

Pauliina Louhi

RESPONSES OF BROWN TROUT
AND BENTHIC INVERTEBRATES
TO CATCHMENT-SCALE
DISTURBANCE AND IN-STREAM
RESTORATION MEASURES IN
BOREAL RIVER SYSTEMS

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DEPARTMENT OF BIOLOGY,
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SYSTEMS**

Academic dissertation to be presented with the assent of the Faculty of Science of the University of Oulu for public defence in Kuusamonsali (Auditorium YB210), Linnanmaa, on 5 November 2010, at 12 noon

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Abstract

Maintaining connectivity in boreal streams by rehabilitation procedures is a challenging task that requires ecological understanding based on empirical research. In this thesis, I examined the effects of stream rehabilitation on densities and growth of brown trout (*Salmo trutta* L.), as well as on benthic biodiversity. As streams are known to be closely connected to their watersheds, I also examined the effects of watershed drainage activities on stream organisms.

The results of this thesis have implications for enhancing salmonid populations, as well for maintaining stream biodiversity. First, regional climatic variability was shown to override local impacts of watershed management on stream biota. This highlights the importance of placing results from local studies in a regional context. Second, increased sedimentation that typically follows anthropogenic actions in the watershed did not only cause direct mortality on the early life stages of brown trout, but also forced them to emerge earlier from gravel and constrained their development. Thus, sedimentation may have far-reaching fitness consequences on juvenile salmonids.

Third, while instream rehabilitation did enhance habitat diversity for salmonid fish, there were only marginal effects on juvenile fish and benthic biodiversity. Therefore, the factors limiting stream biota, and obscuring positive effects of rehabilitation, are to be found elsewhere. For this purpose, my thesis offers at least three potential, not mutually exclusive explanations: (i) land use changes have altered watersheds and this can be seen as decreased stream biodiversity that cannot be corrected through local-scale restoration efforts; (ii) a habitat-forming organism group, stream bryophytes, is dispersal limited, slowing down any positive responses to restoration by fish or invertebrates that depend strongly on bryophytes; and (iii) changes to stream habitat heterogeneity caused by channelization for timber floating were rather modest to start with, and therefore any effects of stream habitat rehabilitation on stream biota are likely to be subtle.

Based on these findings, I suggest that future restoration efforts should be prioritized according to a comprehensive watershed assessment. Also, monitoring of projects should be more rigorous and preferably multidisciplinary, documenting the ecological as well as hydrological and socioeconomic outcomes of rehabilitation projects.

Keywords: brown trout, forest management, lotic macroinvertebrates, restoration

To my family

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List of original publications

This thesis is based on the following papers, which are referred to by their Roman numerals.

- I Louhi P, Mäki-Petäys A, Erkinaro J, Paasivaara A & Muotka T (2010) Impacts of forest drainage improvement on stream biota: a multisite BACI-experiment. *Forest Ecology and Management* 260: 1315–1323.
- II Louhi P, Ovaska M, Mäki-Petäys A, Erkinaro J & Muotka T (2010) Does fine sediment constrain salmonid alevin fitness? Manuscript.
- III Vehanen T, Huusko A, Mäki-Petäys A, Louhi P, Mykrä H, & Muotka T (2010) Effects of habitat rehabilitation on juvenile brown trout (*Salmo trutta*) in boreal forest streams. *Freshwater Biology* 55: 2200–2214.
- IV Louhi P, Mykrä H, Paavola R, Huusko A, Vehanen T, Mäki-Petäys A & Muotka T (2010) Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications*. In press.

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1 Introduction

Connectivity is widely acknowledged as a fundamental property of ecosystems (Moilanen & Nieminen 2002), although different ecological disciplines may use concepts related to connectivity (*e.g.* fragmentation, isolation, migration etc.) in slightly different contexts (Moilanen & Hanski 2001). As streams are naturally hierarchical and heterogenous systems at multiple spatial scales, connectivity across several dimensions is of crucial importance for the biology of many lotic organisms. Hydrological connectivity, defined here as “water-mediated fluxes of material, energy, and organisms within and among components of the hydrologic ecosystem” (Pringle 2001), arguably underpins most ecosystem processes and patterns of riverine ecosystems at multiple scales (Kondolf *et al.* 2006).

In the riverine framework, ecological connectivity can be viewed as operating in longitudinal (upstream-downstream), lateral (river-catchment), vertical (river-channel bottom), and temporal dimensions (Ward 1989) (Fig.1). Longitudinal connectivity (*e.g.* fish migration, nutrient cycling) is probably the best-known dimension, but lateral dimension is also of high importance, involving exchange between the river channel and its watershed, such as allochthonous inputs. Vertical connectivity involves interactions between surface water and groundwater in the interstitial spaces within the bed substrate, primarily affecting organisms within or near the substrate (*e.g.* developing salmonid eggs or invertebrates). The fourth dimension, time, scales the processes and mechanisms occurring along other dimensions.

Running waters have been a source of water for domestic, industrial and agricultural purposes, as well as a means of power generation and waste disposal, routes for navigation, and locations for the pursuit of leisure activities. As a result, river systems are now among the most degraded ecosystems in the world (Malmqvist & Rundle 2002). Today, there are very few river systems that are still near their pristine condition. The ecological connectivity of most running water systems has been interrupted especially through channelization, which impairs the intimate interdependence of the stream and its riparian setting, reduces habitat heterogeneity and simplifies flow patterns (Malmqvist & Rundle 2002).

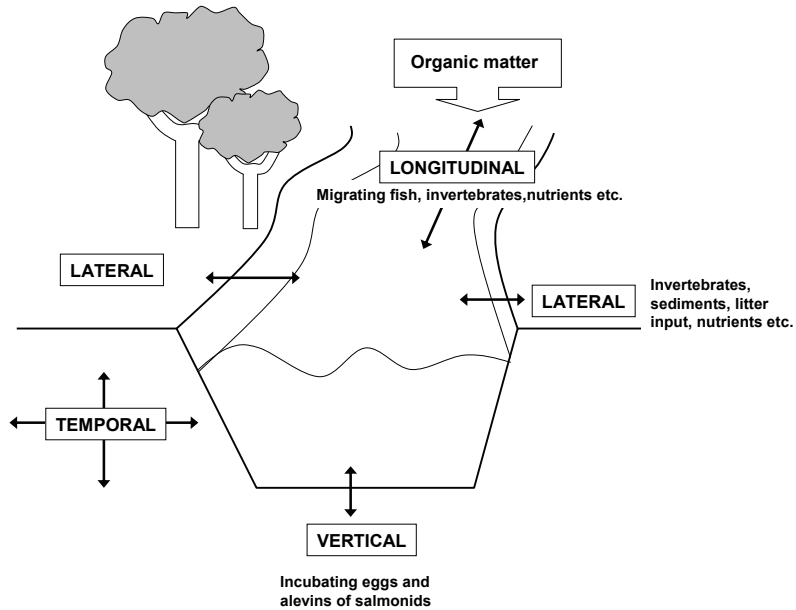


Fig.1. Restoring the four-dimensional nature of lotic ecosystems. Modified from Ward (1989).

As a means of improving degraded riverine ecosystems, restoration (or rehabilitation) has greatly increased during the last two decades, being now a key component of river management programs. Restoration and rehabilitation are defined in many different ways, and there is still disagreement about what constitutes restoration. The term restoration, which in the most formal sense is defined as returning an ecosystem to its original, predisturbance state, has commonly been used to refer to all types of habitat manipulations, including enhancement, improvement, mitigation, habitat creation and other situations (Roni *et al.* 2008). These activities are, however, more accurately termed rehabilitation, as most do not truly restore the original state of a system.

The primary focus of several in-stream restoration attempts is to enhance stream habitat diversity, which is expected to create optimal nursery habitat for fish, particularly salmonids (Roni *et al.* 2008). Increased habitat diversity is in turn expected to increase biological diversity, and this assumption has gained much empirical support from the terrestrial literature (*e.g.* MacArthur & Wilson 1967, Davidowitz and Rozenzweig 1998, Tews *et al.* 2004). Although some

stream studies also show this pattern (*e.g.* Li *et al.* 2001, Brown 2003), recent reviews have found only weak support for the success of in-stream restoration in enhancing salmonid populations and/or benthic biodiversity, even though a majority of projects did enhance physical habitat heterogeneity (Miller *et al.* 2009, Palmer *et al.* 2010). Thus, the basic (though often implicit) assumption underlying most in-stream restoration projects, that restoring the complexity of the physical habitat will translate to improved biodiversity (“if you build it, they will come”, or Field of Dreams principle; Palmer *et al.* 1997), may simply not be true.

In Fennoscandia, dredging of streams to facilitate log transport has probably been the most profound anthropogenic alteration to the physical stream environment. In Finland alone, up to 20,000 km of natural stream channel wider than about five metres was extensively channelized for timber transportation between 1850 and 1970 (Eloranta 2004). Timber floating ceased by the end of the 1980s, and extensive restoration programs imposed by legislation have been launched ever since to rehabilitate these streams to their pre-channelization condition (Yrjänä 2003). Restoration in Fennoscandia is mainly conducted using excavators to add boulders into the stream bed, creating deflectors, boulder dams, weirs, and other in-stream enhancement structures (large woody debris is rarely used) (Eloranta 2004, Nilsson *et al.* 2005). Twenty years ago, however, biodiversity did not have much weight in environmental decision making in Finland, and the primary (if not sole) motivation for restoring the streams used for timber transport was to enhance salmonid fisheries.

Even after a high number of restoration projects and great expenditure of money, time and other resources, there are still only a few attempts to properly monitor and evaluate either the success of the projects, or reasons for their failure (Lake 2001). It is alarming to note that more than 90% of stream restorations in the US, Australia and Europe are still not monitored beyond visual estimation (Bernhardt *et al.* 2005, Brooks & Lake 2007, Kail *et al.* 2007). Biodiversity is rarely defined and measured directly, and even the best monitoring designs rarely incorporate data prior to restoration. Most attempts to monitor restoration impacts have been very short in duration, often no more than a single year. In river restoration, however, the recovery of lost linkages is intended to occur over time and the target endpoint is also likely to be temporally dynamic (Palmer *et al.* 2005). Therefore, lacking properly designed monitoring studies, particularly ones with pre-restoration data, we are seriously limited in our attempts to assess whether stream restoration has successfully attained its goals, be it fisheries enhancement or biodiversity conservation. Also, low publication rates for null

(‘no response’) results may introduce bias into attempts to assess the overall success of restoration (Miller *et al.* 2009).

Overall, when implementing restoration programmes, all four dimensions of connectivity should be taken into account, and stream systems should be viewed as networks. Many instream restoration projects may have been unsuccessful because they were implemented in isolation from the larger catchment context (Bond & Lake 2003, Lepori *et al.* 2005, Wohl *et al.* 2005). Most running waters are closely connected to their catchments (*i.e.* laterally connected), and rely on their riparian areas to provide allochthonous inputs in the form of riparian vegetation and terrestrial invertebrates (Stone & Wallace 1998; Baxter *et al.* 2005). The direct effects of habitat diversity might therefore be overwhelmed by several other factors, *e.g.* flow-related and/or anthropogenic disturbances. In boreal streams, landscape-level disturbances (*e.g.* forestry) may be more limiting to stream communities than lack of in-stream habitat diversity, and restoration efforts should therefore be prioritized according to a comprehensive watershed assessment (Roni *et al.* 2008). In such a scheme, in-stream restoration may not be a top priority but may still be important once other obstacles to restoration of biodiversity have been removed. Unfortunately, in Finland such watershed assessments are rare, and in-stream restoration is forced by legislation, with the assumption that restoration will benefit trout, and what is beneficial for trout must be beneficial for other stream organisms as well. This, however, may be wishful thinking, and remains a largely untested hypothesis (see Muotka & Syrjänen 2007).

In boreal headwaters, forestry is a major form of land use, contributing to long-term changes in lotic ecosystems at multiple spatial and temporal scales. Forest harvest, drainage and fertilization do not only increase wood production, but also affect aquatic ecosystems in close contact. Forest drainage has transformed nearly six million out of 15 million hectares of wetland areas into productive forest in Finland (Statistical Yearbook of Forestry 2006). Since the late 1990s, drainage of pristine peatlands has ceased due to stricter environmental legislation, and emphasis has turned to the maintenance and improvement of the existing ditch networks. Changes to run-off water chemistry after ditch maintenance works have been assumed to be similar to those after the original construction of ditches. Such changes have been observed as increased loading of suspended solids, nutrients and metals due to mobilisation of particulates from mineral soils exposed beneath the peat layer (Liljaniemi *et al.* 2003), and

increased pH and decreased total organic carbon concentration due to immobilisation of organic acids in the same soil layer (Åström *et al.* 2001).

To minimize the impacts of forestry on aquatic ecosystems, forest managers have adopted riparian buffer strips to create protective filters between streams and sites of forestry action (Kiffney *et al.* 2003). In Finland, national legislation imposes the best suitable water protection methods, such as overland flow areas, ditch breaks and sedimentation pits, or plugging of the old ditches, to be used in the context of forest activities. The main standard for reducing loading of sediment and nutrients into streams after drainage works is to decrease flow velocity in ditches before they join the stream. Although methods applied vary across sites, sedimentation pits combined with a ditch break is currently the most commonly used technique in state-owned lands in Finland (Finnish Forest and Park Service 1998).

Vertical connectivity is less readily apparent in rivers, and its reduction through human impacts is rarely acknowledged. Stream water flows into and out of permeable streambeds, *i.e.* downwelling and upwelling respectively. This connectivity can be reduced by physical barriers that reduce permeability, such as sedimentation and clogging of pore spaces of streambed gravels, or by physical changes that reduce hydraulic gradients, such as channelization (Boulton 2007). For instance, under increased sedimentation from the catchment, the conditions for developing salmonid embryos and alevins inside the gravel may be seriously impaired. The early part of the salmonid life cycle occurs within the gravel (termed intragravel stages). The egg hatches into an 'alevin', which remains in the gravel and carries the yolk sac (Crisp 2000). Only when the yolk sac is almost exhausted, the alevin emerges from the gravel, fills its swim bladder with air to attain neutral buoyancy and begins external feeding. This event marks the end of the intragravel life, and the young fish is then termed a 'fry'. Very fine sediments (<2.0 mm) tend to infiltrate into substrate, resulting in a reduction of the redd permeability and thereby lowering the oxygen supply to developing ova (Chapman 1988, Sear 1993, Levasseur *et al.* 2006). Fine sediments larger than 1.0 mm may form a seal on the redd surface that inhibits the emergence of fry from the redd (Kondolf 2000). These changes will result in poor egg survival or otherwise insurmountable fitness costs to alevins. By the time the fry leave the protected inter-substrate environment and emerge into the stream, they have limited swimming ability and are often swept downstream (Daufresne *et al.* 2005), facing a high predation risk (Elliott 1986).

2 Aims of the thesis

The overall objective of this thesis was to identify essential factors for restoring the ecological connectivity of boreal streams. The subprojects include several aspects with direct relevance to restoration ecology, such as the effects of forestry actions on stream biota (I), increased sedimentation effects on salmonid alevin fitness (II), and potential effects of instream restoration on brown trout (III) and benthic macroinvertebrates (IV). The complex interaction of streams and their catchments is not yet fully understood and this renders the outcomes of future restoration projects uncertain. Thus, the present work aims to find a realistic approach for restoring ecological connectivity within boreal stream networks.

3 Material and methods

3.1 Study areas

Forestry impacts on stream biota (I) were studied in small headwater streams (1st and 2nd order) of River Kiiminkijoki and River Utosjoki, which both run into the Gulf of Bothnia in northern Finland. The River Kiiminkijoki (catchment area 3812 km²) is one of the few mid-sized coastal rivers in Finland with no artificial flow regulation and is largely free from industrial and domestic influences. The River Utosjoki (300 km²) is part of the River Oulujoki (22900 km²), which is harnessed for hydropower production with eight dams along the downstream reach of the main stem. Forestry is the main form of land use in the headwater areas of both river systems and large areas of unproductive peatland were drained for forestry in the 19th century.

The effects of instream habitat restoration (III, IV) were studied in the headwater streams of River Oulujoki and in 14 streams in northeastern Finland, a majority of them belonging to the catchment area (14191 km²) of River Iijoki. All restored sites were dredged during the 1950–60's for timber floating. Reference sites for study IV were tributaries of River Oulankajoki near the border between Finland and Russia, representing near-pristine conditions.

3.2 Field surveys

The subprojects of this thesis were based on several types of data: brown trout egg survival and alevin fitness, and sedimentation characteristics in natural streams and experimental channels (I, II), and field surveys of macroinvertebrates, fish and physical instream characteristics (I, III, IV).

3.2.1 Assessing the impacts of sedimentation on stream biota (I, II)

The goal of paper I was to measure, for six consecutive incubation periods (pre-treatment data 2002–2004, post-treatment data 2005–2007), whether there are differences in sediment, brown trout embryo survival and macroinvertebrate community structure between treatment areas affected by forest ditching improvements and unaffected control areas upstream of them. The maintenance and improvement of the existing ditch networks is generally expected to increase

loading of sediment and nutrients into streams (Liljaniemi *et al.* 2003), ultimately having negative effects on stream biota. Therefore, national legislation in Finland imposes the best suitable water protection methods to be used in conjunction of all forest activities. In this study, forest ditching improvements were carried out together with watercourse protection structures (ditch break and/or sedimentation pits) during summer low flows in 2004. Six artificial gravel beds were placed in each stream to mimic natural spawning grounds, three upstream (control section) and three downstream of the ditching areas.

Brown trout egg survival was studied using incubation boxes with 30 eggs evenly deposited among washed gravel in each box. Six incubation boxes and six sediment containers were laid in each gravel bed in October each year of the experiment. Incubation success and sedimentation were monitored twice each year, before and after the spring flood. The incubation period was thus divided into two successive phases, before and after hatching. Water quality was analysed from samples collected four times each year (February, April, May and October). Twelve benthic macroinvertebrate samples were taken at each stream in late September of 2000 to 2006, six at treatment sites and six at control sites. Invertebrates were later identified, mainly to the genus level.

Data were analysed using linear mixed-effect models (LME), which allowed the incorporation of fixed factors and random effects that control for correlation in data arising from grouped observations (Pinheiro & Bates 2000). In the LME, we incorporated three independent categorical variables as fixed factors: 1) 'Before' vs. 'after' forest ditching improvements, corresponding to temporal control; 2) 'Treatment' vs. 'control' (spatial control) sites among streams; 3) Sampling times nested within periods, allowing the time series structure to be taken into account (3-yr data for each 'before' and 'after' stage). Sampling sites were nested within a stream and fitted as random effects to control for the non-independent observations within sites. In this design, particular interest lies in the interaction (period*treatment) of treatment factor which, if significant, implies a long-lived pulse impact of forest ditching (Underwood 1992).

In paper II, we set up an experiment that lasted for one incubation period in Kainuu Fisheries Research facilities in Paltamo. We constructed 24 experimental channels, in each of which we placed three separate cylinders, all containing 30 equal-sized brown trout eggs among washed gravel.

To assess whether alevin growth and emergence were affected by sedimentation and/or chemical cues from predators, we applied a randomized factorial design with three sedimentation (high vs. low sediment addition vs.

control with no sediment added) and two predation-risk (predator present vs. absent) treatments, with four replicates for each treatment combination.

The weekly added volumes of sediment (fine sand and natural sediment <2.0 mm) closely mimicked natural variation in sediment concentration in Finnish streams (Laine & Heikkinen 2000; Louhi *et al.* 2010). We placed a single burbot (*Lota lota*) in half of the channels to ensure that predator odour was present for alevins approximately a month before the peak emergence. No visual connection occurred between alevins and predators.

Fish growth was measured three times during the experiment: (i) early March, when alevins had recently hatched (415 °C days), (ii) late March, when alevins were still inside the gravel (460 °C days), and (iii) late May, after the onset of fry emergence (790 °C days). However, as there were no differences among treatments in any of the response variables on two earlier sampling occasions, we focused on data from the last sampling date. To take into account the developmental stage of the fry, both timing variables (start of emergence; 50% of fry emerged) were counted as degree-days from the beginning of the experiment. The emergence period was considered to have ceased once no new fish had emerged for two successive days.

Standard length of the fish and size of the yolk sac (yolk sac area as seen from the side) were measured from photographs using ImageJ 1.41 (Rasband 1997–2010). In the laboratory, contents of all cylinders were oven dried (105 °C) for 12 hours and then sorted, by sieving, into four size fractions: <0.074 mm, 0.074–0.25 mm, 0.25–1.0 mm and 1.01–2.0 mm. Inorganic and organic contents of each fraction were then measured through combustion at 550 °C for 6 hours.

We used multiple regression with stepwise selection to determine if significant relationships existed between sedimentation (four size fractions in both inorganic and organic sediment) and percent survival. We also used two-way ANOVA to test for the effects of sedimentation on channel-specific mean values for each response variable (start of emergence, 50% of fry emerged, duration of emergence period, and relative yolk-sac size). Because the low-sedimentation treatment differed little from controls in all response variables, we also ran the same set of analyses with this treatment excluded.

3.2.2 Instream habitat restoration, juvenile salmonids, and stream biodiversity (III, IV)

In papers III and IV, we examined how restoration measures aiming at enhancing of habitat conditions for juvenile brown trout affect their target organisms and other stream biota. For this purpose, we used (i) a well-replicated, balanced Before-After-Control-Impact (BACI) design with data from three years before (pre-treatment data 1999–2001) and three years after restoration (post-treatment data 2001–2003) in differently-restored and control reaches of six separate streams. The streams were restored by constructing cross-sectional weirs in July-August 2001, using either boulders or logs. Spawning gravel was added as 20-cm-thick gravel beds, with an area of 1–2 m², to sites with suitable flow conditions.

Three-pass electrofishing was used to assess fish densities three times each year (June, August and October). The fish caught were counted, measured, weighed, and then returned to their initial positions in the stream. Scale samples were taken to estimate trout age. Fish densities by age-group were estimated using the software PROGRAM CAPTURE (model Zippin) (Otis *et al.* 1978). The mean standardized mass-specific growth rate for consecutive sampling periods was calculated according to Ostrovsky (1995).

To quantify rehabilitation-induced changes in habitat structure, and reveal differences between the two rehabilitation practices (boulders vs. logs and boulders) and controls, a two-dimensional hydraulic model (River 2D; University of Alberta (2002–2006)) was used in one stream as an example. A detailed physical habitat survey was carried out in three streams both before and after rehabilitation. These approaches were based on the quantification of the stream bed topography and bank profile, dominant substratum size, mean water velocity, water depth and cover of aquatic vegetation at each site.

To assess the effects of rehabilitation procedures on stream biodiversity, we sampled macroinvertebrates twice a year (June and October) for three years before (1999–2001) and three after (2001–2003) rehabilitation. Eight randomly placed samples were taken from each site within each stream using a Surber sampler. Owing to the high number of replicates (overall n = 1728 samples), only genus level identification could be used.

Three years of post-restoration data may be too short to detect biological responses, and in paper IV we complemented the BACI approach with a space-for-time substitution design including channelized, restored and near-natural

reference streams, with an almost 20-yr perspective on the recovery of benthic invertebrate communities from restoration. Rehabilitation measures used in these streams were typical of stream rehabilitation projects in Finland (see Yrjänä 2003). At each site, we selected a relatively uniform riffle of ca. 50 m and collected a 2-min kick-net sample comprising four 30-s subsamples, aiming to cover most benthic microhabitats present at a site. All samples were collected during a two-week period in September-October 2007 and invertebrates were identified mainly to species level.

The impact of restoration in the BACI-design, was tested using linear mixed-effect model (LME), which allows the incorporation of fixed factors and random effects that control for correlation in data arising from grouped observations (Pinheiro and Bates 2000). We incorporated three independent categorical variables as fixed factors: (1) Period (B): ‘before’ (temporal control) vs. ‘after’ restoration; (2) Treatment (TR): boulder enhancement structures vs. both boulders and large woody debris (LWD) vs. control (no enhancement structures; spatial control); and (3) Seasons (S) (two surveys each year) nested within periods (S (B)) as an additive factor stabilizing variation among sampling times. Streams and sampling sites nested within streams were fitted as random effects to control for the non-independence of observations within streams and sites.

Data interpretation followed the logic of beyond-BACI designs (Underwood 1994), with two simplifications: (i) our design was symmetric, and (ii) we had independent replicates ($n = 6$) for each treatment and control. In this design, particular interest lies in the interaction (B x TR) which, if significant, implies a long-lasting pulse effect of anthropogenic disturbance (Underwood 1994). In our case, a significant period*treatment interaction indicates a difference between treatments in how they vary from before to after restoration. We further constructed separate contrasts for the interaction terms between each restoration type and the control. LME models were fitted using the restricted maximum likelihood (REML) method. Statistical significance of period, treatment, season and period x treatment interaction were tested using F-statistics in lme function (nlme library) available in the free software R 2.11.1. (R Development Core Team, 2010).

To test the hypothesis that the streams restored 15–17 years prior to sampling in 2007 ($n = 15$) differed from the channelized streams ($n = 8$) and/or near-natural reference streams ($n = 8$) in macroinvertebrate abundance and species richness, we used *a priori* contrasts. To control for differences in abundance, samples were rarified to the lowest abundance observed (476 individuals) using EcoSim version

7.0 (Gotelli & Entsminger 2001). Patterns in macroinvertebrate community structure were assessed by a three-dimensional solution of Nonmetric Multidimensional Scaling (NMDS; McCune & Mefford 2006) based on the Bray-Curtis dissimilarity coefficient. Differences in community composition among the channel types were analysed by Multi-Response Permutation Procedure (MRPP), which is a nonparametric method for testing differences in assemblage structure between *a priori* defined groups (Zimmermann *et al.* 1985). If MRPP returned a significant difference, we used Indicator Value (IndVal) analysis to identify species that best discriminated among groups (channel types).

4 Results and discussion

4.1 The influence of sedimentation on the early stages of salmonid fishes (I, II)

We found no evidence that forest drainage improvement, combined with water protection methods, increases inorganic or organic sedimentation in small forest streams (study I). This supports the finding of Joensuu *et al.* (1999) that sedimentation pits are relatively effective in retrieving the coarse fraction of suspended solids. Nevertheless, fine sediment from the stream catchment may infiltrate the spawning beds and alter water quality within them, potentially resulting in reduced survival of salmonid eggs (see Chapman 1988, Armstrong *et al.* 2003) or delayed emergence of alevins from the gravel (Roussel 2007). However, no such effect was detected in our study, *i.e.* the effect of sedimentation on brown trout egg mortality was non-significant (I).

Interestingly, stream discharge in the smaller streams increased slightly more through time in treatment than control sections, suggesting that drainage improvement had a subtle additive effect on stream flow. Similarly, brown trout egg mortality rate increased after drainage works in the four smaller streams, but only in areas upstream of the drainage and before the spring flood. Discharge was significantly lower in the control than treatment sites, but, as this difference was detectable throughout the study, it cannot provide a direct explanation for the increased mortality rate in the control sites, particularly because egg survival was relatively high during winters 2002 and 2003, despite a much lower discharge then. This unanticipated difference between treatment and control sections was more likely due to small-scale differences in ice cover formation at the onset of winter. This highly dynamic process was, however, not directly measured in our study.

The fact that no direct effect of sedimentation on brown trout egg mortality was found does not preclude its possible influence on fitness-related traits of alevins. For juvenile fish, high mortality rates have been reported shortly after emergence from the gravel into the open water (Webster 2002). In this respect, salmonids are of special interest, because they typically have a long intragravel period, and they undergo an ontogenetic habitat shift when emerging into the open water and starting exogenous feeding. At that stage, they are confronted with multiple predators (Armstrong *et al.* 2003). Our results in the experimental study

(II) support earlier findings that human-induced and land-derived fine sediments may result in poor embryo survival or premature emergence of fry (for reviews, see Chapman 1988, Armstrong *et al.* 2003). In particular, an increase in the finest organic sediment fraction (<0.074 mm) was harmful to developing embryos. Levasseur *et al.* (2006) similarly concluded that very-fine sediment (<0.063 mm) was highly detrimental to embryo survival; whereas larger sediment (up to 2.0 mm) had no corresponding effect. According to Greig *et al.* (2005), very fine clay-sized sediments may create a thin, poorly permeable seal around the eggs, restricting the availability of oxygen to developing embryos.

In addition to direct mortality, high sedimentation caused detrimental effects on fitness-related traits of emerging fry. For example, fish exposed to high sedimentation at the embryonic stage had on average a larger yolk sac at emergence than did fry receiving no or little sedimentation. This finding was most likely caused by the fact that high sedimentation decreases intragravel oxygen content via decreased permeability (Chapman 1988) and, under hypoxic conditions, complete absorption of the yolk is delayed (Roussel 2007). Fry, which have not completed their ontogenetic development and therefore emerge with a large yolk sac, are poor swimmers, encountering a high predation risk and/or increased risk of downstream displacement upon emergence (Elliott 1986, Olsson & Persson 1986). Furthermore, poor oxygen conditions during the ontogenetic development affect muscle development of fish (Matschak *et al.* 1997; 1998). It is therefore likely that fry exposed to high sedimentation as developing embryos suffer a “carry-over effect” of reduction in swimming performance, increasing their vulnerability at the transition stage from intragravel to open-water way of life.

Emergence in the high-sedimentation treatment started later than in the controls, as has also been observed for embryo developed under hypoxic conditions (Geist *et al.* 2006, Roussel 2007). This response was detected, however, only in the absence of the piscivorous fish, whereas, when exposed to predator odour, fish receiving little or no input of fine sediment delayed their emergence by as much as four days (about 25 degree days), emerging several days later than fish exposed to excessive sediment and predator odour. Earlier emergence could be advantageous when competing for feeding territories, and strong selection against late emergence has indeed been documented in Atlantic salmon (*Salmo salar* L.) fry (Einum & Fleming 2000). Even a difference of one day may provide a priority effect that cannot be overcome by bigger size when establishing territories (Huntingford *et al.* 1999, O'Connor *et al.* 2000). However, any

advantage of earlier emergence may be easily traded off if smaller and/or less developed individuals with large yolk sacs face intense predation pressure (Brännäs 1995). Jones *et al.* (2003a) observed such a trade-off on the timing of emergence in Atlantic salmon embryos in the presence of burbot, with alevins in the burbot treatment emerging over a day later than the control fish. Our results showed, however, that abiotic stress in the form of excessive sedimentation overcame any effects of fish presence on the timing of emergence, with fry from the high-sedimentation treatment showing little response to burbot.

4.2 Influence of forest drainage on the benthic macroinvertebrate community (I)

Stream discharge in our study sites increased from before to after drainage improvement works (study I), but, because a corresponding pattern was also observed in other streams and rivers in the same and adjacent watersheds, this increase was not related to drainage works but rather reflected regional variability in precipitation. This had a direct impact on stream macroinvertebrates whose densities and diversity decreased in years following drainage works. The adverse effects of increased flow on stream invertebrates have been documented in numerous studies, and it is now one of the basic premises of modern stream ecology (Allan & Castillo, 2007). Our results thus add to the growing body of literature indicating that regional climatic variability may cause stream invertebrate communities to respond similarly over time across a number of streams (Bradley & Ormerod 2001, Daufresne *et al.* 2003, Gilbert *et al.* 2008), highlighting the importance of placing results from short-term local experiments in a regional context (Heino *et al.* 2002).

The fact that drainage works had little impact on benthic macroinvertebrates emphasizes the importance of considering the original state of the community. All these watersheds were drained in the 1970s, and it may well be that invertebrate communities before the drainage improvement works already consisted of taxa tolerant of the prevailing environmental conditions. As the initial drainage works in this area were extremely extensive, more sensitive taxa may already have been missing from the regional species pool at the time of our sampling. Generally, anthropogenic changes to stream systems have favoured organisms with broad tolerances over more specialized taxa, depending on the nature of the manipulation and characteristics of the streams in question (Hawkins *et al.* 1982). Changes to habitat structure caused by forestry actions have often shifted the

invertebrate community towards higher production and increased abundance of generalist species, such as *Baetis* spp. and chironomids, and towards less diverse communities (Richardson 2008, Larsen *et al.* 2009).

In conclusion, through the use of temporal and spatial controls, we were able to demonstrate that regional forcing by climatic factors largely overwhelmed any effects of local management actions on stream biota in small forested catchments. With the design used, we should have been able to detect most impacts of forest drainage improvement on stream habitat and organisms. Therefore, we feel safe to conclude that the water protection methods used were sufficient in reducing sediment loading into our study streams, and that the relatively strong temporal trends exhibited by stream communities were mainly caused by regional climatic variability rather than by drainage works *per se*.

4.3 Efficiency of instream habitat rehabilitation in enhancing salmonid populations and other stream biota (III, IV)

Using a BACI-design, we observed that in-stream habitat rehabilitation clearly increased streambed complexity. The rehabilitated reaches were characterised by deeper water, lower water velocities and larger substrates than the control reaches. The most conspicuous immediate change caused by rehabilitation was, however, the loss of aquatic vegetation (mainly mosses: average decrease of percent moss cover was 42% in boulder additions and 39% in LWD+boulder additions), which showed no sign of recovery during the three years of post-restoration monitoring.

While rehabilitations most likely increased the abundance of microhabitats suitable for fry foraging (see Nislow *et al.* 1999), we found no effect of rehabilitation on early juveniles (0+ and 1+) of brown trout. These younger age-classes decreased in abundance similarly in all treatments. For age 2+ -fish, however, densities in control sites typically exceeded those in other sites before but not after rehabilitation and, although densities after rehabilitation decreased in all reaches, they did so less in the rehabilitated than control reaches. No effect of rehabilitation on the growth rate of juvenile fish was detected.

Both in a short-term BACI approach and in a long-term comparative approach, in-stream rehabilitation had little influence on macroinvertebrate communities. We therefore feel confident with the conclusion that the in-stream habitat enhancement measures used to improve salmonid fisheries did not enhance benthic biodiversity. This observation may seem unexpected in the light of general ecological theory, where a positive relationship between habitat

diversity and species richness is often taken as granted. However, a corresponding pattern to our study was also detected by Palmer *et al.* (2010) in a comprehensive review of stream restoration studies. These authors concluded that the direct effect of habitat diversity on stream macroinvertebrate communities is likely overwhelmed by several other factors, *e.g.* flow-related and/or anthropogenic disturbances.

Some studies have shown that enhancing habitat heterogeneity through structures such as logs and boulders may increase the density of juvenile salmonids (*e.g.* Roni & Quinn 2001, Lehane *et al.* 2002). However, for in-stream rehabilitation to be effective, habitat availability should be limiting fish densities and/or biodiversity before rehabilitation. In boreal streams, landscape-level disturbances (*e.g.* forestry) may well be more limiting to fish or macroinvertebrate communities than lack of in-stream habitat diversity. Rehabilitation efforts should therefore be prioritized according to a comprehensive watershed assessment scheme (Roni *et al.* 2008). In such a scheme, in-stream restoration may not be a top priority but may still be important once other obstacles to restoration have been removed.

Because extreme hydrological events are expected to become more frequent in the future (*e.g.* Hintzman *et al.* 2005), many monitoring studies will likely be plagued by unpredictable broad-scale variability. This was exactly what happened in our BACI design, because a year after restoration in 2002, discharge was at a record-low in Finnish rivers (Finnish Environment Institute 2002). By contrast, precipitation was exceptionally high in 2004, which led to unusual flooding in the middle of summer (Finnish Environment Institute 2004). Importantly, trout densities in all of our six study streams responded in a similar way, suggesting that trout populations were limited by the same regional-scale factor. It therefore seems that exceptional hydrological events may have masked any local effects of rehabilitation, and positive population responses may only be detected after fish and other stream biota have fully recovered from events such as those that occurred during our study – unless such exceptional events turn out to be less exceptional in the future, re-appearing at a much more frequent interval than before.

Drought may also have partly confounded the detection of restoration-induced changes to macroinvertebrate density and diversity, both of which decreased after rehabilitation. As a parallel decrease also occurred in unmodified controls, this response could not have been caused merely by rehabilitation. Importantly, however, the response was stronger in rehabilitated than control

reaches, and densities had already decreased strongly by October 2001, soon after rehabilitation and well before the onset of drought. Therefore, rehabilitation-induced disturbance must also have been involved. Tullos *et al.* (2009) suggested that channel reconfiguration acts as a “disturbance filter” that may affect macroinvertebrates for many years following rehabilitation. In our case, recovery from rehabilitation may have been further slowed down by the subsequent drought.

Another possibility is that the recovery of macroinvertebrate communities reflects the very slow renewal rate of their key habitat resource, aquatic bryophytes. Owing to the use of heavy machinery, moss cover decreases radically during restoration works (Muotka & Laasonen 2002). This is also likely to have a direct impact on trout, because macrophytes represent an important in-stream cover for juvenile fish (Eklöv & Greenberg 1998, Heggenes & Saltveit 2002). Aquatic mosses and other macrophytes often have a key role in stream ecosystems, and the loss of mosses may therefore impact trout populations indirectly. Mosses not only provide optimal nursery habitat for stream invertebrates (Suren & Winterbourn 1992), but they also contribute importantly to a stream’s organic matter input retention efficiency (Muotka & Laasonen 2002). As the reduction of organic matter is known to propagate upwards in lotic food webs (Wallace *et al.* 1997), loss of macrophytes during rehabilitation works may have far-reaching effects on benthic invertebrates and, ultimately, juvenile fish. However, as mosses were only reduced in the treatment but not in control reaches, yet trout populations responded similarly in all treatments, their loss cannot explain the lack of a positive density response in this study.

In conclusion, stream habitat rehabilitation had slight and variable effects on the densities of brown trout and macroinvertebrates in our study streams. Density fluctuations were fairly similar between the sites, and seemed to be mainly related to large-scale climatic processes causing a severe drought after rehabilitation. It therefore seems that, in our case and probably in many others as well, a central reason for the apparent failure of rehabilitation was probably the adverse regional climatic conditions that overwhelmed any positive impact that the measures might have had, making short-term local rehabilitation attempts futile. Finally, merely increasing the heterogeneity of the stream bed may be insufficient; instead, enhancing salmonid stocks and/or other stream biota may also require action in the off-channel riparian habitats, and further beyond in the catchment area, to rehabilitate not only the in-stream habitat, but also (and more importantly) ecosystem conditions of the river basin as a whole.

5 BACI-designs within restoration projects

Restoration projects are amenable to analysis by BACI designs, because their general aim is to detect a change in a set of locations over time (Downes *et al.* 2002). An appropriate design to detect restoration effects on stream biota would consist of replicated sampling several times before and several times after the onset of restoration, in both potentially impacted and in replicated control locations. Based on this kind of design, it would be possible to ascertain whether there is an interaction between the impacted and control sites through time, indicative of a restoration-induced change in the restored sites.

However, as promising as BACI-designs may appear, their practical application is not straightforward. BACI-designs are vulnerable to external factors (“demonic intrusion” *sensu* Underwood 1994) that happen to vary on the same time scale as the human impact studied. The use of spatial and temporal controls should help avoid false conclusions about the anthropogenic impact on biota. However, long monitoring periods are needed to make sure that both pre-and post-impact periods will include a sufficiently wide range of natural hydrological variability, otherwise the detection of human impacts will be easily compromised. Although the change in habitat structure is immediate, and the effect is available for stream biota directly after rehabilitation, recovery of benthic invertebrates, or their key habitat resource, mosses, to pre-rehabilitation levels may take several years (Muotka *et al.* 2002, Jones *et al.* 2003b). It may therefore be that to detect any response, monitoring of biota should continue for much longer than three years. Hierarchical spatial controls (similar sites in other watersheds) (Underwood 1994) may also be needed, but are rarely available in environmental impact studies.

Some authors have questioned the use of population parameters in BACI designs because, due to logistical constraints, most studies will be based on a relatively low number of temporal and spatial replicates, particularly in the Before period (Osenberg *et al.* 1994). In addition, wide variation among sampling units, inherent to most natural phenomena, makes effects of a given size hard to detect. This potentially renders the power of a BACI analysis very low for detecting impact, even when one exists. Overall, calculating power analysis can be problematic in more complex beyond-BACI-designs (Benedetti-Cecchi 2001).

In some cases, the decision to restore only a subset of impacted locations and leave controls available for adequate sampling may involve ethical and practical problems. In most restoration projects, there will be a shortfall of funds and other

resources available compared to what is actually needed; this shortfall will always reduce the number of control sites. Therefore, logistical and financial factors usually constrain the implementation of complex BACI-designs.

6 Restoring ecological connectivity of stream system networks – a challenging puzzle

A puzzle is defined as a problem or enigma that challenges ingenuity. Although different kinds of puzzles are created, they usually have one thing in common: they have a solution. Solving a puzzle may require the ability to recognize patterns and create a particular order out of what may look like a chaos. So does my puzzle, restoring biological communities, have a single solution? Because my results demonstrated that habitat heterogeneity was not limiting either brown trout populations or macroinvertebrate communities in our streams, it seems that the answer is to be found somewhere else than in in-stream restoration.

Although we lack historical, pre-channelization data, as well as data from the active timber floating period (*i.e.* prior to the 1980s), it seems that, when Fennoscandian forest streams were channelized for log floating, the loss of habitat heterogeneity was only partial (Nilsson *et al.* 2005). Since the channelized streams in our study did not differ strongly from the near-natural reference streams, one might ask whether these streams should ever have been restored. In fact, although the channelized streams were hydromorphologically simplified to some degree, their biological communities did not differ strongly from regional references or control sites. Therefore, under current criteria emphasizing biodiversity, these streams would not have been defined as in need of restoration. Nevertheless, stream restoration in its present form has strong public acceptance in Finland, mainly because it is considered beneficial for commercially important fishes, ecotourism, and the well-being of local people (Olkio & Eloranta 2007).

Properly designed monitoring programs of restoration projects are still rare. As restoration is often constrained by financial resources, funds are only rarely provided for ecological monitoring. Most often monitoring is limited to visual surveys of the restored site, or to channel cross-sections and snapshot electrofishing surveys. It may not be worth wasting initially small amounts of money, time and other resources to monitoring of restoration projects that lack pre-treatment data and temporal and spatial replication.

However, it is not the practitioners who are to be blamed for the unwillingness to learn from prior experience, but environmental policymakers clearly need to be better informed about the importance of measuring the outcomes of restoration. In general, rehabilitation projects should always have a satisfactory monitoring plan before starting the actual work.

Ecologists generally accept that longitudinal, lateral and vertical connectivity of streams underpin many ecosystem processes and patterns in rivers at multiple scale (Ward *et al.* 2001). Concepts and strategies in river restoration have been slower to acknowledge the significance of all these dimensions and how these vary along the stream. There is nothing cryptic about the nature of these dimensions; there are just a lack of adequate data on stream networks, and practical issues of sampling and monitoring, that have contributed to the lag in recognition of their significance to restoration efforts.

National guidelines for prioritizing stream and river restoration projects, including their monitoring, should be developed and implemented. These guidelines need to be based on scientific information about which problems can be mitigated via restoration. As the trophic links between streams and their riparian forests are easily disturbed by human intervention (Baxter *et al.* 2004), future restoration projects should pay more attention to the reciprocal effects of stream and riparian restoration and to feedbacks between these two strongly inter-connected ecosystems.

Overall, to solve the puzzle of ecological restoration, there are five crucial issues that need to be addressed:

1. There is a need of explicit criteria to (i) identify the restoration activities needed and to (ii) set the ultimate goal(s) of restoration to be able to assess the overall success of river restoration. Instead of defining a single reference condition or conducting single-goal restorations, we need to identify a probabilistic range of possible outcomes and expand our goals towards community level and ecosystem functioning (Palmer *et al.* 2005).
2. Future restoration projects should shift the focus towards watershed areas, with the aim of identifying and targeting limiting factors.
3. Long-term monitoring of restoration projects in order to determine their success, or reasons for their failure are needed. Learning from our mistakes is the only way to design better restoration projects in the future. Therefore, permits and funding should favor projects with clear priorities to document the ecological as well as socioeconomic outcomes of restoration projects.
4. An ecological ‘insurance’ should be added to all restoration projects (Palmer *et al.* 2007). Bottlenecks for the target species may occur at multiple points during their lifecycle (*e.g.* overwintering survival, lack of suitable spawning habitat or refugia from flood or drought). Therefore, to direct restoration towards alleviating the most important limiting factors is not possible without

sound ecological knowledge. As a result, scientists and practitioners need to work in close contact throughout the entire restoration project, spanning from the design to the implementation and monitoring of projects.

5. The documentation of the entire restoration process needs to be accessible to other practitioners and scientists (Palmer *et al.* 2007). Mechanisms ensuring that funding sources and citizens will remain involved throughout the project help to grow a wider understanding of the needs for restoration.

The above selection of important issues is by no means exhaustive, nor should individual issues be seen as mutually exclusive. At the moment, however, the ecological connectivity puzzle is being solved blind-folded. Only by improving the links between restoration activities and ecological theory will we be able to develop the means by which ecosystems may be effectively restored in the long term.

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