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## Implications for Stream Restoration

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
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UNIVERSITY OF JYVÄSKYLÄ

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# ABSTRACT

Allochthonous organic matter originating from streamside vegetation is of
central importance in maintaining food webs and diverse life forms in small
woodland streams. In this thesis I studied how the seasonal availability of
particulate organic matter (POM) is reflected in the seasonality and community
composition of stream macroinvertebrates. I also studied the breakdown rates
of leaves from three deciduous tree species and their colonization by fungi and
macroinvertebrates, as well as the distributional patterns of detritivores and
their food resources in the streams of contrasting retentivity. The input of
allochthonous detritus in stream Rutajoki, Central Finland, was highly pulsed,
peaking in September-October. The standing stocks of benthic organic matter
were among the lowest reported for woodland streams. Minimum biomasses
and densities of total macroinvertebrates occurred in summer, and maximum in
mid-winter. Seasonality was most distinct among shredders, with 40–fold
higher biomasses in March than during the summer. The breakdown rates of
alder and birch leaves were fast, while willow leaves were processed at a
medium rate. Birch leaves contained the highest fungal biomasses while alder
supported the highest invertebrate numbers. Invertebrate community
composition was similar between the three leaf types, but differed distinctly
from the surrounding benthos. The aggregation of detritivores to retentive
stream patches was most pronounced in the channelized stream, while in the
natural stream they showed only weak association with benthic leaves. Due to
simplified habitat structure, channelized streams contained a group of indicator
species, whereas shifts between restored and natural streams were more
gradual. The poor retention capacity may severely limit the production of
detritivorous invertebrates. The presence of various leaf species is one of the
key elements in supporting vital populations of detritivores.

Key words: Benthic invertebrates; detritivores; forest streams; leaf litter
breakdown; Particulate Organic Matter, seasonality; stream restoration.

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# CONTENTS

# LIST OF ORIGINAL PUBLICATIONS

This doctoral thesis is based on the following articles, which will be referred to by their Roman numerals. I have designed, performed and mainly written the studies no. I-IV. In the study V, I participated in the statistical and graphical treatments of the data, and to a lesser extent, in writing of the manuscript.

I       Haapala, A. & Muotka, T. 1998: Seasonal dynamics of detritus and associated macroinvertebrates in a channelized boreal stream. Archiv für Hydrobiologie 142: 171-189.

II      Haapala, A., Muotka, T. & Markkola, A. 2001. Breakdown and macroinvertebrate and fungal colonization of alder, birch and willow leaves in a boreal forest stream. Journal of the North American Benthological Society 20: 395-407.

III     Haapala, A. & Muotka, T. 2001. Stream macroinvertebrate communities in leaf packs vs. benthos: does leaf type matter? Verhandlungen der internationale Vereiningung für theoretische und angewandte Limnologie (accepted).

IV      Haapala, A., Muotka, T. & Laasonen, P. 2000. Distribution of benthic macroinvertebrates and leaf litter in relation to streambed retentivity: implications for headwater stream restoration. Manuscript, submitted.

V       Muotka, T., Paavola, R., Haapala, A., Novikmec, M. & Laasonen, P. 2001. Long-term recovery of stream habitat structure and benthic invertebrate communities from in-stream restoration. Conservation Biology (accepted).

# 1 INTRODUCTION

All biotic communities, as well as individual organisms constituting these communities, depend on an energy supply for their activities. Organic matter generated within a community is called *autochthonous*, while the energy fixed in other systems and imported to the community as dead organic matter is called *allochthonous* (Begon et al. 1990). Small woodland streams, as forest soils and ocean beds as well, are treated as heterotrophic ecosystems: there most of the energy for consumers is of allochthonous origin (Cummins et al. 1973, Vannote et al. 1980, Wallace et al. 1997). A typical woodland stream with an overhanging canopy of vegetation is too shady for effective autochthonous production, i.e. the photosynthesis of algae and macrophytes. Most of the energy is derived from the litter shed by the surrounding vegetation; thus, allochthonous detritus dominates carbon and energy budgets. Furthermore, with the exception of streams flowing through tundra and desert, allochthonous inputs exceed those of autochthonous sources for most of the streams studied worldwide (Webster & Meyer 1997). In the streams of temperate zones, the autumnal senescence and shed of deciduous leaves create a vast amount of organic matter available for stream organisms (Bird & Kaushik, 1981, Weigelhofer & Waringer 1994, Benfield 1997). In the streams of northern latitudes with mixed coniferous forests, the absolute input rates are much lower (Cowan & Oswood 1983, Conners & Naiman 1984), but the seasonality of the input is probably even more pronounced (Haapala & Muotka 1998). Given that small shaded streams in temperate and boreal zones have limited algal productivity and a highly pulsed input of allochthonous detritus, it is not surprising that the maximum number (and even the maximum biomass) of benthic invertebrates occurs during the coldest period of the year (Mortensen & Simonsen 1983, Petersen et al. 1989, Meyer 1991, Haapala & Muotka 1998).

In aquatic ecology, leaves and other dead organic matter has been divided into fractions based on their size and solubility. Here I concentrate on fractions used by stream macroinvertebrates. Entire leaves and their parts, twigs, bark, fruit and seeds are termed Coarse Particulate Organic Matter (CPOM), consisting of particles larger than 1.0 mm. **Shredders** (e.g. Nemouridae

stoneflies, freshwater shrimp) are benthic invertebrates, which feed on CPOM, and thus fragment the coarse material by splitting and defecation. Fine Particulate Organic Matter (FPOM) is less than 1.0 mm in diameter and constitutes of dead algal cells, fragmented CPOM, and particles from e.g. forest floors. **Collector-filterers**, such as net-spinning caddisflies, remove FPOM suspended in water by various modes of filtration. **Collector-gatherers,** or deposit feeders, (e.g. *Ephemera* mayflies) collect FPOM from debris and sediments. The other Functional Feeding Groups (*sensu* Cummins 1973) may, at least in theory, control the rate at which their resources are produced. Grazers or **scrapers** consume mainly algae periphyton, but they also grasp other components of organic microlayer such as bacteria attached to stones and other types of substratum. Finally, **predators** consume other invertebrates as their food, and they could also be termed as carnivores. As it can be noticed, this classification of stream invertebrates is concerned more with the ways these organisms obtain their food, and less with the trophic roles of these consumers. In this thesis, I decided to combine shredders, collector-gatherers and collector-filterers to a collective group of **detritivores** which better describes their trophic role, i.e. feeding on dead organic matter. I used *a priori* classifications based on the scientific literature rather than considered the local differences in the utilization of varying food resources. Though relevant in a scientific context this may be misleading e.g. in the case of some omnivorous species.

The categorization of stream animals into distinct feeding groups has been occasionally critisized, because it neglects some important biological aspects, and its ecological relevancy is therefore questionable (Mihuc 1997, Ledger & Hildrew 2000). Some predatory invertebrates, for example, exhibit ontogenic changes during their life cycle, so that a larva eats algae and fine detritus during the earliest phases of its life, and later ingests only animal prey (Feminella & Stewart 1986, Malmqvist et al. 1991). Grouping animals only by their feeding mode may also be misleading if trophic relationships, seasonality and omnivory are taken into consideration (Hildrew et al. 1984, Friberg & Jacobsen 1994, Ledger & Hildrew 2000, Murphy & Giller 2000). For example, nymphs of *Heptagenia* (usually treated as scrapers) ingest diatoms as their main food item but they also consume detritus (Huhta et al. 1995). The growth rate of a shredding caddis, *Sericostoma personatum*, is distinctly higher when it feeds on filamentous green algae, compared with spruce needles and alder leaves (Friberg & Jacobsen 1999). The role of amorphous detritus and microbial loop (e.g. particle-associated bacteria and Protozoa) can also be substantial or even crucial in the energy uptake of stream macroinvertebrates (Hall & Meyer 1998).

Several stream ecologists have suggested that the spatial distribution and seasonality of detritivorous invertebrates is highly dependent on riparian inputs, and even on the composition of the riparian tree assemblages (Ross 1963, Vannote et al. 1980, Cummins et al. 1989, Grubbs & Cummins 1996). Therefore, modelling the stream ecosystem requires detailed knowledge on the input, retention and processing of the terrestrial leaf litter. Once the leaves fall into a stream, they break down in a sequence of leaching, conditioning and fragmentation. It has been stated that these processes occur distinctly (Webster

& Benfield 1986, Allan 1995), while Gessner et al. (1999) stressed that it may not be meaningful to separate these interactive and partly overlapping phases. In any case, a short period of leaching (dissolving of soluble organic compounds) and some degree of conditioning by microbes is usually needed before macroinvertebrates can use the leaves as their food (Kaushik & Hynes 1971, Graça et al. 1993). According to current knowledge, fungi overall constitute a majority (88-100%) of the microbial biomass on submerged, decaying leaves (Baldy et al. 1995, Weyers & Suberkropp 1996). However, the role of fungi in the breakdown process has been eagerly debated recently (for a review, see Gessner et al. 1999). Gessner et al. (1999) stated that fungi not only make the leaves more palatable for shredders, but also contribute to breakdown *per se*. Whatever the role of fungi is, the importance of detritivorous invertebrates usually overrides it in cold areas (Irons et al. 1994). However, experimental studies suggest that the relative contribution of stream invertebrates to leaf breakdown is around 20-35% (Petersen & Cummins 1974, Cuffney et al. 1990). Non-biotic factors affecting leaf breakdown include water temperature, pH, concentrations of nutrients, and water velocity through physical abrasion. While the consumption of stream organisms reduces the standing stocks of leaf litter gradually, spates and other disturbances during autumn and winter may have more dramatic effects on the availability of benthic leaves (Cummins 1980, Cowan et al. 1983, Grubbs & Cummins 1996). Therefore, seasonal food limitation of shredders inhabiting boreal streams is most likely to occur at the onset of spring, when shredders reach their maximum annual biomass and start a period of rapid growth prior to emergence, but nearly all of the fast-decaying leaf litter has disappeared (Grubbs & Cummins 1996, Haapala & Muotka 1998).

The input and breakdown rates of terrestrial leaf litter are not the only determinants of the availability of organic matter to detritivores. One of the most important factors regulating the standing stocks of benthic CPOM is the retention efficiency of a stream channel (Smock et al. 1989, Dobson & Hildrew, 1992, Dobson et al. 1995). Streams with natural channel morphology have heterogeneous substrate, turbulent flow patterns, a meandering channel form, and pool-riffle alterations. Channelized streams typically have weakened retention efficiency, due to homogenous bed morphology, more laminar flow patterns and lack of pool-riffle alterations and side-channels, leading to reduced residence time. Obstructions to stream flow, like boulders and large woody debris, effectively enhance the stream retentiveness (Bilby & Likens 1980, Smock et al. 1989). Because many stream invertebrates have a tendency to aggregate in retentive stream patches (Dobson & Hildrew 1992, Dobson et al. 1995, Murphy & Giller 2000), it has been theoretized that the association of detritivorous invertebrates with leaf accumulations is strongest in streams of lowest retentiveness (Dobson 1991). Furthermore, there is a good reason to assume that shredding invertebrates may face severe food limitation in channelized streams with negligible amount of benthic leaves, especially in late spring (Haapala & Muotka 1998). Therefore it has been suggested that adding retentive structures to stream bed would be a valuable management tool for improving acidified upland streams with poor retentiveness (Dobson et al.

1995). Restoration of channelized rivers using such retentive structures has clearly enhanced the retention efficiency, but the effects on stream macroinvertebrates have not been as positive as might be expected (Laasonen 2000, but see Friberg et al. 1998).

Small streams are transition zones between terrestrial and aquatic ecosystems, and therefore of central importance in maintaining aquatic biodiversity, as well as good water quality in rivers and lakes (Allan 1995, Dobson & Cariss 1999). The degradation of water resources often begins in upland areas of watersheds, as human activity alters the plant cover. The removal of riparian vegetation leads to many changes, including higher water temperatures, a possible shift from heterotrophy to autotrophy, a decrease in the production of many invertebrates, reduced bank stability, and the loss of natural capacity to prevent sediments and nutrients from reaching the stream channels (Allan 1995, Wallace et al. 1999). Channelization and dredging of streams, in turn, has resulted in simplified flow patterns, lower retentiveness for organic matter, an increased load of nutrients and fine sediments, and the loss of nursery habitat for many valuable fish species (Petersen et al. 1992, Laasonen et al. 1998). The result of intensive forestry, agriculture, and hydraulic engineering has produced a need to restorate the vegetation to more natural-like conditions. Maintaining or re-establishing the inputs of riparian detritus is an essential element of the conservation or restoration of diverse riverine food webs (Wallace et al. 1997).

Research reported in this thesis was related to stream macroinvertebrates and their association with allochthonous organic matter. One of the most important questions was how these organisms are distributed in relation to patches rich in leaf litter in natural and channelized streams, and how stream restoration affects these relationships. The seasonality of particulate organic matter and functional feeding groups was studied during a year-round survey in a channelized woodland stream to identify potential bottlenecks limiting the production of detritivorous invertebrates. For this purpose, the life cycles of the three most abundant shredders were also studied as a by-product of the same sampling protocol. The breakdown rates of leaves from three common deciduous tree species, as well as their colonization by aquatic fungi and invertebrates, were examined in winter to assess their relative importance for detritivores. The invertebrate community composition of benthic leaf packs was compared with random patches on the stream bed, and the invertebrate communities of channelized, restored and natural streams were examined to identify the indicator taxa for each stream type.

The applied nature of this thesis is related to in-stream restoration and its biological effects in headwater woodland streams. Restoration of channelized streams is nowadays being carried out in a large number of Finnish rivers and streams, but relatively little is known about its ecological consequences (see, however, Laasonen 2000). One of the prime objectives of this thesis was to evaluate how restoration measures planned to enhance the production of juvenile salmonids affect other stream biota, using invertebrates and the allochthonous food-chain as indicators for these changes.

# 2    MATERIALS AND METHODS

## 2.1 Study streams

Small rivers and streams in central and northeastern Finland have been the scene for this thesis. River Rutajoki in central Finland (62°N, 26°E) belongs to the river Kymijoki water catchment, draining 180 km² of bogs and woodlands and emptying into Lake Päijänne. All the studies except V were performed there. Study no. IV was partly conducted in a small second-order stream Merenoja, a tributary to river Oulankajoki near the Russian border (66°N, 29°E). The last study consisted of 14 streams in northeastern Finland (63°-66° N, 27°-30° E), a majority of them belonging to the catchment area of river Iijoki. All these rivers run through mixed coniferous forests, whereas the riparian zone of river Rutajoki is dominated by deciduous tree species, like silver birch (*Betula pendula* Roth.), grey alder (*Alnus incana* L.), European aspen (*Populus tremula* L.) and willows (*Salix* spp.). Therefore, the annual litter input is two to threefold in the river Rutajoki when compared to small streams in northeastern Finland (Haapala et al. unpub.). Study streams are circumneutral, oligotrophic and oligohumic streams (water colour between 20-40 mgPt/l), with some mesohumic streams (colour range: 50-100 mgPt/l) in the Iijoki water district. Water temperature varies annually between 0-25 °C, with the annual termal sum ranging between 2600-2740 degree days in Rutajoki (Syrjänen et al. unpubl.) and 1920 degree days in Merenoja (Muotka & Virtanen 1995). Ice covers these streams from three to six months, and the melting of snow causes spring floods between the end of April and the beginning of June. Streamside forests have intensively been used in forestry, and most of the streams have been channelized for timber floating in the 1950's. Most of the previously channelized streams have now been restored. In Rutajoki, the restoration took place in October 1997, after which the stream bed became more heterogeneous. A majority of streams included in study no. V was restored in the early 1990's.

## 2.2 Seasonality of stream macroinvertebrates and allochthonous organic matter (I)

Benthic samples were collected in the river Rutajoki once a month from 15 September 1993 to 19 August 1994 to find out the seasonal fluctuations in the quantities of benthic invertebrates and detritus. Three standardized kick net samples (each from a 0.33 m² area) were taken on each occasion from randomly selected cross-transects. In the field, these samples were stored in 70% ethanol, and macroinvertebrates and detritus were later sorted in the laboratory. Invertebrates were identified to the lowest feasible taxonomic level (mainly species or genus) and assigned to functional feeding groups (FFG) according to Merritt & Cummins (1978; see also Malmqvist et al. 1978). The abundances and biomasses of FFG's, as well as the total number of invertebrates, were measured from each sample. All the remaining material was sieved, and detritus particles larger than 10 mm were divided into leaves and wood. Particles between 1-10 mm were treated as miscellaneous CPOM, and particles less than 1.0 mm as FPOM. The different fractions of organic matter were dried at 60 °C for 24 h, weighed, ashed in a muffle furnace (3 h 550 °C) and reweighed to determine their ash free dry masses (AFDM).

Sampling of leaf litter was performed both at the streamside forest and stream channel to find out how the food base of detritivores varies seasonally. Leaves, woody fragments, seeds and other plant litter were collected near the shoreline using eight boxes, placed along both shores of the study section. These boxes were set up on 4 June 1996 and emptied regularly until 12 November, when leaf falling had ceased. Litter samples were divided into species-specific leaf detritus, woody detritus and miscellaneous plant detritus. AFDM for each category was measured to the nearest 0.01 g. For the estimation of the in-stream autumnal accumulation of leaf litter, 12 sampling squares were established in the same study section. A 25 x 25 cm -frame was used to delineate the square, and all leaf material within it was collected by hand at weekly or biweekly intervals from 1 September to 15 November. The dry mass of each sample was measured, and the standing stock of benthic leaves was calculated using linear regression between the dry mass and AFDM. Since retention is known to affect the standing stocks of benthic CPOM, a series of leaf release experiments were done to examine the retention capacity of the study site. Five hundred plastic strips (4 * 8 cm) were released into water surface at the upstream end of a 50-m long study stretch. After 3 h those leaves that had travelled through the study section were counted. These leaf release experiments were performed at five discharges from 0.46 to 1.52 m³/s.

## 2.3 Breakdown and colonization of alder, birch and willow leaves in a boreal stream (II)

This study was set up to examine the processing rates of the leaf types commonly dominant in the riparian zones of boreal woodland streams, as well as their importance as food for shredders. Before this study, there were no published studies of the breakdown rates and associated animal and microbial colonization of leaves from Scandinavian deciduous tree species. Leaves of grey alder (*Alnus incana* L.), silver birch (*Betula pendula* Roth.) and willows (mainly *Salix myrsinifolia* L.) were collected in October 1996 and dried to a constant weight. Leaf portions of 2.0 grams of each leaf species were packed into mesh bags, and placed into a riffle site in the stream Rutajoki. A total of 90 bags were attached firmly on the stream bottom on October 18. Thereafter, 4-5 randomly selected replicates for each species were collected 1, 7, 33, 82, 111 and 169 days from the start of the experiment to determine (i) species-specific leaching and breakdown rates, (ii) fungal colonization and (iii) invertebrate colonization. Each mesh bag was carefully transferred to a plastic box filled with tap water, and the bags were then returned to the laboratory in a cool box. In the laboratory, the leaves were rinsed to remove attached sediment particles and macroinvertebrates. Leaves were then dried at 60°C for 24 h to determine their dry masses. Animals retained by a sieve with a mesh size of 0.25 mm were preserved in 70% ethanol and later identified to species or genus. Larval blackflies were excluded from further analyses, because they mainly colonized the anchoring structures, not the mesh bags themselves. All the other invertebrates were assigned to functional feeding groups according to Malmqvist et al. (1978) and Merritt and Cummins (1996). Chironomids were divided into 3 feeding groups: filterers (mainly *Rheotanytarsus* spp.), collector-gatherers (Orthocladiinae) and predators (Tanypodinae) (see Wiederholm 1983, Chauvet et al. 1993). The biomasses of the dominant shredder species were measured using regression equations between head capsule widths and dry masses (Meyer 1989). Fungal biomasses were estimated at each sampling day except day 1 using the ergosterol bioassay (Newell 1992). Ergosterol concentrations were converted to fungal biomass using the ratio of 5.5 μg ergosterol per 1 mg fungal dry mass (e.g. Robinson and Gessner 2000).

To examine how the life cycles of some shredder taxa are related to seasonal variation in the availability of leaf litter, we used independent material collected during study I. The head widths of the specimens of *Amphinemura borealis* (Mort.), *Protonemura meyeri* (Pict.) and *Nemoura cinerea* (Retz.) were measured from samples taken at ca. monthly intervals from September 1993 to August 1994. Growth increments were expressed as mean specific growth rates, calculated according to exponential growth model and expressed as percent body mass/day.

## 2.4 Community structure of stream macroinvertebrates in leaf bags of alder, birch and willow vs. benthos (III)

During winter 1996-97, quantitative random samples of the stream benthos were collected concurrently with the study of leaf breakdown (II) to find out whether the leaf bag colonists consist of a random sample of the local species pool or whether a distinct subgroup of benthic animals are involved in the colonization process. These samples were taken in October, January and the beginning of April, corresponding to 7, 82 and 169 days of exposure of the leaf bags. On each occasion, six Surber samples were taken from the stony benthos adjacent to the leaf breakdown and colonization study. Invertebrates were treated as in studies I, and II, without any biomass and growth estimations. Hovever, to make comparisons with the leaf bag samples more reliable, larval blackflies were excluded from all analyses (see previous chapter). In all statistical treatments, absolute numbers were converted to relative abundances in each sample type (Surber samples, leaf bags of alder, birch and willow leaves) because of the differences in sample area. Taxonomic composition of the different sample types (leaf bags of the three leaf types and benthos) was then compared using an index of similarity and Non-metric Multidimensional Scaling (NMDS) ordination method. Indicator value method (Dufrene & Legendre 1997) was performed to identify the species characteristic for each sample type.

## 2.5 Distribution of macroinvertebrates and benthic CPOM in streams with contrasting retention properties (IV)

An extensive sampling programme of benthic detritus and macroinvertebrates was carried out in order to determine if invertebrates are spatially aggregated to most retentive stream sites, and if there are any differences in this pattern between a channelized, restored and natural stream. A total of 150 quantitative samples were taken after leaf abscission from a natural stream Merenoja, as well as from stream Rutajoki before and after its restoration during years 1996 and 1997. Before sampling, a leaf release experiment was conducted to characterize retentive stream structures. Benthic samples (0.04 $m^2$ Surber sampler) were then collected from microhabitats that retained leaves ('retention sites') and randomly located stream patches ('random sites'), taking 25 samples for each patch type. Macroinvertebrates were picked and identified to species or genus level (except for Dipterans), and divided to functional feeding groups. Leaves and leaf fragments were oven dried at 60 °C for 24 hours and weighed for dry masses.

The three stream types were treated separately in statistical tests, because there was no replication for the stream type. Differences in the mass of benthic leaves and densities of functional feeding groups between the sample types were tested using independent sample t-tests. Morisita's index was used to examine the distribution patterns of various macroinvertebrate groups. Regression analysis was used to examine the relationships between leaf litter and animal densities in the benthic samples. The analysis of covariance was used to test the homogeneity of the regression slopes for each stream.

## 2.6 Long-term recovery of benthic habitat structure and macroinvertebrate communities from in-stream restoration (V)

The retention capacity of a stream is one of the key processes shaping the biotic communities of headwater streams, and the restoration of channelized streams should enhance their retention efficiency (Laasonen et al. 1998). Despite this apparent environmental gradient, little is known about the long-term effects of stream restoration on organisms other than game fish. The prime objective of this study was to evaluate how restorations conducted for fishery purposes affect other stream biota, using benthic invertebrates as the target organisms. In 1997, the channelized, restored and natural streams previously sampled by Laasonen et al. (1998) were resampled taking samples from three streams of each group. The time for recovery in restored streams was now four, six and eight years, each 'restoration year class' having three replicates. Samples of benthic invertebrates were collected using standardized kick netting, with four 60 -second samples being taken at each stream. The preservation and laboratory methods were the same as in the previous studies (I-IV), except that biomasses were not measured. Macroinvertebrates were identified to the lowest feasible taxonomic unit, usually to species level. Simuliids and chironomids were identified only to the family level, and they were therefore excluded from all statistical analyses.

Physical variables were measured to quantify changes in the stream habitat structure during the time elapsed since restoration. At each stream site, we measured water depth (D), current velocity, substrate size and percentage moss cover at 30-50 random points along evenly placed transects. Stream bed heterogeneity was quantified as relative bed roughness (k/D). The amount of benthic leaf litter was quantified by collecting all the leaves and leaf fragments from eight 0.1 m² quadrates at each site. The differences between the groups in physical habitat characteristics were examined by discriminant analysis.

The data from the study by Laasonen et al (1998) and this study was combined and analysed using NMDS, an ordination method highly suitable for discontinuous data sets (McCune & Mefford 1995). Our primary interest was to

find out if the invertebrate community structure in the restored streams resembles more natural streams as the recovery period gets longer. The Indicator Value method was used to identify the species characteristic of each of the five stream groups (the channelized and natural streams, and the streams restored 4, 6 and 8 years before sampling). Finally, we examined the persistence in species rankings for all the sites that were sampled in both studies. This was done by calculating Spearman rank correlations between the abundances in the years 1992-93 and 1997 of the 15 or 20 species that were the most abundant at each site on the earlier sampling occasion. This was done to test whether the benthic communities at the restored sites varied more between the years than the natural stream benthic communities.

# 3  RESULTS AND DISCUSSION

## 3.1 Seasonality of macroinvertebrates and their allochthonous food base (I and II)

Seasonal variation in the biomasses and abundances of functional feeding groups, as well as total macroinvertebrates, was statistically significant. Generally, most feeding groups attained their maximum densities and biomasses during winter, while seasonal minimum occurred in June or July. Seasonality was most distinct among shredders with fivefold higher densities and 40–fold higher biomasses in March than during the summer months. The maximum shredder biomass occurred five months after the peak availability of whole-leaf detritus. This pattern was also observed by Petersen et al. (1989), and it may be connected to the "conditioning times" required to make leaves palatable for shredders. Cummins & Klug (1979) proposed that the maximum ratio of shredder biomass to benthic leaf biomass occurs at a point when leaves have lost about 50 % of their original weight. This hypothesis was not supported by our results, since the maximum biomasses of shredders (both as absolute biomass and biomass related to leaf mass) occurred when 85-98 % of the fast-decaying leaves were processed. The biomasses and densities of total invertebrates tracked closely the seasonality of total benthic CPOM, and reached their annual peaks in March (1.2 g DW / m² and 2300 individuals / m²), while the minimum density (620 ind./ m²) occurred in July and the minimum biomass in August (0.3 g DW / m²).

There can be some risks when interpreting these differences between summer and winter densities to be merely the influence of seasonality not to mention the influence of availability of CPOM. Some source of error my be caused by the semi-quantitative sampling method, low number of replicates and the seasonal differences in the spatial distribution of stream animals. For example, strong aggregation of stream invertebrates is caused by the late autumnal transition to mid-channel from areas prone to freezing (Olsson 1981). However, many previous studies have also reported the annual maximum of

biomasses during the coldest period of the year (Mortensen & Simonsen 1983, Petersen et al. 1989, Meyer 1991), but seasonal differences in those temperate streams were not as distinct as in our study. However, Murphy & Giller (2000) found a peak in total invertebrate densities during early autumn in two Irish streams. Total invertebrate abundances in all these studies mirrored closely fluctuations in benthic detritus (but see Petersen et al. 1989), which may indicate that these communities are highly dependent on the autumnal pulse of leaf input, and thus on the vegetation growing in the streamside forests.

The seasonality was also pronounced in the litter input and benthic accumulation studies. Roughly 75 % of the direct litter input occurred during one month – from the beginning of September to early October. The daily input rate varied from a maximum of 13 g AFDM / $m^2$ in late September to a minimum of 0.1 g / $m^2$ in November. Leaf litter alone consisted 87 % of the total annual input, with birch leaves being the major contributor. Total annual litter fall, 310 g AFDM / $m^2$, was in the lower end of values reported for similar-sized watersheds in temperate regions (Weigelhofer & Waringer 1994, Benfield 1997). Closely similar values have been reported for alder-dominated watersheds in southern Sweden (Otto & Svensson 1983) and Canadian woodland streams (Conners & Naiman 1984, Richardson 1992).

The accumulation of benthic leaf litter followed closely the autumnal leaf input. A distinct peak with 17 g AFDM / $m^2$ occurred during the first half of October, followed by a steady decline, until practically no new leaves appeared in November. A similar pattern of leaf accumulation is documented for a north Swedish stream by Malmqvist & Oberle (1995), except that benthic leaf biomass was overall somewhat higher in Rutajoki. Nevertheless, the mean annual standing stocks of total CPOM and FPOM in our study stream are among the lowest reported in the literature. Even in a subarctic stream in Alaska, where litter input was 4-5 times lower than in Rutajoki, the maximum standing stock of CPOM was nearly twice that in Rutajoki, and the standing stocks of FPOM were much higher throughout the year (Cowan & Oswood 1983). Since our stream was poorly retentive (on average, 26 % of the artificial leaves were retained within a 50 meter section), this apparent controversy is probably caused by lower substratum heterogeneity in Rutajoki.

The growth patterns of *Protonemura meyeri* and *Nemoura* spp. nymphs tracked the seasonal variation in the standing stocks of benthic leaves. Small nymphs first appeared in benthic samples during August-September, then entered a period of rapid growth, coinciding with the increasing availability of their food. The growth of these two taxa nearly ceased in late November, but then proceeded more slowly from February onwards. An almost opposite pattern was noticed in *Amphinemura borealis*; the nymphs of this species developed slowly during the peak availability of benthic leaves, but started to grow rapidly during spring. Thus, *Amphinemura* may be considered as a spring-summer shredder, while *N. cinerea* and *P. meyeri* are more likely autumn-winter shredders (see Cummins et al. 1989). Obviously, if *A. borealis* is an obligatory shredder, it should benefit from the presence of slowly decaying leaves in spring, as for example from willow.

## 3.2 Breakdown and colonization of alder, birch and willow leaves (II)

Leaf litter decomposed relatively fast in this study, despite cold water temperatures and partial ice cover during the winter. The loss of leaf mass was fastest in the beginning of experiment; thus, the exponential breakdown model described best the dynamics of weight loss in all three leaf types. The loss of mass due to leaching (first 24 hours) was 14 – 19 % of the original dry weight. Alder leaves were processed fastest, while the breakdown of willow leaves was slowest during all phases of the study. According to leaf breakdown rates, alder and birch were assigned to 'fast' processing category, while willow leaves were processed at a slow-to-medium rate. In early April, after 169 days of exposure, alder leaves had lost 98 % of their original mass, whereas 85 % and 61 % were lost from birch and willow leaves, respectively. Thus the deciduous tree species studied here formed a range of processing rates, translating into a continuum of litter availability for invertebrates.

Ergosterol concentrations during the study were relatively low, as compared to values reported in other studies in cold areas (e.g. Gessner et al. 1998, Robinson & Gessner 2000; but see Griffith & Perry 1994). Birch leaves contained the highest overall fungal biomass. Fungal colonisation increased markedly during the first month of exposure in all leaf types, after which it remained almost constant in birch and willow, but decreased in alder. The abundances of macroinvertebrates also increased markedly during the first month, after which they stabilised for alder and willow. A somewhat different colonization pattern was observed for birch, with a steady increase until January and a maximum density at the end of the experiment. Shredders and collector-gatherers were the most numerous leaf-pack colonists. There were significant differences in total macroinvertebrate numbers per g leaf mass between the leaf types, alder leaves being generally the most densely populated.

The fastest breakdown rates reported for the leaves of alder and birch are likely to occur because they have the highest initial nitrogen content (Gessner & Chauvet 1994) whereas inhibitory substances, such as lignins and phenolics, occur at highest concentrations in willow leaves (see e.g. Keinänen et al. 1999, Kull 1998, Nyman & Julkunen-Tiitto 2000). This should lead to higher palatability and feeding rate for invertebrate consumers. In this study, alder supported greater amounts of total macroinvertebrates than birch and willow (see also Cowan et al. 1983). However, shredder abundances were a bit higher in birch leaves, which also contained the greatest concentrations of ergosterol throughout the study. The differences in shredder abundances between the leaf types were, however, non-significant.

The facilitative role of stream microbes for shredder feeding has recently been questioned by Gessner et al. (1999). They stated that "fungi also promote mass loss directly in that they release enzymes that cleave structural plant

polymers, and assimilate and convert the resultant organic matter to $CO_2$ and biomass". The decreasing ergosterol concentrations found in alder leaves after the first month of exposure could partly reflect this phenomenon. The colonization sequence of shredders suggests that they first prefer leaves of highest palatability, which in turn causes the fastest breakdown of alder leaves. At a certain point, when alder leaves approached the completion of processing, invertebrate abundances increased somewhat on birch and willow leaves. This phenomenon (i.e. increase in invertebrate abundances on birch and willow leaves) occurred at a time when dominant shredder species entered their winter-spring growth period. Given that seasonal food limitation is likely to occur by the end of winter in this stream, this continuum of processing and availability of various leaf types may be a key element in supporting vital populations of detritivores.

## 3.3 Community structure of stream macroinvertebrates in leaf bags of alder, birch and willow vs. benthos (III)

Invertebrate communities inhabiting mesh bags of alder, birch and willow showed remarkable similarity with the surrounding benthic communities in January (mid-experiment), but not in the beginning and especially at the end of the experiment in April. The percent similarity between the leaf bag samples and the benthic samples attained its maximum value in January. Similarity values (leaf type vs. benthos) did not differ between the leaf types, whereas seasonal differences were highly significant. These results were also supported by the NMDS –ordinations: in January, the leaf bag communities differed less from the adjacent benthos than on the other two occasions.

Species assemblages between the four sample types were overall distinctly different, but this was mainly due to the fact that benthic samples contained many taxa that were completely lacking from, or occurred in low numbers, in the leaf bag samples. Indicator value analysis revealed that Surber samples were characterized by greater abundances of Oligochaetes, elmid beetles and *Agapetus ochripes*, *Chimarra marginata* and *Hydroptila* sp. caddis larvae. Very few taxa could be regarded as indicators for any of the leaf types, the only exceptions being the shredder species *Protonemura meyeri* (birch leaf bags), *Potamophylax cingulatus* (alder) and a predator *Isoperla* spp. (willow). Collecting-gatherers and shredders occurred in much higher relative proportions in the leaf bags than in the benthos. On the other hand, filterers and especially scrapers were clearly underrepresented in the leaf bag samples, especially from January onwards. The relative proportion of predators was rather constant, irrespective of the sample type. An interesting detail is that the relative abundance of collectors and shredders in the leaf bag samples was still quite high at the end of the experiment, when only 5-15 % of the initial weight of

alder and birch leaves remained. These highly decomposed leaves are probably not optimal food for shredders, but they do support relatively high fungal biomass (II). This fading resource, and especially the less fragmented leaves of willow, is probably important in the nutrition of detritivores in late spring, when many shredder species approach their emergence.

Alike the few earlier documents of the taxonomic composition of faunal assemblages inhabiting different leaf types (Short et al. 1980, Malmqvist & Oberle 1995), we found only minor differences in the community composition between alder, birch and willow leaves. Although the apparent similarity was observable in both the ordination method and the indicator value analysis, this pattern may be partly due to the relatively long sampling interval used. According to Dobson (1994), macroinvertebrate communities colonizing a leaf type should differ most from the surrounding benthos when that leaf is most palatable for shredders. Furthermore, a leaf type should be most palatable to consumers when about 50 % of the leaf material has been decomposed (Cummins et al. 1989). This stage was reached after 36 to 63 days of exposure for alder and birch, respectively (II). Therefore, a set of mesh bag and benthic samples collected between our first and second sampling dates (between 7 and 82 days) might have revealed more distinct differences in the structure of species assemblages inhabiting different leaf types.

## 3.4 Distribution of benthic macroinvertebrates and leaf litter in relation to streambed retentivity (IV)

The retention capacity of stream Rutajoki increased via restoration from 25 % (channelized) to 75 % (restored) of artificial leaves retained, attaining the levels of a natural stream Merenoja (76 % of leaves retained). The most retentive substratum feature in the natural stream was the stream bank. Stones and boulders trapped the majority of leaves in the channelized stream before restoration, whereas debris dams were the most effective retention structure thereafter. The quantity of benthic leaves was significantly higher in the retention sites than in random sites in all the three stream types, but the difference between the patch types was most distinct (28 fold difference) in the channelized stream before its restoration. After restoration, the overall benthic standing crop of leaves was remarkably higher, as it was also indicated experimentally by the higher rate of retention.

Total macroinvertebrate densities were higher in the retention than in random sites in all the streams, although the difference was not significant for stream Merenoja. The highest mean densities, exceeding 500 individuals / 0.04 $m^2$, were found in the retention sites of stream Rutajoki after restoration. In Rutajoki, densities in the retention sites were roughly twice as high as in random sites, both before and after restoration. The densities of shredders and other detritivores were significantly higher in the retention than in the random

sites in Rutajoki, both before and after restoration, but not in Merenoja, which supported the highest overall shredder densities. The densities of predatory and algae-scraping invertebrates differed very little or not at all among the patch types in any of the streams. In all the stream types, some shredder taxa (e.g. nemourid stonefly nymphs and limnephilid caddis larvae) were significantly more abundant in the retention than in the random sites. According to Morisita's index of dispersion, total macroinvertebrates and detritivores exhibited a strongly aggregated distribution in all the stream types. However, invertebrates and benthic leaves tended to be most aggregated in the channelized, and least so in the natural stream.

The regression analysis showed that the dry weight of leaves was good predictor of macroinvertebrate densities. In all the stream types, except the natural stream Merenoja, there was a significant relationship between the leaf mass and density of total invertebrates. The mass of benthic leaves explained even better variation in the densities of detritivores, but not in densities of shredding invertebrates in any of the stream types. However, the major shredder *Nemoura* spp. displayed a strong positive relationship to the amount of leaves in all the stream types, most strongly so in the channelized stream.

Our results parallel those of Dobson & Hildrew (1992) for southern English streams with contrasting retentivity. Overall, the densities of shredders were higher in the stream Merenoja, whereas the association of detritivores with leaf packs was more distinct in the less retentive stream Rutajoki, both before and after restoration. 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). In natural streams other variables, like stream velocity and substrate composition, may also regulate the densities and distribution patterns of detritivores.

The restoration of river Rutajoki reduced slightly the dependence of detritivores on leaf packs, with the exception of *Nemoura* stoneflies. After restoration, the densities of most detritivorous taxa were still higher in the retention than the random sites, although then the difference between the patch types was usually less distinct. This change was relatively small, however, considering the fact that the retentive capacity of the stream was clearly enhanced by the restoration.

## 3.5 Long-term recovery of benthic habitat structure and macroinvertebrate communities from in-stream restoration (V)

Physical habitat structure showed a distinct improvement from recently restored streams to the oldest restorations ('+8 streams') along a gradient in

moss cover (DFA axis 1). The second discriminant function displayed a gradient from channelized to natural streams and streams restored three years before sampling, based on the streambed complexity. Streams restored 8 years before sampling and the natural streams supported significantly higher amounts of benthic leaves than the channelized streams, and they also contained higher densities of shredders and detritivores.

The overall community structure was significantly different between the five stream groups. Channelized streams supported a characteristic set of indicator species, whereas shifts in the species composition between the restored and the natural streams were more gradual. Species almost exclusively found in the channelized streams included the filterers *Sphaerium* sp. and *Hydropsyche siltalai*. This stream type was also characterized by some algae-feeding species, and the predators *Rhyacophila nubila* and *Wiedemannia* sp.. The higher heterogeneity of the other stream groups was revealed by the generally lower indicator values for species in these groups. Almost all the indicator species typical for +8 streams were shredders, like *Leuctra* and *Protonemura* stoneflies, but the natural streams were characterized by a functionally more variable set of invertebrates. NMDS ordination, where the two sampling occasions (1991/1992 vs. 1997) were compared, as well as Spearman rank correlations between the species rankings, showed that macroinvertebrate communities in the natural streams changed only little between the two surveys. On the contrary, most of the restored streams had undergone considerable changes in the community structure, e.g. taxon richness had increased significantly in more recently restored streams. It thus appears that macroinvertebrate communities vary drastically during the first few years after restoration, but soon turn more persistent with less year-to-year variability in the relative abundances of the species. One possible reason for the fluctuations after restoration may be the loss of mosses due to the restoration practises used (see Laasonen et al. 1998). Aquatic mosses are slowly growing organisms (e.g. Sand-Jensen et al. 1999) and they have a key role in the trophic dynamics of many streams because of their importance as beneficial microhabitats for benthic invertebrates (e.g. Suren & Winterbourn 1992, Wallace et al. 1997). Since the mosses had recovered after the disturbance caused by restoration works, the restored stream habitat resembled to some extent the natural reference streams we studied.

# 4    CONCLUDING REMARKS

The aim of this thesis was to evaluate the role of allochthonous organic matter, mainly in the form of deciduous leaf litter, in the seasonality and community composition of stream macroinvertebrates and the life cycles of the dominant leaf-shredding invertebrates in boreal woodland streams. Considering the changes caused by in-stream restoration to these dynamics, I attempted to find out how the increased retention capacity in a stream affects the distribution and community composition of stream invertebrates and which species benefit from restoration on a longer time scale. A secondary question was how fast leaf litter from different deciduous trees is processed and how much this litter contributes to the feeding of detritivores. All the studies were performed in small woodland streams with good to excellent water quality and an intact riparian zone, but a considerable variation in their retentive properties.

The results of the study no. I revealed that a strong seasonality is likely to occur in the biota of small headwater streams with an intact riparian canopy. A vast majority of leaf litter input occurred within one month in the beginning of autumn, followed by a rapid accumulation of benthic leaves in early October. The availability of whole-leaf detritus decreased thereafter, whereas the amount of miscellaneous CPOM and FPOM increased at the same time. The densities of most functional feeding groups followed the same pattern, increasing from November onwards. The majority of species attained their maximum densities and biomasses during winter, while a distinct annual minimum occurred in June or July. This may indicate that of the whole community has a strong dependency on coarse particulate organic matter in small woodland streams such as in Rutajoki. Seasonality was most pronounced among shredders, with 40-fold higher biomasses in March than during the summer months. The maximum shredder biomass occurred five months after the peak availability of unprocessed leaf detritus, when only remnants of the fast decaying leaves were left. Building on the studies I, II and IV, I concluded that shredding invertebrates must face a severe and long-lasting seasonal food shortage in channelized boreal streams. The poor retention capacity of such streams may

limit the whole invertebrate community, keeping the densities of macroinvertebrates at a low level (see also Laasonen et al. 1998).

The aggregation of many detritivorous taxa to patches containing leaf litter was obvious, especially in the channelized stream. This result supported Dobson's (1991) hypothesis that the association of benthic invertebrates with leaf accumulation is strongest in streams of lowest retentiveness. A weaker aggregation by most detritivores to retentive patches in the natural stream also suggests that these invertebrates are less food-limited in natural streams with plenty of leaf packs. While this study was not designed to test the importance of leaf packs as food vs. microhabitat, it provided circumstantial evidence that detritivores inhabit leaf accumulations primarily for the food they offer (see also Dobson et al. 1992, Richardson 1992). Furthermore, given the limitations in recovery time, stream restoration clearly enhanced the retention of stream bed, but only slightly reduced the dependency of detritivores on benthic leaves.

I found no evidence to support the idea that willow should be treated as a weed in the management of small streams (see Kärkkäinen 1998). Grey alder leaves broke up most rapidly, but neither fungal biomasses nor invertebrate parameters differed much between alder and willow leaves. Obviously, the abundance of high-quality food like alder leaves should benefit shredder welfare (see e.g. Irons et al. 1988). However, it has been stated that the existence of both 'slow' and 'fast' leaf types ensures food availability for shredders throughout the year, and thus supports a diverse macroinvertebrate community (Golladay et al. 1983, Cummins et al. 1989, Vought et al. 1999). Our results clearly indicate that all riparian species of deciduous trees have an important role in providing food for detritivores, and there is no reason to ignore any native tree or shrub species in riparian re-vegetation projects (see also Dobson & Cariss 1999).

Several land-use practises throughout the world have been directed to riparian zones, and an increasing demand for wood and arable land will degrade the biodiversity of streamside forests and wetlands still in natural state (Allan 1995). Therefore, maintaining the integrity of riparian vegetation, as well as re-vegetation of bare stream banks with a diverse tree community, should be an ultimate task in the future stream management programs. In addition, streamside buffer strips are also efficient in the processing and retention of suspended solids and nutrients, which should also be taken into account in the re-vegetation programs of streams draining cultivated lands (e.g. Petersen et al. 1992).

These results provide valuable information for improving stream restoration measures, keeping in mind that the central finding of this thesis was the strong seasonality of detritus dynamics and benthic communities in small streams of the boreal zone. One of the implications is that performing restoration activities during winter and early spring is not recommendable, if the goal is to increase the benthic macroinvertebrate production in these streams. This conclusion is based on two case studies conducted in Finnish woodland streams. Tikkanen et al. (1994) reported a rapid recovery of benthic animals after in-stream restoration performed in midsummer; this was mainly

caused by high rates of colonization. It may be possible that the rate of colonization is slower during winter, although Korsu (unpubl.) has noticed relatively fast recovery of invertebrate densities in a lake-outlet stream during January-March.

In addition to ordinary restoration structures, some amount of large woody debris (LWD) may also be beneficial for the stream biota, because of its effectiveness in trapping leaf litter and sediments (Dobson & Cariss 1999). In addition, LWD provides a suitable habitat for invertebrates and fishes (Cowx & Welcomme 1998). Finally, the conservation of intact riparian zones with diverse communities of trees and shrubs must be a major goal in any management project of headwater streams, and the clearance of streamside vegetation should strongly be avoided.

A general theme covering all the studies in this thesis was the questionable nature of functional feeding group categorization (see the Discussion in the papers I, II, and III). This categorization has often been critisized because it largely ignores ontogenic changes, seasonality and omnivory (e.g. Malmqvist et al. 1991, Friberg & Jacobsen 1994, Ledger & Hildrew 2000). For example, assigning first instar larvae of *Isoperla* stoneflies to the predatory feeding guild, or early larval stages of *Amphinemura borealis* to the shredder guild, may be highly misleading. Finally, in order to understand better the relative role of terrestrially derived detritus in the food webs of boreal streams, more has to be known about the role of autochthonous production, as well as about the microbial loop in these streams. What is the role of periphytic algae in relatively cold, boreal woodland streams? Could algae possibly provide food for 'shredders' during the springtime food depletion? Answering these questions would require an extensive research programme, including the analysis of the gut-contents of detritivorous taxa from a wide variety of stream habitats, not to mention feeding experiments in the laboratory.

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# YHTEENVETO

## Hiukkasmaisen orgaanisen aineksen merkitys pohjoisten metsäjokien pohjaeläinyhteisöille – huomioita virtavesien kunnostushankkeisiin

Pohjoisen Euraasian virtavesien pohjaeläimistön vuodenaikaisvaihtelun ja lajikoostumuksen riippuvuutta syksyisin jokien pohjille kertyvästä lehtikarikkeesta ei tähän asti ole tutkittu juuri lainkaan. Kuitenkin brittiläisissä ja pohjois-amerikkalaisissa lauhkean ilmastovyöhykkeen pienvirtavesissä lehtikarikkeen määrän ja laadun on havaittu ratkaisevasti säätelevän edellä mainittuja ilmiöitä, ja lehtikarikkeen kertymisen estämisen on todettu voimakkaasti heikentävän koko pohjaeläinyhteisöjen tuotantoa hajottajista petoihin. Tässä väitöskirjassa selvitettiin rantametsistä jokiin kulkeutuvan eloperäisen aineksen, etupäässä syksyllä varisevien lehtipuiden lehtien, merkitystä koskien pohjaeläimistölle. Eri puulajien tärkeyttä koskiekosysteemissä tutkittiin talven yli kestäneellä koivun, lepän ja pajun lehtien hajoamis- ja kolonisaatiokokeella. Eri pohjaeläinryhmien tilajakautumisen yhteyttä lehtikariketta pidättävien rakenteiden jakautumiseen tutkittiin pidätyskyvyltään toisistaan poikkeavissa koskiuomissa. Kunnostettujen koskien elinympäristöjen ja pohjaeläinlajiston palautumista tutkittiin vertaamalla eri-ikäisiä kunnostuskoskia perattuihin ja luonnontilaisiin koskiin.

Koko pohjaeläinyhteisön ja eri ravinnonottoryhmien (pilkkojat, pohjakerääjät, suodattajat, kaapijat ja pedot) tiheyksien ja biomassojen vuodenaikaisvaihtelua seurattiin vuoden kestäneellä näytteenotolla keskisuomalaisessa pienjoessa. Tämän yhteydessä seurattiin karkean ja hienokarikkeen (CPOM ja FPOM) määrien vuodenaikaista vaihtelua. Rantametsistä tulevan eloperäisen aineen kertymisen huippu oli syys-lokakuussa, jolloin reilun kuukauden aikana kertyi 75 % vuotuisesta karikkeen määrästä. Lokakuun alun jälkeen koskikivikon lehtimassat alkoivat tasaisesti vähetä, mutta muun karikkeen määrät kasvoivat siitä eteenpäin keskitalveen asti. Runsaimpien pohjaeläinlajien tiheydet noudattivat samaa kaavaa: eläimistön kokonaistiheys ja biomassa olivat suurimmillaan keskitalvella ja pienimmillään loppukesällä. Useimpien ravinnonottoryhmien biomassojen maksimit ajoittuivat lopputalveen tai kevääseen ja minimit kesään. Vuodenaikaisvaihtelu oli selkeintä pilkkojilla, joiden tiheys oli maaliskuussa viisinkertainen ja biomassa 40 -kertainen verrattuna kesäkuukausien vastaaviin arvoihin. Pilkkojakillan biomassan maksimi havaittiin vasta viisi kuukautta sen jälkeen, kun koskien pohjilla oli eniten hajoamatonta lehtikariketta. Nopeasti hajoavista ja ravintoarvoltaan hyvälaatuisista lehtilajeista (koivu ja leppä) oli tuolloin jäljellä lähinnä lehtiruodit ja -suonisto. Monilla pilkkojalajeilla, kuten Nemouridae -koskikorennoilla, alkaa toinen nopean kasvun vaihe kevättalvella ao. hyönteistoukkien valmistautuessa aikuistumiseen. Lehtikarikkeen

saatavuus voikin muodostaa populaatiokokoa rajoittavan pullonkaulatilanteen ainakin peratuissa ja kariketta huonosti pidättävissä koskiuomissa.

Lepän ja koivun lehtien havaittiin hajoavan nopeasti pohjaeläinten kolonisaatiolle alttiissa näytepusseissa, kun pajun lehdet hajosivat näitä huomattavasti hitaammin. Mikrobien, lähinnä sädesienten, aktiivisuutta kuvastavan ergosterolin määrät poikkesivat suhteellisen vähän eri puulajien lehdillä ollen pääsääntöisesti suurimmat koivulla. Lepän lehdillä oli koko kokeen ajan suurimmat pohjaeläinmäärät, jotka eivät kuitenkaan poikenneet tilastollisesti merkitsevästi eri lehtilajien kesken. Kokeen loppuvaiheessa pajun lehtien merkitys hajottajapohjaeläinten ravintona korostui, sillä lepän lehtien alkuperäispainosta oli huhtikuun alussa jäljellä enää 2 %. Pohjaeläinten lajistokoostumus ei poikennut juurikaan eri lehtilajien välillä, mutta yhteisöjen erot olivat huomattavia verrattuna ympäröivän koskikivikon lajistoon etenkin kokeen alussa ja lopussa. Osatöiden II ja III tulokset osoittivat, että kaikilla tavanomaisilla rantametsien puulajeilla on oma merkityksensä pilkkojien ja pohjakerääjien ravinnossa, ja jokirantojen sekä puronvarsimetsien hoidossa tuleekin jatkossa panostaa monimuotoisen puu- ja pensasvalikoiman suosimiseen.

Tässä väitöskirjatyössä saatiin koskien kunnostustöissä tarpeellista taustatietoa virtavesiekosysteemin toiminnasta. Pohjaeläimistön ravintovarojen ja tiheysmaksimien keskittyminen talviaikaan saattaa joissain tapauksissa hidastaa yhteisörakenteen elpymistä loppusyksyllä tai talvella toteutettavan koneellisen kunnostuksen jäljiltä. Pohjaeläimistön tiheyksien palautuminen on ollut nopeaa keskikesällä toteutetun kunnostuksen jälkeen, sillä ainakin osa kunnostustöiden aiheuttamasta häiriöstä kompensoituu silloin vesihyönteisten elinkiertomuutoksilla ja nopeammalla kolonisaatiolla. Loppusyksyllä ja talvella pohjaeläinten ravintovarat ovat laikuttaisesti jakautuneita ja etenkin hajottajien osalta keskittyneet pidättävimpiin uoman osiin, minkä ohella jäätyminen aiheuttaa pohjaeläimistön voimakasta keskittymistä. Tällöin kunnostuksen aiheuttama hävikki voi olla suurempaa kuin kesällä, jolloin osa eläimistöstä elää aikuisvaiheena ei-akvaattisessa elinympäristössä. Kunnostustöiden toteutuksessa voitaisiin lisäksi nykyistä enemmän huomioida puuston merkitys virtavesieliöstölle niin virran sisäisenä suojaavana ja kariketta pidättävänä rakenteena kuin jokirantojen eheyttä ylläpitävänä, uomaa varjostavana ja sinne ravintoa tuottavana elementtinä.

Osatöiden I, II ja III perusteella esitän, että pohjaeläimistön klassinen jaottelu ravinnonottoryhmiin ei kenties toimi kaikissa tilanteissa. Esimerkiksi perinteisesti pilkkojina pidettyjen *Amphinemura borealis* -koskikorennon toukkien kasvun vuodenaikaisrytmiikan ei havaittu olevan yhteydessä lehtikarikkeen saatavuuteen. Onkin mahdollista, että kyseisen pilkkojalajin ravinnonkäyttö voi kohdistua esimerkiksi pienempijakoiseen detritukseen. Ravinnonottotapojen mukainen ryhmittely tarjosi kuitenkin käyttökelpoisen työkalun virtaveseselkärangattomien luokittelussa ja kuvasti pääsääntöisesti niiden ravintoresurssien vuodenaikaismuutoksia.

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# ORIGINAL PAPERS

## I

## Seasonal dynamics of detritus and associated macroinvertebrates in a channelized boreal stream

by

Haapala, A. & Muotka, T. 1998

II


**Breakdown and macroinvertebrate and fungal colonization of
alder, birch and willow leaves in a boreal forest stream**


by


Haapala, A., Muotka, T. & Markkola, A. 2001

III


**Stream macroinvertebrate communities in leaf bags vs. benthos: does leaf type matter?**


by


Haapala, A. & Muotka, T.

**IV**

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

by

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

Manuscript, submitted

V

# Long-term recovery of stream habitat structure and benthic invertebrate communities from in-stream restoration

by

Muotka, T., Paavola, R., Haapala, A., Novikmec, M. & Laasonen, P.