Restoration of streams used for timber floating: Egg to fry survival, fry displacement, over-wintering and population density of juvenile brown trout (*Salmo trutta* L.)

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Abstract

The construction of floatways during the 19th and 20th century profoundly changed the habitat conditions for fish and other aquatic organisms in lotic environments. Increased mortality during early life stages, reduced habitat quality and availability probably had large negative consequences for populations of salmonids. As timber floating ended during the 1970's, restoration programs were initiated that aimed to reverse the damage caused by floatway activities and to increase the production of salmonids. We predicted that restoration would have positive effects on egg to fry survival, fry displacement, over-wintering and population density of juvenile brown trout and on fish species diversity. To test these predictions, I conducted studies in restored (treatment) and unrestored (control) reaches in tributaries to the rivers Ume-, Vindel, Pite- and Kalixälven in northern Sweden. Egg-to-fry survival was approximately six times higher in restored (10.3%) compared to unrestored (1.7%) gravel beds. Displacement of newly emerged fry was reduced from 10.1% to 2.3% and first summer recruitment increased approximately three fold (from 0.2‰ to 0.6‰) following habitat restoration. Trout density increased significantly (>360%) in restored stream reaches whereas no change was evident in unrestored control reaches during a period of eleven years. Tracking of PIT-tagged individuals revealed that brown trout managed to over-winter within a restored stream. Minimum habitat suitability index explained a large portion (66.8 %) of the variation in the proportion of individuals that over wintered within different stream reaches. Although more fish species were caught in restored reaches, restoration did not result in significantly higher fish species diversity. These results show that restoration of streams utilized for timber floating can be an efficient method to enhance and conserve populations of trout and salmon. However, success of restoration relies on good knowledge about other species occurring in the system and their ecology. For instance, using wrong substrate sizes during restoration of spawning habitat can result in increased rates of egg predation by benthic predators. As brown trout utilize a variety of different environments during their lifecycle, including streams, lakes and sea, maximal response to habitat restoration will not be achieved as long as other factors, i.e. migration barriers and over exploitation, also constrain populations.

Keywords: channelization, log driving, salmonids, substrate, incubation, ice, habitat enhancement, migration, PIT-tag, spawning, habitat suitability, electrofishing, predation, recruitment, species diversity, habitat heterogeneity.

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Till Pappa

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Appendix

Papers I-VI

This thesis is based on the following papers, which will be refereed to by their Roman numerals:

I. Nilsson, C., Lepori, F., Malmqvist, B., Törnlund, E., Helfield, J.M., Palm, D., Östergren, J., Jansson, R., Brännäs, E., and Lundqvist, H. 2005. Forecasting environmental responses to restoration of rivers used as log floatways: an interdisciplinary challenge. *Ecosystems* 8, 779-800.

II. Palm, D., Brännäs, E., Lepori, F., Nilsson, K., and Stridsman, S. 2007. The influence of spawning habitat restoration on the density of juvenile brown trout (*Salmo trutta* L.). *Canadian Journal of Fisheries and Aquatic Sciences 64: 509-515.*

III. Palm, D., Brännäs, E. Östergren, J., Lindberg, M., and Lundqvist, H. The influence of bullhead (*Cottus gobio* L.) on Atlantic salmon (*Salmo salar* L.) recruitment – implications for spawning habitat restoration. *Manuscript.*

IV. Palm, D., Lepori, F., and Brännäs, E. Post-emergence displacement of brown trout *Salmo trutta* L., fry in a northern Swedish stream: influence of habitat restoration. *Manuscript.*

V. Palm, D., Brännäs, E. and Nilsson, K. Over-winter migration strategies of juvenile brown trout (*Salmo trutta* L.) in a restored ice-covered stream: influence of habitat suitability. *Manuscript.*

VI. Lepori, F., Palm, D., Brännäs, E., and Malmqvist, B. 2005. Does restoration of structural heterogeneity enhance the diversity of fish and macroinvertebrates? *Ecological Applications* 15, 2060-2071.

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Introduction

Streams worldwide are subject to human impacts that degrade habitat conditions and threaten biodiversity (Malmqvist and Rundle 2002). Over the last decades, growing public concern about environmental degradation (Ormerod 2003) and the ecological importance of spatial heterogeneity in streams (Petersen and Petersen 1991, Cooper *et al*. 1997, Brown 2003) have spurred numerous attempts to restore degraded systems (e.g., Hildebrand et al. 1997, Linløkken 1997, Scruton *et al*.1998, Muotka and Laasonen 2002, Roni *et al*. 2002, Pretty *et al*. 2003, Rubin *et al*. 2004). However, this increasing implementation of restoration methods has not been accompanied by a parallel development of scientific evaluations (Lake 2001). Therefore, the potential of restoration to fulfill its anticipated benefits, the recovery process, and the identification of conditions that cause either success or failure all remain poorly understood. Streams in northern Sweden provide good opportunities for the study of restoration effects on fish populations and biodiversity. Here, beginning two decades ago, hundreds of kilometers of streams that were channelized in the 19th and 20th centuries to transport timber from the interior to coastal sawmills (Törnlund 2002, Törnlund and Östlund 2002, paper I, Törnlund 2006, Törnlund and Östlund 2006) are having physical habitat restored via the replacement of boulders, gravel, large woody debris, and removal of constraining embankments.

Among the organisms which have shown a high sensitivity to habitat degradation in lotic environments are salmonids, especially during their early life stages. Their complex ecology, where intact and heterogeneous stream habitats play an essential role, have been thoroughly described, i.e. Armstrong *et al*. (2003), Klementsen *et al*. (2003). In degraded habitats, salmonid eggs and embryos often suffer high mortality due to high concentrations of sand and fine particulate matter in the spawning substrate which reduce water circulation, oxygen supply and the possibility to emerge from the redd (Hausle and Coble 1976, Olsson and Persson 1988, 1989, Laine *et al*. 2001, Lapointe *et al*. 2004) or simply due to shortage of potential spawning habitat (Milner *et al*. 2003). Restoration of spawning habitat, including cleaning of spawning gravel from sand and fines, will hence have positive effect on egg to fry survival (Shackle *et al.* 1999). As egg survival is not only affected by the circulation of water and the supply of oxygen (Rubin 1998, Ingendahl 2001, Armstrong *et al*. 2003) but also by bentic predators (DeVries 1997), the size of the substrate is important. Biga *et al*. (1998) concluded that the size of the substrate regulates to what extent predators can descend and access egg pockets within spawning beds. Knowledge about substrate sizes when spawning habitats are restored and potential predators is therefore of great importance to minimize predation.

After emerging, fry attempt to settle, start to feed and establish territories - a time of great risk. At this stage fry are very susceptible to displacement by high water velocities (Ottaway and Forrest 1983, Crisp and Hurley 1991, Daufresne *et al*. 2005) and therefore dependent on finding low velocity microhabitats (Heggenes 1988, Moore and Gregory 1988, Meyer and Griffith 1997). Uncontrolled movements may increase the risk of mortality due to starvation or predation (Elliott 1994, Einum and Fleming 2000, Einum and Nislow 2005). Restoration of habitat heterogeneity in channelized streams is assumed to increase the amount of flow refuges and thus reduce fry displacement.

In seasonal environments juvenile salmonids annually have to face several critical periods, i.e. drought during seasons of low precipitation, which may have large negative effects on populations (Elliott and Elliott 2006). In northern boreal regions winter is one of the most critical periods (Quinn and Peterson 1996, Mäki-Petäys *et al*. 2000, Huusko *et al*. 2007, Hurst 2007). As lotic environments often have highly dynamic ice conditions, salmonid habitats in winter are largely unpredictable which forces individuals to move and continuously seek new habitat and this can have a negative influence on survival (Huusko *et al.* 2007). Stream habitats that provide high local variation in depth, water velocity and substrate size provide refuges from various ice conditions and are thus preferred by juvenile salmonids (Huusko *et al.* 2007). Restoration that generates habitat heterogeneity will therefore probably improve over-wintering success. Given that restoration increases survival at the egg stage, reduced displacement at the fry stage and increases survival during winter, restoration should result in greater population density.

Besides enhancement of salmonid fisheries, one of the most compelling basis behind restoration projects is to moderate the current alarming rate of biodiversity loss due to human activities (May 1988, Wilson 1992). Maximizing biodiversity, therefore, is often a key goal of restoration schemes (Young 2000). According to current ecological theory, patterns of biodiversity are largely controlled by the local heterogeneity of the physical environment (cf., Brooks *et al*. 2002, Brown 2003). Therefore, in physically homogenized streams, attempts to achieve increased biodiversity typically focus on the restoration of structural heterogeneity (Hildebrand *et al*. 1997, Muotka *et al*. 2002, Lewis and Williams 1984). As this is also the rationale for restoration of streams utilized for timber floating, an increased number of fish species is a likely outcome.

Thesis objectives

This thesis is a part of an interdisciplinary research project aiming to assess the effects of restoration on stream ecosystems and aquatic organisms used as float ways.

The objectives were to asses the effects on salmonid egg survival, fry displacement, juvenile over-wintering and population density using brown trout as a model species. In addition the aim was also to identify responses in the fish community. This was done in two steps; first, we reviewed the literature to produce predictions about how brown trout and the fish community would respond to restoration (paper I); second, these predictions were tested in the field and experimental studies (paper II-VI).

We predicted the following responses to restoration:

1. Increased egg-to-fry survival (II, III)
2. Reduced rate of post emergence fry displacement (IV)
3. Successful over-wintering in restored systems (V)
4. Increased population density (II, IV, VI)
5. Increased diversity of fish species (VI)

History of timber floating and restoration

To facilitate the water-based timber transport during the 19th and 20th centuries, extensive transformations of streams and rivers into float ways were made. Timber floating was particularly widespread in Sweden. In 1950, approximately 60% (i.e. 30 000 km) of all streams in Sweden had been modified for this purpose. Streams were narrowed and deepened, boulders and large woody debris were removed or blasted from the channel and secondary channels were often cut off (Fig. 1 and 2). To further improve efficiency, many streams were gradually turned into flumes. As the technique developed, and especially with the help of bulldozers, the effects on aquatic systems increased. These actions resulted in a network of fast flowing channels with low habitat heterogeneity (Törnlund 2002; Törnlund and Östlund 2002; paper I; Törnlund 2006; Törnlund and Östlund 2006).

Removal of boulders and large woody debris have multiple impacts on stream dwelling salmonids. First, these physical structures are essential elements of both juvenile and adult salmonid habitat, as they provide refuge from predators and fast flows, as well as hydraulically suitable feeding stations. Second, boulders retain finer particles such as gravel and sand which would otherwise be eroded, with an armoring layer of coarse particles developing on the streambed (Merz *et al.* 2004). Given that most salmonids spawn in depressions (redds) excavated into gravel, the presence of suitable gravel is essential for the reproduction and recruitment of these fish. Therefore, any removal of boulders due to channelization might reduce salmonid densities not only because of the loss of juvenile and adult habitat, but also because of the loss of spawning substrate. Other anthropogenic actions such as dam constructions, cutting off secondary channels, and the narrowing of the channel also had severe effects due to reduced connectivity and loss of habitat area.

Since the use of water for timber transport ended in the 1970's, several streams and rivers utilized for timber floating have been restored in attempts to reverse the human-induced negative impacts. One important goal of these restoration programs was to increase production of brown trout and Atlantic salmon. From a fishery management point of view, stream habitat restoration has been conducted through two different methods: 1) nursery and rearing habitat restoration, and 2) spawning habitat restoration. Nursery and rearing habitat restoration have generally aimed to increase channel heterogeneity (e.g. variation in depth, water velocity and substrate size) and channel width (Fig. 1). This has largely been implemented by the replacement of boulders that was removed from the channel and placed along the channel margins during the timber floating era using bulldozers. Addition of large woody debris and reopening of cut off secondary channel have also been performed. During spawning habitat restoration, the reconstruction of erosion tolerant gravel patches has been the main strategy. This has been conducted by local removal of armored stream beds and reconditioning of present substrate or through the addition of external substrate.

Fig. 1. Above, River Gillerån before (left) and after (right) clearing 1937. Below, River Gargån before (left) and after (right) restoration 2006 (Photo: Daniel Jonsson).

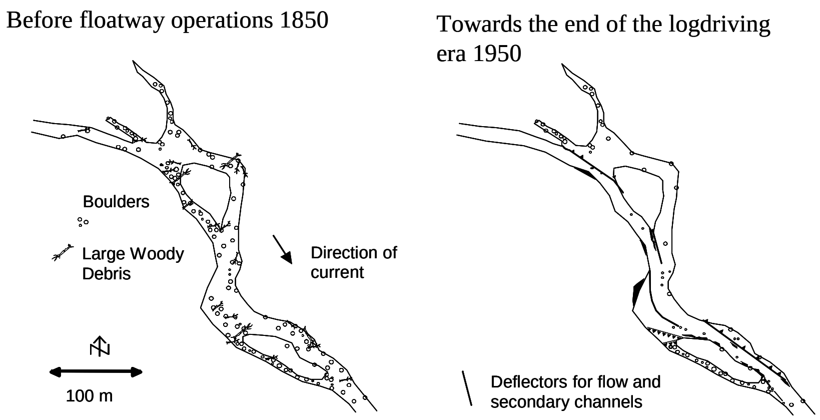

Fig. 2. The development of a floatway from the mid 1800's to the mid 1900's including secondary channel disconnections, flow deflectors and removal of boulders. The example is from the River Bjurbäcken, a tributary of the River Vindelälven in northern Sweden. Modified from paper I.

Material & methods

Study area

The field studies (paper II, IV and V) were conducted in 2nd to 3rd order tributaries of the rivers Ume, Vindel, Pite and Kalixälven in northern Sweden (Fig. 3). Paper V was carried out in the main stem of River Vindelälven. The streams are characterized by tranquil reaches interspersed with steeper (gradient 1–3%), fast flowing sections (runs), which typically extended for tens to hundreds of meters. The streams follow a nival flow regime with continuous ice covers from November to April. The oligotrophic, circumneutral, and moderately humic water in the streams is consistent with the organic-rich soils and crystalline geology (Precambrian gneiss) that characterize the watersheds. The fish fauna is dominated by brown trout, Atlantic salmon, bullhead (*Cottus gobio* L.), pike (*Esox lucius* L.), minnow (*Phoximus phoximus* L.), burbot (*Lota lota* L.), and European grayling (*Thymallus thymallus* L.). The streams are surrounded by managed forest consisting of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.); scattered riparian broadleaved trees include gray alder (*Alnus incana* L.), birch (*Betula* spp.), and willow (*Salix* spp.). The experimental study (paper III) was conducted at Umeå Marine Research Station located 35 km south of Umeå (63° 47´N, 20° 17´E).

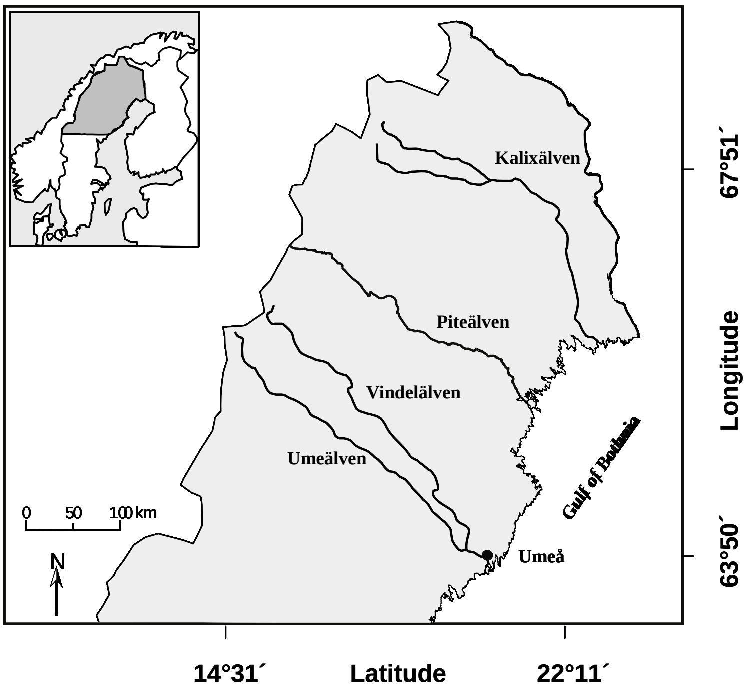

Fig. 3. The location of River Ume-, Vindel-, Pite- and Kalixälven.

Habitat characteristics

Habitat measurements in paper II, IV and V were conducted at fixed points along multiple equidistant transects covering stream reaches from 50 to 150 m in length. Water velocity was estimated using an electromagnetic flow meter and substrate size was measured along the b-axis. Stream bed topography was measured at multiple scales. At the patch (<1m) scale we used a streambed profiler whereas at the reach (50-150 m) scale we used single point depth measurements. In paper II we used sieves to calculate substrate size distribution of spawning gravel. For further details regarding habitat measurements see paper II, IV and VI.

Habitat suitability

In paper V we related habitat suitability in different reaches of a small stream to over-wintering of juvenile brown trout. Habitat suitability was estimated at fixed points along multiple equidistant transects covering the stream reaches. At each sampling point water depth, velocity and dominant substrate size was measured after which a winter habitat suitability index, obtained from river Kuusinkijoki in Finland (Mäki-Petäys *et al*. 1997), were calculated. To get the joint habitat suitability for each point, including all three habitat parameters, habitat data were combined in three different ways using the procedures described in USGS (2001); multiplicative, geometric mean and the minimum value.

Egg-to-fry survival

In paper II differences in brown trout egg-to–fry survival between restored and unrestored gravelbeds in a tributary to river Kalixälven was studied. A known amount of brown trout eggs was placed into a set of incubation boxes and buried in gravel beds within 24 hours after fertilization. At the stage of emergence the incubation boxes were retrieved and the survival rate was measured.

Egg predation

In paper III bullhead predation on Atlantic salmon eggs is related to substrate size. This was conducted at an indoor laboratory using stream aquariums. A known number of Atlantic salmon eggs were buried in artificial spawning redds constructed out of different substrate sizes, after which wild captured bullheads were released into the aquariums. After two weeks the eggs that escaped predation were counted and predation rates were calculated.

Fry displacement

Paper IV evaluates the consequences of rearing habitat restoration on post emergence fry displacement and juvenile recruitment of brown trout. This was done by comparing the drift of newly-emerged hatchery-reared brown trout fry that was released into restored and unrestored stream reaches.

Sampling of fish

Electrofishing was used as the main method to sample fish. Fish density was calculated using single or multiple removal techniques according to Bohlin *et al*. (1989).

Tagging and re-locating fish

In paper V we studied over-wintering of juvenile brown trout by tracking the movement of individually tagged fish. Wild brown trout were caught by elecrofishing and tagged with Passive Integrated Transponders (PIT-tags) (length 23 mm). After anaesthetizing (with MS 222) the fish, a five mm abdominal incision was carefully made, after which a PIT-tag was inserted and the incision closed by one suture. Each tagging was performed in approximately 30 seconds. Before release, the fish were allowed to recover in a holding net for several hours.
To track the position of tagged fish we used Mobile RFID Leoine system, Technology Aquartis SENC Quebec, Canada, witch consists of a backpack-carried 12 volt PIT-tag antenna (60 cm in diameter) which has a maximum detection range (for a 23 mm PIT-tag) of 125 cm. The operator walked in the middle of the stream in the flow direction slowly sweeping the antenna from bank to bank approximately 1 cm above the water, ice or snow surface (Linnansaari *et al*. 2007).

Results – summary of papers

I.

This paper describes the history of log driving, reviews its impact on physical and biological conditions and processes, and predicts the responses to restoration. We hypothesized that restoration measures will make rivers wider and more sinuous, and provide rougher bottoms, thus improving land-water interactions and increasing the retention capacity of water, sediment, organic matter and nutrients. Some habitat components, i.e. beds of large boulders and bedrock outcrops, and availability of sediment and large woody debris, were assumed to be extremely difficult to restore. The geomorphic and hydraulic/hydrologic alterations were supposed to favor production, diversity, migration and reproduction of riparian and aquatic organisms. Time for response is likely to vary according to the types of processes and organisms. Regarding responses of brown trout and the general fish community we predicted increased egg survival, reduced fry displacement, successful over-wintering, increased population density and species diversity.

II.

Between 1992 and 2003, we measured the density of age 0+ brown trout in a channelized stream in northern Sweden, which was restored using two different schemes. One section of the stream was restored by the addition of boulders and reconstruction of gravel beds, whereas another section was restored through addition of boulders only. In addition, we compared the substrate-size composition of gravel beds and the egg-to-fry survival between the two stream sections, and related the density of age 0+ brown trout to the area of reconstructed gravel beds. After the restoration, the density of age 0+ trout increased significantly in the ”boulder+gravel” section (>360%) and was positively correlated with the area of reconstructed gravel beds. By contrast, the density of age 0+ trout did not change in the ‘boulder only’ treatment. Egg-to-fry survival was significantly higher, ca. six times, in the ”boulder + gravel” section (10.3%) compared to the ”boulder-only” section (1.7%), probably because of the higher content of sand and fine sediment in the gravel beds of the latter treatment. This study shows that the density of 0+ brown trout was limited by the availability and quality of spawning substrate rather than the structural habitat complexity.

III.

This paper investigates whether bullhead influence the recruitment of age 0+ Atlantic salmon within the river Vindelälven in northern Sweden. We also tested the hypothesis that the size of the spawning substrate influences the ability of the bullhead to predate on salmon eggs.

The analysis of combined data from radio-tagged spawning female salmon and juvenile salmon density, obtained through electrofishing, revealed significant differences in recruitment of juvenile salmon. Recruitment was eight times higher in areas without bullhead compared to areas with bullhead.

In stream aquaria, artificial spawning redds containing salmon eggs were constructed from four different substrate sizes, 12.7, 23.1, 37.1 and 62.1 mm in mean diameter. Fifteen days after the introduction of wild-captured bullhead to the

aquaria, egg predation rates were calculated. Predation averaged 83% in the aquaria containing the largest substrate size whereas only 2-3% predation was observed in the other substrate sizes.
We conclude that bullhead influence the recruitment of juvenile salmon within the river Vindelälven, probably through predation on eggs. The possibility of bullhead to access spawning redds and consume salmon eggs was influenced by the size of the substrate. For salmon spawning habitat restoration, selecting gravel large enough for sufficient water circulation but small enough to exclude bullhead, is therefore crucial in order to minimize the risk of egg predation in areas with bullhead.

IV.

This paper tests the hypothesis that habitat restoration decreases the post-emergence displacement of brown trout fry. The short-term (24 h) displacement of released trout fry was reduced from 10.1 % to 2.3 % following restoration. Water velocity was the most important factor controlling fry displacement, accounting for 89.4 % of the variation. Moreover, the restoration increased the post-summer recruitment (the proportion of introduced juvenile trout remaining in the study reaches 60 days post release) approximately three fold (from 0.2 ‰ to 0.6 ‰). These findings demonstrate that habitat restoration substantially reduces the magnitude of fry displacement and contributes to higher recruitment.

V.

Over-winter behavior in brown trout was studied in a restored ice-covered stream in northern Sweden. We monitored movements of 238 individually-tagged juvenile trout (body length 120-204 mm) from late summer until late winter using portable PIT-tag equipment and related it to body length and habitat suitability. We found three different over-winter strategies: 1. Individuals that over-wintered close to the site at which they were tagged (stationary strategy), 2. Individuals that conducted reach-scale movements (short migration strategy), 3. Individuals that left the study stream (long migration strategy). There was no difference in body length between individuals undertaking different strategies. Habitat suitability explained a large portion (66.8 %) of the variation in the proportion of individuals that undertook the stationary over-wintering strategy in different reaches from late summer until late winter. We conclude that several over-winter strategies can exist within a single trout population and is not related to body length. Also, we suggest that habitat suitability indices can be useful tool to asses over-wintering conditions in stream reaches.

VI.

Structural heterogeneity together with fish and invertebrate diversity was compared at restored, unrestored, and reference sites on tributaries of the Ume River, northern Sweden, where several kilometers of streams have been restored from channelization through placement of boulders into the channel. Structural heterogeneity, measured as variation in depth, at the study sites was assessed at two spatial resolutions likely to be affected by restoration. These are the patch scale (0.7 m), reflecting substratum characteristics, and the reach scale (50 m), reflecting general channel topography. Fish and invertebrate samples were used to assess taxonomic richness, taxonomic density, evenness, and assemblage composition at the study sites. Measures of structural heterogeneity were substantially higher at restored relative to channelized sites (55-81%); however, indices of fish and invertebrate diversity were similar between these treatments. At restored sites, measures of structural heterogeneity and fish and invertebrate diversity were consistent with, or slightly exceeded reference levels. This implies that local (patch to reach) heterogeneity did not structure fish and invertebrate assemblages in the study streams. Our results suggest that restoration might have little beneficial effect on biodiversity if the restoration schemes (and the original impacts, which are the target of amelioration attempts) do not affect structural heterogeneity relevant to the target organisms.

Discussion

Floatway constructions during the 19th and 20th century resulted in large changes of stream habitats across northern Scandinavia (I). From our current knowledge about the habitat requirements of juvenile Atlantic salmon and brown trout, the most important changes were probably the reduction in structural habitat heterogeneity (variation in depth) which resulted in increased water velocity, reduction of channel width, and loss of gravel (i.e. spawning substrate). Commonly, restoration projects rely on the assumption that stream geomorphology and hydrology will change following the removal of float way constructions and replacement of boulder and smaller substrates (I). Indeed, our results supports this assumption. Measurements of these key habitat parameters showed that habitat heterogeneity and channel width was higher and that water velocity was lower in restored compared to channelized stream reaches (IV, VI). These findings are supported by studies from similar systems in Finland (Muotka and Laasonen 2002, Muotka *et al.* 2002).

Did restoration result in higher egg-to-fry-survival?

The results of paper II showed that brown trout egg-to-fry survival was significantly higher in restored compared to unrestored gravel beds. Visual observations of the recovered eggs suggested that the most likely mortality cause was suffocation caused by fine sediments or fungal infections. Survival rates were consistent with the rate of survival observed in other studies where incubators were used at natural spawning sites (Bernier-Bourgault and Magnan 2002). It is likely that the improved egg survival was mainly caused by the removal of sand and fine sediment conducted as a part of the gravel bed restoration. In agreement with this suggestion, cleaning of sand and fines from spawning gravel significantly increased the survival of brown trout embryos in four English rivers (Shackle *et al.* 1999), and several studies have shown that the survival of embryos tend to be low in substrates containing high amounts of sand and fines (Hausle and Coble 1976, Olsson and Persson 1988, Lapointe *et al*. 2004). Salmonids naturally clean the substrate of sand and fines during the excavation of redds (Kondolf *et al*. 1993, Gottesfeld *et al.* 2004), but such actions may be insufficient to ensure high embryo survival where the spawning habitat has been highly degraded, which was probably the case of our study stream before restoration.

In our egg study, the egg-to-fry survival rate was low in both restored and unrestored gravel beds. In part, the low survival might reflect artifacts due to the use of incubators, which tend to accumulate more sediments and impose higher mortality on embryos than natural redds (Harshbarger and Porter 1982). The low survival might also have natural causes, such as the development of fungal infections, which might have been exacerbated by the relatively high densities of eggs in the incubators (0.1 eggs•cm^{-3}). However, the aggregation of eggs is natural in salmonids, which typically lay eggs in pockets excavated into the streambed (Crisp and Carling 1989, Fleming 1996, De Gaudemar *et al*. 2000). Moreover, the survival of salmonid embryos seems to be unrelated to egg density (Raddum and Fjellheim 1995, Rubin 1995). In any case, the range of survival rates observed in our study (0-47%) was not substantially different from the range observed in other egg incubator assays at enhanced spawning sites, where densities of 0.3-0.5 eggs·cm^{-3} have resulted in average survival rates of 22% to 51% (Rubin and Glimsäter 1996, Shackle *et al*. 1999, Mertz *et al.* 2004).

Because egg survival is not only affected by the substrate composition but also of benthic predators, i.e. bullhead, the effect of four different substrate sizes on egg predation was investigated (III). This study revealed that predation rate of bullhead on Atlantic salmon eggs was significantly higher (82.3%) in large substrates (size 62.1 mm) compared to smaller substrates (sizes 12.7-37.1 mm) where predation ranged between 1.6-2.8 %. These results fully support the conclusions by Biga *et al*. (1998) that the size of the substrate regulates to what extent predators can descend and access egg pockets within spawning beds. In our study we used size-sorted substrate so we could not fully reflect the substrate size composition of natural spawning reeds (Kondolf *et al*., 1993). Variation of substrate sizes in natural spawning redds likely regulates access by interstitial predators. The more substrate is sized below some threshold value, the lower the predator access probably is. Nevertheless, substrate used in spawning habitat restoration projects often originates from commercial gravel mines that only supply sieved and sorted fractions with low size variation.

Did restoration reduce the rate of post emergence fry displacement?

The results of paper IV indicate that in-stream restoration can significantly reduce post-emergence displacement of brown trout fry and thereby contribute to higher recruitment. Approximately 6-8 % of the released fry was displaced from the canalized control site whereas almost no fry were displaced from the restored control site (0.0 - 0.2 %). At the canalized impact site, fry displacement was significantly reduced from 10.1 % before restoration to 2.3 % after restoration. Also, the reduction of fry displacement was strongly associated with the decrease in water velocity caused by the restoration. The effects of restoration on water velocity and fry displacement were evident as early as one year after restoration. However, the effects are likely to increase with time. In Sweden and Finland, recently restored stream reaches are characterized by a lack of woody debris and aquatic mosses, which were extensively dislodged by bulldozers during restoration work (Muotka *et al*. 2002). The re-colonization by mosses and other aquatic plants and the accumulation of large woody debris might take several years, but will further reduce water velocity and increase habitat heterogeneity, and thereby further decrease the post-emergence displacement of fry.

The effects of the restoration on the displacement of trout fry is of great interest from several aspects. First, these results further support the previous suggestions that water velocity plays a primary role in controlling the post-emergence displacement of fry (Ottaway and Forrest, 1983; Crisp and Hurley, 1991; Daufresne *et al*., 2005). Second, the practical implications of the results emphasize the importance of stream restoration for the self-sustaining of brown trout populations. Whereas adult trout easily resist and even require fast flows in streams, e.g. for reproduction, juveniles can only settle in habitats with lower water velocities. In the absence of slow-flowing areas, brown trout fry emerging from the spawning substratum are inevitably washed downstream for tens (Elliott 1987; IV) of meters, where a large proportion of them likely will die from starvation or predation (Elliott 1994, Einum and Fleming 2000, Einum and Nislow 2005). The sensitivity of brown trout fry to higher water velocities was observed by Heggenes and Traaen (1988), who found that brown trout fry at temperatures between 6-14 °C could only resist water velocities in the range 0.15-0.19 m s^{-1} before being displaced. In channelized streams, where water velocities often are well above this tolerance threshold, post-emergence mortality of brown trout juveniles due to displacement is likely to be so high that long-term sustainability of brown trout populations is jeopardized.

Given that the mortality of juvenile brown trout is naturally high (80-90%) (Elliott, 1994), any factor causing additional mortality might negatively affect trout populations. Whether the loss of fry because of displacement can be considered as additional mortality is not clear, due to a lack of knowledge about the fate of displaced fry (Daufresne *et al*., 2005). However, when displacement due to high water velocities results in mortality and not in the relocation of fry, the loss can be considered additional. Therefore, any actions that reduce fry displacement will probably also reduce the total mortality during the fry stage.

In contrast to water velocity, streambed roughness (i.e. habitat heterogeneity) did not appear to be an important factor affecting the displacement of fry at the study sites (IV). These results contradict Elliott (1987) and Gustafson-Greenwood and Moring (1990), who suggested that increased habitat heterogeneity should reduce the displacement of fry by increased availability of flow refuges. Habitat heterogeneity is also believed to influence displacement by reducing competition between fry, as it effectively increases the habitat area per unit of channel length (Höjesjö *et al*. 2004, Einum and Nislow 2005). However, Daufresne *et al*. (2005) noted that the downstream displacement of trout fry during the first days following emergence is controlled primarily by flow conditions rather than by intraspecific competition. We hesitate to conclude, however, that habitat heterogeneity does not influence the displacement of fry. Indeed, the reduced water velocity after restoration is certainly a consequence of increased channel roughness (habitat heterogeneity) due to the addition of boulders. Therefore, the changes in water velocity were intimately connected to changes in habitat heterogeneity (IV). However, this study suggests that water velocity is a stronger proximate control of the displacement of fry than habitat heterogeneity *per se*. Alternatively, the apparent lack of effect of habitat heterogeneity on fry displacement and the similarity in heterogeneity between the restored and canalized control sites might suggest that the scale at which heterogeneity was measured was not fine enough. In paper V habitat heterogeneity was measured at the reach (50 m) and patch (< 1m) scale and differences between restored and channelized sections were substantial. In paper IV heterogeneity was measured at a slightly larger scale (150 m). As newly emerged salmonid fry initially use only small areas (e.g. 100 cm^2, Gustafson-Greenwood and Moring 1990), the risk of displacement is probably influenced by habitat heterogeneity at scales finer than the one considered here. Another possible reason for the apparent lack of effect of the enhanced heterogeneity on the displacement of fry is that we introduced newly emerged fry originating from a hatchery, and their behavior may have differed from that of naturally-emerged fry. However, even though experimental introduction of fry has been criticized (Daufresne *et al*. 2005), the sensitivity of fry to displacement due to high water velocity seems similar between introduced (e.g. Crisp and Hurley 1991) and naturally-emerged (Daufresne *et al*. 2005) brown trout fry.

Were juveniles over-wintering successfully in restored systems?

According to our data juvenile brown trout undertook three different over-winter strategies. Most detected individuals spent the winter close to the sites at which they were tagged whereas only a few individuals conducted any short or long migrations.

Given the high efficiency in tag detection, 90-100 % (this study) and 93-100 % (Linnansaari *et al*. 2007) only few individuals might have escaped detection within the surveyed tagging sites. Nevertheless, a substantial number of individuals that migrated short distances might have gone undetected as we were only monitoring a small portion of the entire stream.

Habitat suitability explained a large portion (66.8 %) of the variation in the proportion of individuals that over-wintered and remained within different tagging sites from late summer until late winter. Rimmer *et al*. (1983); Heggenes and Dokk (2001) suggested that if a given habitat fulfills species specific preferences for both summer and winter conditions, no or little seasonal migration would be necessary. Therefore, as winter habitat suitability gets lower the proportion of over-wintering individuals should decrease.

Meyer and Griffith (1997); Harvey *et al*. (1999) found that the availability of cover determined the number of fish that held positions at different sites during winter. Further more, Mitro and Zale (2002) discovered that habitats of low heterogeneity were abandoned in favor of sites with higher heterogeneity during winter. Probably, our study stream did not provide enough habitat complexity to host all tagged individuals during winter. However, individuals that migrated and switched tagging sites prior to the start of the winter did not end up at sites that had higher winter habitat suitability compared to their tagging site of origin, which suggests that selection of over-wintering site must at least partly be explained by other factors than the condition of the habitat. Never the less, we suggest that habitat suitability indices can be useful tools to asses over-wintering conditions in stream reaches at our study site.

To answer if over wintering was successful or not, the behavior of brown trout in our restored system should be compared to behavior in an unrestored control system. However, the tagged individuals in paper V performed three different over-wintering strategies, of which one was to remain within their summer and fall habitat from late summer to late winter. This suggests that the habitat conditions in this restored site must have been acceptable and over wintering successful.

Did restoration increase population density?

Paper II showed that the restoration of spawning habitat by the removal of the armored streambed, together with replacement of large boulders into the channel, influenced the density of age 0+ brown trout, whereas the addition of boulders alone did not. Consistent with these results, several studies have shown that the availability of spawning habitat is one of the most important predictors of the density of juvenile salmonids in running waters (Beard & Carline 1991, Beland 1996, Magee *et al*. 1996). The increased availability of spawning habitat probably reduced the mortality of embryos associated with spawning activities. Where salmonids are forced to spawn in confined areas, the redd excavated by any fish can be disturbed by overcutting by other spawners (Milner *et al*. 2003).The addition of spawning areas therefore allows fish to distribute themselves more widely and thus avoid interference during the excavation of redds. Supporting this hypothesis, as demonstrated in paper II, the densities of 0+ brown trout were positively correlated to the mean area of restored gravel beds. Still, a relatively high variation (38 %) was noted, which probably reflected fluctuations in the number of returning spawners or variations in nursery and rearing conditions. The existence of other sources of variation is also indicated by the stepwise increase in population size during the time periods 1992-1993, 1994-2000, and 2001-2003, which does not completely mirror the increase in the area of reconstructed gravel beds. Another important factor causing the increase in brown trout density is of course the enhanced egg-to-fry survival in the restored gravelbeds.

Although the addition of boulders alone had no positive effects on brown trout density (paper II) and on fish density in general (paper VI), benefits of boulder addition still exist. Paper III demonstrates that rearing habitat restoration notably reduced the displacement of newly emerged brown trout fry and that recruitment was increased. Furthermore, as restoration increased the wetted channel width (+40%), the area of available habitat per unit stream length also increases. This partly explains the higher fish biomass in restored compared to channelized stream reaches observed in paper VI.

Did restoration increase the diversity of fish species?

Paper V provides no support for the hypothesis that restoration of structural heterogeneity in the study streams promoted biotic diversity. We considered three possible explanations for these results. First, patterns of fish diversity at the study sites might not be controlled by spatial heterogeneity at the scales affected by restoration. Second, biotic differences might have existed between treatments, but were not detected because of insufficient statistical power. Third, the physical and biological recoveries at restored sites might have been incomplete at the time of the study.

Although research on associations between biotic diversity and spatial heterogeneity has a long history (Thienemann 1954), only recently has the scale dependence of these associations been explicitly recognized (e.g., Cooper *et al*. 1997). While there is debate about which scales of structural heterogeneity control fish diversity in streams, the relevant scales are expected to match the scales at which these organisms perceive their environment, in turn determined by factors such as home-range dimensions, behavioral patterns of response to resources, and larger scale movements (Cooper *et al*. 1997). Fish typically have broad home ranges that encompass different habitats (often taxon specific), each fulfilling different functions, including spawning, feeding, and refuge provisioning (e.g., Mäki-Petäys *et al*. 1997). As a result, the diversity of fish is probably dependent on heterogeneity in these functional habitats. The lack of correlation between heterogeneity and diversity measures in paper VI suggests that the restoration acted at scales of structural heterogeneity that were irrelevant to fish. For instance, the restoration did not create substantially new habitats such as deep pools, vegetated margins, or backwaters that encouraged colonization of additional fish and invertebrate species. The habitat remained essentially lotic in character (runs and riffles with coarse mineral substrata), and thus probably suitable for species that were already present. In this study, the strong similarity in faunal characteristics between sites from the same streams shows that factors at the watershed scale were more relevant to invertebrate diversity than the restoration status i.e., whether the site was channelized or restored.

A temporary lack of biotic changes following restoration work may arise due to biological time-lag or physical isolation delaying colonization by new taxa (Fuchs and Statzner 1990). However, our study sites were located within a relatively intact drainage system, where nearby lakes, deep pools, and larger rivers could act as sources of fish species to restored sites. Under these conditions, fish may respond quickly to habitat improvement via immigration from neighboring zones (Riley and Faush 1995, Harvey 1998). Therefore, we suggest that the three to eight years separating restoration from evaluative work in this study should have been sufficient to allow considerable biological recovery at the restored sites. In contrast to our study area, the potential for recolonization of restored reaches would be limited where whole river systems have been degraded and disconnected from their floodplains, such as in many urbanized lowland areas in Europe and North America. However, in a Finnish restoration project similar to ours, restored sites showed erratic changes in invertebrate-assemblage structure for up to eight years following restoration, suggesting that full equilibration with changed habitat conditions might take a considerable time (Muotka *et al*. 2002). Without more long-term quantitative data it will not be possible to conclusively assess the time needed for biotic recovery from restoration in our study area, or in general.

Estimates of fish community attributes in streams sometimes show errors so large that their usefulness in detecting the effects of habitat changes has been questioned (Brooks *et al*. 2002). In paper V, however, consistency of mean values between channelized and restored sites and small errors suggest that in most cases the lack of significant biotic differences was not an artifact due to type-two errors. In effect, the power of the comparisons between channelized and restored sites would have been adequate to detect 10% or 20% increments in diversity components relative to channelized streams. Increments of 10% and 20% were chosen to represent the lower limits of what might be considered a biologically meaningful change.

Broader perspectives on stream restoration

Restoration of streams utilized for timber floating seems to offer a practical solution to fishery managers under the increasing demand to enhance salmonid fisheries. However, the well being of salmonid populations depends on factors besides than the condition of freshwater habitats. The development of hydroelectric power plants and the expanding net work of logging roads have caused obstructions to fish migration which in many places have resulted in the extinction or weakening of populations (Laine *et al*. 2002, Rivinoja 2005, Östergren 2007). Intense harvest at sea along with diseases constitutes other threats to salmonid populations (McKinnell 1998, Ikonen 2006). Given this complex situation, positive effects from restoration in freshwater habitats can be difficult to demonstrate if populations can not respond due to constraints in other parts of their lifecycles. Therefore, in restoration programs, where the goal is to benefit fish populations, all constraints to population development must be ranked by their impairment and dealt with accordingly. For instance, there is no point to restore spawning habitats if they can not be reached by spawners due to migration barriers, i.e. hydroelectric power plants. In this scenario, it is better to improve connectivity before conducting habitat restoration. However, restoration of upstream habitat could be used as a strategy to promote measures of migration barriers downstream.

Stream restoration schemes serve multiple purposes, besides improvement of salmonid fisheries, i.e. enhancement of riparian plant diversity (Helfield *et al*. 2007). Furthermore, restoration might also be justified even where benefits to the fauna and flora are not expected. Placement of boulders in channelized streams, for instance, can contribute to the efficient use of base resources by reducing downstream losses of leaf detritus due to poor retentiveness and mechanical fragmentation (Muotka *et al*. 2002, Lepori *et al*. 2005).

Future research needs

- To further explore the effects of stream restoration, projects focusing on fish production on the catchments scale are necessary. Studies focusing on small scale (reach) are important to understand what factors may limit populations (Rosenfeld *et al*. 2000) and how these may be affected by restoration, i.e. changes of habitat. However, since brown trout and Atlantic salmon use and shift habitats at a larger scale (catchments) throughout the juvenile stage, all mechanisms regulating production cannot be encompassed within reach scale studies (Everest *et al*. 1991).

- Although restoration and associated evaluation projects have been conducted at many places during the last two decades, we still lack knowledge about the time scale required for full recovery including fauna, flora and geomorphology. To be able to completely evaluate the results of restoration the effects should be assessed when the response organisms or variables have had time enough for full recover. To fill this information gap, long-term restoration projects and monitoring programs are necessary (Muotka *et al*. 2002).

- Because winter in northern Scandinavia includes approximately half the year with continuous ice cover, knowledge about winter ecology of stream-dwelling fish is important, including survival and habitat requirements, and how it relates to different restoration activities.

Although the number of winter studies has increased during the last decade, more research is still needed (Huusko *et al*. 2007).

- Different species of stream-dwelling fish have evolved and adapted to different types of habitat. These adaptations not only influence their ability to dwell in different habitats, but also their ability to compete with other species. Because stream habitat restoration generates large changes in the physical habitat, the competitive situation between species will probably also be affected. In Scandinavia, restoration programs commonly aim to increase production of brown trout and Atlantic salmon. However, it is known that the two species compete and that brown trout is the more aggressive species and prefer low velocity holding sites (Heggenes and Saltveit 1990; Heggenes *et al*. 1999; Heggenes *et al*. 2002). As restoration generally reduces water velocities, trout that generally dwell in lower water velocity compared to salmon, can move into habitats previously predominated by salmon and start to compete and potentially reduce salmon production. To reduce the risk of negative consequences of restoration, additional research on how changes in physical habitat effects the competitive situation between species, i.e. through physical and bioenergetic habitat modeling (Rosenfeld 2003; Rosenfeld *et al*. 2005), is required.

- As the climate is gradually changing, from a Scandinavian view, with higher temperature, more precipitation and more extreme flow events the effects of restoration needs to be considered in light of climatic conditions. Possibly the current restoration methods need to be adapted to match climatic changes. Potentially, the benefits of restoration we find today might be overshadowed by negative effects of climatic change in the near future (2007 Battin *et al*. 2007; Walsh and Kilsby).

Swedish summary – Svensk sammanfattning

Konstruktionen av flottleder under 1800 och 1900-talet medförde radikala förändringar av levnadsmiljöerna för fisk och andra akvatiska organismer i rinnande vattendrag. För fiskarterna öring och lax medförde förändringarna sannolikt ökad ägg- och yngelmortalitet samt reducerad kvalitet och yta av tillgängligt habitat. Efter att timmerflottning upphörde på 1970-talet började natur och fiskevårds organisationer successivt försöka återställa de skador som orsakats vattendragen under flottningsepoken. Genom dagens kunskap om öringens och laxens krav på sin livsmiljö förutspår vi att flottledsåterställningen kommer att medföra positiva effekter för dessa fiskarter. I syfte att testa detta antagande genomförde vi ett antal studier i flottledsrensade och återställda biflöden till Ume-, Vindel-, Pite- och Kalixälven. Ägg till yngelöverlevnaden visade sig vara ca. sex ggr. högre i restaurerade grusbottnar (10.3%) i jämförelse med orestaurerade (1.7%). Driften av yngel reducerades från 10.1% till 2.3% och rekryteringen över första sommaren ökade ca. åtta ggr. (från 0.2‰ till 0.6‰), till följd av restaurering. Som ett resultat av detta ökade tätheterna av öring med >360 % på restaurerade sträckor medan orestaurerade kontrollsträckor inte uppvisade någon förändring. Kontinuerlig positionering av individuellt märkta fiskar (PIT-tag) visade att öring övervintrade inom restaurerade vattendrag. Habitatets lämplighet för övervintring förklarade en stor del (66.8 %) av variationen av andelen individer som övervintrade inom olika delsträckor. Trots att ett större antal fiskarter fångades under elfiske i restaurerade sträckor kunde ingen signifikant effekt på artantalet påvisas. Dessa resultat visar att flottledsåterställning kan vara en bra metod för att både förstärka och bevara populationer av öring. För att inte få oönskade effekter och för att lyckas med restaureringar krävs god kunskap om alla arter som förekommer i berörda vattendrag. Till exempel, används fel sorts substrat vid lekbottenrestaureringar för kan en ökad äggpredation av stensimpa bli resultatet, vilket kan radera ut andra positiva effekter som uppnåtts med restaurering. Då öring och lax använder och behöver många olika typer av miljöer under sina livscykler, inklusive sjöar och hav, kommer inte full respons på restaureringsåtgärder i rinnande vattendrag att kunna uppnås så länge andra faktorer, t.ex. vandringshinder och högt fisketryck, också medför begränsningar för populationerna.

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