rehabilitation of hydraulic habitats in streams using principles of fluvial behaviour'. *Freshwater Biol.* 29: 195-210.
- Osborne, L.L., Bayley, P.B., Higler, L.W.G., Statzner, B., Triska, F. & Iversen, T. M. 1993. Restoration of lowland streams: an introduction. *Freshwater Biol.* 29: 187-194.
- Petersen, L-B. M & Petersen, R.C. 1991. Short term retention properties of channelized and natural streams. *Verh. int. Ver. Limnol.* 24: 1756-1759.
- Petersen, R.C., Gislason, G.M. & Vought, L.B.-M. 1995. Rivers of the Nordic Countries. In: C. E. Cushing, K. W. Cummins & G. W. Minshall (eds), *Ecosystems of the World 22: River and Stream Ecosystems*: 259-341. Elsevier, Amsterdam.
- Poff, N. L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *J. N. Am. Benthol. Soc.* 11: 86-92.

- Quinn, J.M., Williamson, R.B., Smith, R.K. & Vickers, M.L 1992. Effects of riparian grazing and channelization on streams in Southland, New Zealand. *N. Z. J. Mar. Freshwat. Res.* 26: 259-273.
- Raikow, D.F., Grubbs, S.A. & Cummins, K.W. 1995. Debris dam dynamics and coarse particulate organic matter retention in an Appalachian Mountain stream. *J. N. Am. Benthol. Soc.* 14: 535-546.
- Reice, S. R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia* 67: 90-97.
- Reice, S.R. 1991. Effect of experimental spates on benthic community in New Hope Creek, North Carolina, USA. *Verh. int. Ver. Limnol.* 24: 1691-1693.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.B., Wallace, J.B. & Wissmar, R. 1988. The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.* 7: 433-455.
- Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 73: 873-887.
- Robinson, C T. & Minshall, G. W. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *J. N. Am. Benthol. Soc.* 7: 77-86.
- Smith, C.D, Harper, D.M. & Barham, P.J 1990. Engineering operations and invertebrates: linking hydrology with ecology. *Regul. Rivers* 5: 89-96.
- 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.
- Snaddon, C.D., Stewart, B.A. & Davies, B.R. 1992. The effect of discharge on leaf retention in two headwater streams. *Arch. Hydrobiol.* 125: 109-120.
- Sousa, P.W. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.* 15: 353-391.
- Speaker, R.W., Moore, K.A., & Gregory, S.V. 1984. Analysis of the process of retention of organic matter in stream ecosystems. *Verh. int. Verein. Limnol.* 22: 1835-1841.
- Speaker, R. W., K. J. Luchessa, J. F. Franklin & S. V. Gregory, 1988. The use of plastic strips to measure leaf retention by riparian vegetation in a coastal Oregon streams. *Am. Midl. Nat* 120:22-31.
- Statzner, B. Gore, J. A. & Resh, V. H. 1988. 'Hydraulic stream ecology: observed patterns and potential applications'. *J. N. Am. Benthol. Soc.* 7: 307-360.
- Suren, A. M. 1991. Bryophytes as invertebrate habitat in two New Zealand streams. *Freshwater Biol.* 26: 399-418.
- Suren, A. M. & Winterbourn, M. J. 1992. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. *Freshwater Biol.* 27: 327-340.
- Ter Braak, C. J. F. 1988. CANOCO a FORTRAN Program for Canonical Community Ordination by Partial Detrended Canonical Correspondence Analysis, Principal Component Analysis and Redundancy Analysis (version 3.10), Agricultural Mathematics Group, Wageningen.
- Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. *J. N. Am. Benthol. Soc.* 8: 36-50.

- Trotter, E.H. 1990. Woody debris, forest-stream succession, and catchment geomorphology. *J. N. Am. Benthol. Soc.* 9: 141-156.
- Vuori, K.-M. & Muotka, T. 1999. Benthic communities in humic streams. In: J. Keskitalo & P. Eloranta (eds), *Limnology of humic waters*: 193-207. Backhuys Publishers, Leiden, The Netherlands.
- Vuori, K.-M. and 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
- Wallace, J.B., Jackson, R.W. & Meyer, J.L. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. *Can J. Fish. Aquat. Sci.* 52: 2120-2137.
- Wallace, J.B., Eggert, S.L., Meyer, J.L. & Webster, J.R. 1999. Effect of resource limitation on a detrital-based ecosystem. *Ecol. Monogr.* 69: 409-442.
- Webster, J. R., Benfield, E. F., Golladay, J. W., Hill, B. H., Hornick, L. E., Kazmierczak, R. F. & Perny, W. B. 1987. Experimental studies of physical factors affecting seston transport in streams. *Limnol. Oceanogr.* 32: 848-863.
- Wiederholm, T. 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomologica Scandinavica Supplement* 19. Borgströms Tryckeri AB, Motala.
- Young, W. J. 1993. Field techniques for the classificatoin of near-bed flow regimes. *Freshwater Biol.* 29: 337-383
- Yrjänä, T. 1998. Efforts for in-stream fish habitat restoration within the River Iijoki, Finland: goals, methods and test results. In: L. DeWaal, A. R. G. Large & M. Wade (eds), *Rehabilitation of Rivers, Principles and Implementation*: 239-250. Wiley & Sons, Chichester.

ORIGINAL PAPERS

I

**Short-term recovery of benthos following disturbance
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II

Recovery of macroinvertebrate communities from stream habitat restoration

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III

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

by

Haapala, A., Muotka, T. & Laasonen, P.

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IV

**Enhanced leaf retention as a mechanism of
recovery in restored headwater streams**

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