

# Habitat compensation in nature-like fishways

effects on  
benthos and fish



STINA GUSTAFSSON



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Faculty of Health, Science and Technology

Biology

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## **Abstract**

The construction of nature-like fishways has become an increasingly common measure to restore longitudinal connectivity in streams and rivers affected by hydroelectric development. These fishways also have the potential to function as habitat compensation measures when running waters have been degraded or lost. The habitat potential has however often been overlooked, and therefore the aim of this thesis was to examine the potential of nature-like fishways for habitat compensation, with special focus on the effect of added habitat heterogeneity.

This thesis examines the effects of habitat diversity on the macroinvertebrate family composition and functional organization in a nature-like, biocanal-type fishway. The biocanal contained four habitat types; riffle, pool, braided channel and floodplain. The effects of habitat diversity and large woody debris on brown trout habitat choice was also investigated in the biocanal. In addition, and prior to introduction of the threatened freshwater pearl mussel into the biocanal, the suitability of different brown trout strains as hosts for the mussel was examined.

The results show that the habitat heterogeneity in the biocanal contributed to an increased macroinvertebrate family diversity. The functional organization of the macroinvertebrate community suggests that it was a heterotrophic system and more functionally similar to the main river than to the small streams that it was created to resemble. Brown trout habitat choice studies showed that high densities of large woody debris increase the probability of fish remaining at the site of release. Testing of different brown trout strains as host for the freshwater pearl mussel revealed that both wild and hatchery-reared brown trout strains were suitable hosts. In summary, the results indicate that it is possible to create a fish passage with added value through its high habitat function and that nature-like fishways can be designed to reach multiple species restoration goals.

## Svensk sammanfattning

Att bygga naturlika fiskvägar har blivit en allt vanligare åtgärd för att återställa fria vandringsvägar för fisk i vattendrag som är påverkade av vattenkraftsutbyggnad. Dessa fiskvägar har också potential att fungera som kompensationsåtgärder när viktigt habitat har förstörts. Habitat-potentialen har emellertid ofta blivit förbisedd, och därför var syftet med denna avhandling att undersöka i vilken utsträckning naturlika fiskvägar kan kompensera för förlorat habitat, med särskilt fokus på effekten av en ökad habitatheterogenitet.

Denna avhandling undersöker effekterna av fyra olika habitattyper i en naturlig fiskväg av biokanalstyp; pool, ström, kvill och svämplan, på bottenfaunans kolonisation samt sammansättning av familjer och funktionella grupper. Inför ett projekt där den hotade flodpärlmusslan (*Margaritifera margaritifera*) planerats sättas ut i biokanalen undersöktes även lämpligheten av olika öringstammar (*Salmo trutta*) som värdfisk för musslan. För att undersöka biokanalens lämplighet som habitat för musslans värdfisk studerades vilken effekt de olika habitat-typerna i biokanalen, samt mängden död ved hade på öringens habitatval.

Resultaten av denna avhandling visar att habitatheterogeniteten i biokanalen bidrog till en ökad familjers diversitet av bottenfauna. Förhållandet mellan de olika funktionella grupperna av bottenfauna visade att biokanalen var ett heterotroft system som till sin funktion var mer lik Västerdalälven, från vilken den får sitt vatten, än de mindre bäckar som den morfologiskt skapats för att efterlikna. Både öring från de vilda och de odlade stammarna tycktes vara lämpliga värdar för flodpärlmusslan. Undersökningar av öringens habitatval visade att en hög densitet av död ved ökar sannolikheten för att öringen ska stanna i det habitat som den släppts ut i, något som i framtiden kan komma att påverka var i biokanalen flodpärlmusslan kommer att introduceras. Sammanfattningsvis visar resultaten att naturlika fiskvägar kan utformas för att återskapa habitat för hotade arter, samt bidra till en ökad biodiversitet. Naturlika fiskvägar kan således bidra både till att ersätta förlorat habitat och återskapa fria vandringsvägar, något som bör beaktas när framtida naturlika fiskvägar designas.

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## **List of papers**

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

- I.** Gustafsson, S., Österling, M., Skurdal, J., Schneider, L. D., & Calles, O. (2013). Macroinvertebrate colonization of a nature-like fishway: The effects of adding habitat heterogeneity. *Ecological engineering*, 61, 345-353.
- II.** Gustafsson, S., Calles, O., Skurdal, J., Vezza, P., Comoglio, C., Österling, E.M (2017). Functional organization and colonization of macroinvertebrates in a nature-like fishway with added habitat heterogeneity. *Manuscript*
- III.** Gustafsson, S., Calles, O., Österling, M. (2017). A test for suitable fish hosts for the threatened freshwater pearl mussel (*Margaritifera margaritifera*) prior to reintroduction. *Manuscript*
- IV.** Gustafsson, S., Österling, M., Nilsson, PA., Calles, O. (2017). Brown trout (*Salmo trutta*) habitat choice: relative importance of woody debris and river morphology in nature-like fishways. *Manuscript*

Paper I is reprinted with the permission of Elsevier.

## **Contribution**

The idea for **papers I-II** was given by OC and MÖ. The field work and identification of macroinvertebrates was carried out by SG with the help of project assistants, of which the most prominent was LS. The data for paper I was analyzed by SG with the aid of LS and the manuscript was written by SG, with contributions from OC, MÖ and JS. The data for paper II was analyzed by SG and the manuscript was written by SG, with contributions from OC, MÖ, PV, CC and JS. The ideas for **papers III-IV** were jointly developed by SG, OC and MÖ. The experimental design for paper III was developed by SG, MÖ and OC. SG conducted the study with the aid of project assistants. The data for paper III was analyzed by SG, with the aid of AN and the manuscript was written by SG, with contributions from MÖ and OC. The experimental design for paper IV was developed by SG, OC and MÖ. SG performed the field work with the help of OC and MÖ as well as project assistants. SG analyzed the data with statistical aid from AN, and wrote the manuscript with contributions from OC and MÖ.

Stina Gustafsson (SG), Olle Calles (OC), Martin Österling (MÖ), Jostein Skurdal (JS), Lea Schneider (LS), Paolo Vezza (PV), Claudio Comoglio (CC), Anders Nilsson (AN)

## **Introduction**

The development of human societies has led to overexploitation and degradation of freshwater biomes (Vörösmarty et al. 2010). Rivers have for example been manipulated for irrigation and power generation for generations (Jones 1954; Kellogg 1922) and in 2005, it was estimated that between three to six times as much water was being stored behind large dams, compared to what was free flowing in rivers (Millennium Ecosystem Assessment 2005). Dam construction generally alters the shape of the river, and shallow fast flowing stream sections are typically replaced by deep and slow flowing areas. Large dams, and reservoirs, also cause changes in the natural flow-regime as they disrupt seasonal flow patterns generated by natural variations in precipitation and snowmelt. Other effects are changes in water quality or temperature (Poff et al. 1997). In addition, dam construction disrupts fish migration, e.g. preventing fish from moving between feeding and spawning areas. Hydropower development usually provides economic and climatic benefits. Due to its negative effects on fish migration it is, however, considered the main reason behind the declines of more than 50% of the threatened fish species in Europe (Northcote 1998).

Rehabilitation of rivers and the surrounding landscape is becoming an increasingly common practice to remedy the negative impact of human activities on riverine ecosystems. Such mitigating and rehabilitating efforts typically target connectivity and habitat. In many cases, stream restoration efforts consist of habitat enhancement by adding or relocating in-stream structures such as coarse substrates, gravel and large woody debris (LWD). The goal is to restore habitats by increasing structural complexity and creating a more diverse flow pattern. In some cases physical manipulations of the channel can be made, for example by reconnecting floodplains or even re-meandering of the main channel (Palmer et al. 2014; Wohl et al. 2015). In areas where the original habitat has been irreversibly lost and restoration therefore is impossible, one remedial action may be the construction of new habitats. The creation of artificial spawning and/or nursing areas for fish have long since been a common rehabilitative measure (Rosberg et al. 1986) and large spawning

channels were constructed in Canada as early as the 1960's (Essington et al. 2000).

The flow in a stream largely determines the availability of different habitats in the watercourse, thus affecting the species composition. Riverine species are adapted to the natural flow regimes and it is important that natural flow regimes are maintained to ensure the viability of these species (Bunn and Arthington 2002). A common measure to preserve flow patterns that benefit the ecosystem is to implement environmental flows (E-flows). E-flows has been defined as 'the quantity, quality and timing of water flows required to sustain freshwater and estuarine ecosystems and the human livelihoods and well-being that depend on these ecosystems' (Brisbane Declaration, 2007). In watersheds regulated by hydropower dams this entails allowing the regulated flow regime to reflect the natural flow regime with a variation that mimics the natural flow variability (Bratrich et al. 2004). This can be especially important during times of spawning migration as water flow stimulates migration for several fish species (Almeida et al. 2002; Lucas et al. 2009; Spedicato et al. 2005; Thorstad et al. 2008).

Barriers in rivers cause fragmentation, which prevents migration and dispersal of aquatic organisms, which in some cases are obligate for life-cycle fulfillment. The most common way of improving longitudinal connectivity is the construction of fishways. Until recently most fishways were what one calls technical types, i.e. constructed out of wood and/or concrete (Katopodis et al. 2001). Such structures may work satisfactory for passage of salmonids and other strong swimmers and occasionally even for other species (Katopodis et al. 2001). The water velocity in technical fishways does however tend to be too high for weak swimmers that often require velocities of 0.3 m/s or less to maintain longer migrations (Pavlov 1989). Technical fishways are also often steep and drops as low as 25 cm can act as migration barriers for young brown trout and other small fish (Jungwirth 1996). Consequently, technical fishways tend to be selective in that they pose a problem for juvenile life-stages and fish species that are weak swimmers.

### ***Nature-like fishways***

During the last decades more attention has been paid to providing passage for all naturally occurring fish species and to meet such multi-species restoration goals the construction of nature-like fishways have become increasingly common. Nature-like fishways are created according to a design philosophy called physiomimesis, which means to imitate nature (Katopodis et al. 2001). The aim of nature-like fishway construction is to mimic the traits of a similarly sized natural stream in the area of the fishway, with the goal to create a structure that both facilitates passage and can act as habitat for all species in the area. There are several types of nature-like fishways; for example rock ramps, step-pool fishways and bypass channels. Bypass channels, or biocanals, are by definition the nature-like fishways that are most similar in structure to natural streams and due to their length have the greatest potential to act as habitat (Cowx and Welcomme 1998; Welcomme 2001).

Most nature-like fishways are primarily built to facilitate fish passage and consequently most studies of nature-like fishways have focused on evaluating passage performance (Aarestrup et al. 2003; Eberstaller et al. 1998; Mader et al. 1998). The use of nature-like fishways as habitats by fish has not been focus of much research; however, some species have been observed to use nature-like fishways as spawning or rearing habitat (Calles and Greenberg 2007; Jansen et al. 1999; Jungwirth 1996). The habitat quality aspect of nature-like fishway design is often overlooked; hence, a potential benefit of habitat mitigation is generally not realized. Ideally, nature-like fishways should allow a natural and variable flow regime and have a low gradient and a diverse substrate (Eberstaller et al. 1998), this is however rarely the case. In addition to creating an 'as natural in-stream environment as possible', the habitat potential of nature-like fishways can be further developed. As different species have different habitat preferences, a nature-like fishway with a highly variable habitat could hold the potential to promote a high biodiversity. Another relatively unexplored area of use for nature-like fishways is their potential as habitat compensation measures. In areas where, for example, stream habitats have been lost, even the relatively small stream-area

provided by a fishway may be important for rheophilic organisms. The fishways may also be adapted to suit a specific species, i.e. creating habitats targeting certain endangered species or species that have been severely affected by dam construction and the subsequent habitat degradation in the area (Enders et al. 2007).

## **Study organisms**

### ***Macroinvertebrates***

Macroinvertebrates are animals that are large enough to be seen with the naked eye, such as insects, mussels, snails and worms. The aquatic macroinvertebrates are key components in the nutrient and energy cycling of stream ecosystems (Webster and Benfield 1986) and they also represent an important food source for fish (Sanchez-Hernandez et al. 2011; Skoglund and Barlaup 2006). As nature-like fishways are created to resemble natural streams, the presence of macroinvertebrates within the fishways is therefore vital to achieve functioning ecosystems. The macroinvertebrates, especially the insects, are fast colonizers of new stream habitats (Malmqvist et al. 1991) and much is known about the habitat preferences of different taxa (Allan 1975; Cairns and Pratt 1993). In addition, benthic faunal assemblages have been used as indicators of habitat quality for a long time (Cairns and Pratt 1993) and they are therefore suitable study organisms when investigating whether habitat modifications in nature-like fishways are successful in mitigating for lost habitat. Taxa in the benthic community can also be divided into functional feeding groups (FFG: sensu Cummins, 1973); depending on in which manner they acquire their food. Due to the link between FFG structure and the stream energy base, information on FFG composition can give indications on whether a system is autotrophic or heterotrophic (Merritt et al. 1996; Yoshimura et al. 2006). Such information can be used to assess whether a nature-like fishway created to resemble a small forest stream is not only physically, but also functionally similar to its natural counterpart.

### **Freshwater pearl mussels**

The Freshwater pearl mussel (*Margaritifera margaritifera* L.) (Henceforth referred to as 'the FPM') has declined substantially and is now considered to be highly vulnerable or threatened with extinction almost everywhere throughout its holarctic range (Young et al. 2001). They are long-lived organisms with a complex reproductive strategy and disruption to any part of its life cycle may be detrimental. The mussel larvae, or glochidia, develop on its mother's gills and the adult mussels will release the glochidia synchronal (Hastie and Young 2003) when the glochidia are approximately 0.07 mm in length (Bauer 2001b). For the glochidia to survive, they must attach and encyst on the gills of a host fish (Fig. 1). In Europe the FPM host fishes are brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) (Young and Williams 1984).

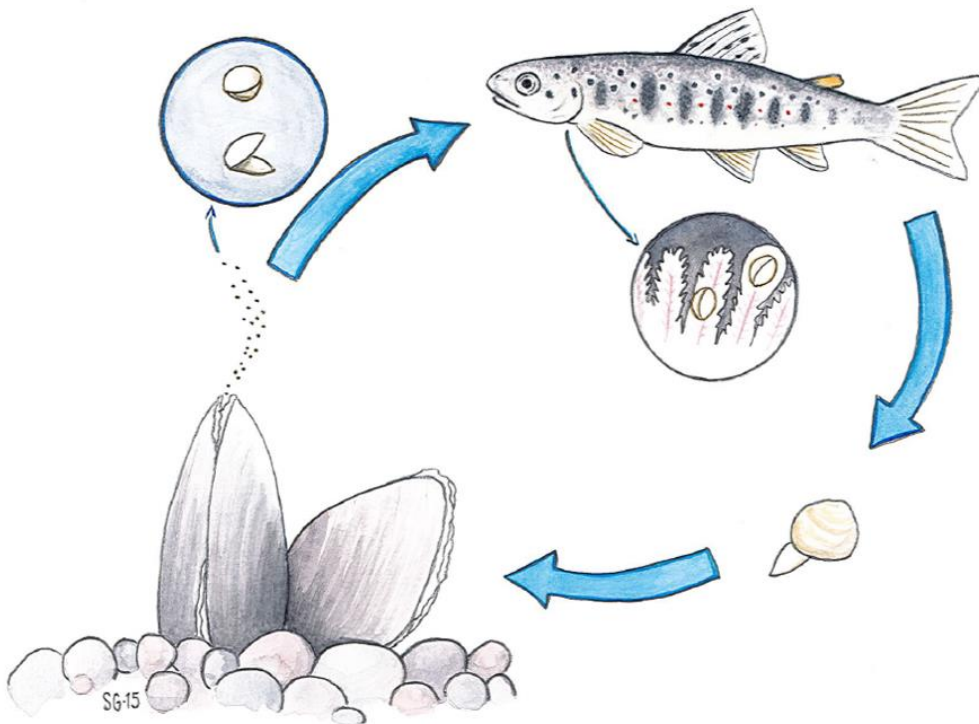


Figure 1. Life cycle of the Freshwater pearl mussel

Surviving glochidia will stay on the host's gills for about 10-12 months and will fall off the following summer when they have reached an approximate size of 0.4 mm (Bauer 2001a). The juvenile mussels will stay in the substrate for several years before emerging (Geist and Auerswald 2007). About one third of Europe's populations of FPM exist in Sweden, and regrettably, in recent decades juvenile mussels are found in less than half of the Swedish populations. The decline can be directly linked to habitat destruction and degradation negatively affecting juvenile survival (Osterling and Hogberg 2014). The close relationship to their host fish may imply that factors affecting the parasitic stage also contribute to the impaired mussel recruitment. As already mentioned, dam constructions, for example, both change flow regimes and disrupts connectivity in running waters (Bednarek 2001 and references therein). This may prevent host fish from reaching areas with FPM, impeding mussel life cycle completion, and obstructing mussel dispersal by larvae attached to fish (Österling and Söderberg 2015). In rivers where dam construction have disrupted fish migration and inundated FPM habitat, nature-like fishways may be created to both facilitate fish migration as well as to some extent mitigate for lost FPM habitat.

### ***Brown trout***

The brown trout is originally a European species that through its polytypic nature has been successfully introduced in many places all over the world. The brown trout can exhibit a wide range of life history traits where some populations remain stationary in small streams, whereas individuals of some populations migrate to lakes or the sea to feed and grow. The brown trout spawns in autumn or early winter and the eggs are buried in gravel redds. The newly hatched alevins stay in the gravel until most of their yolk is consumed, at which point they emerge from the gravel, start to feed and become fry. The fry in turn is called parr once its yolk sack is fully consumed. The most important factors limiting brown trout is water temperature, which if it exceeds 15 C° may impede egg hatching, and water oxygen content, of which both for adults and eggs require high levels (Elliott 1994). Dam construction is also known to influence brown trout populations as it may degrade stream habitat, impede migration and in the end have negative impacts on brown trout



densities and reproduction (Almodóvar and Nicola 1999). As the brown trout is a commercially important species, large amounts of hatchery-reared trout are released every year in Sweden to compensate for the loss of natural reproduction. In 2015 a total of 215 tons of trout were produced for stocking purposes and 802 000 individuals of young brown trout were released (Statistics Sweden 2016).

## **Objectives**

The aim of this thesis was to explore the potential of using nature-like fishways to increase macroinvertebrate family diversity and to compensate for lost FPM and brown trout habitat.

**Papers I and II** explored how artificially creating different habitat types in a biocanal influenced benthic fauna colonization, family composition and trophic level. Aquatic macroinvertebrates are important components in stream ecosystems, and yet few aquatic habitat compensation projects have been evaluated for this group of organisms and hence information about the macroinvertebrate community composition within nature-like fishways is largely lacking.

**Papers III and IV** focused on host fish function and habitat selection by brown trout. Plans were made to introduce FPMs to the biocanal using mussels from a stream in the same catchment. As FPMs are dependent on their trout host fish to complete their life cycle, the suitability of wild and hatchery-reared brown trout strains for hosting glochidia was tested (**Paper III**). FPM glochidia remain infective for a few hundred meters after release, which means that suitable hosts must be present in the immediate surroundings. Consequently, trout habitat selection experiments were carried out to study the potential of habitat diversity and large woody debris as a tool for habitat improvement in the biocanal where FPMs are to be introduced (**Paper IV**).

## **Summary of methods**

The studies in this thesis were conducted both in field (**I, II and IV**) and laboratory conditions (**III**). The field studies were performed in a nature-like fishway and in small forest streams in the central part of Sweden and the laboratory experiment was carried out in the aquarium facility at Karlstad University.

### ***Study area***

The studies in papers **I, II** and **IV** took place in Eldbäcken, a nature-like fishway of biocanal type (henceforth referred to as 'the biocanal'), situated in the Västerdalälven river system (Fig. 2). The biocanal is fitted with four different habitat types to increase the potential for a high biodiversity (Fig. 3):

- 1) Deep pools, with a low water velocity and gravel substrate, were created to compensate for lost freshwater pearl mussel habitat.
- 2) Floodplains with winding waterways and shallow ponds were constructed as brown trout habitats with a riparian zone with high plant diversity.
- 3) Braided areas, where the canal has been diverted into narrow channels with islands in-between, were constructed to accommodate young individuals of brown trout.
- 4) Riffles with a straight watercourse and high water velocity were created for rheophilic taxa, and represented a conventional nature-like fishway.

To be able to evaluate the effect of the different habitat types, each habitat type was replicated three times within the canal according to a randomized block design. To reduce any habitat effect to spill over to neighboring habitats, the habitats were separated by 18 m long buffer zones, identical in design to the riffle habitats.

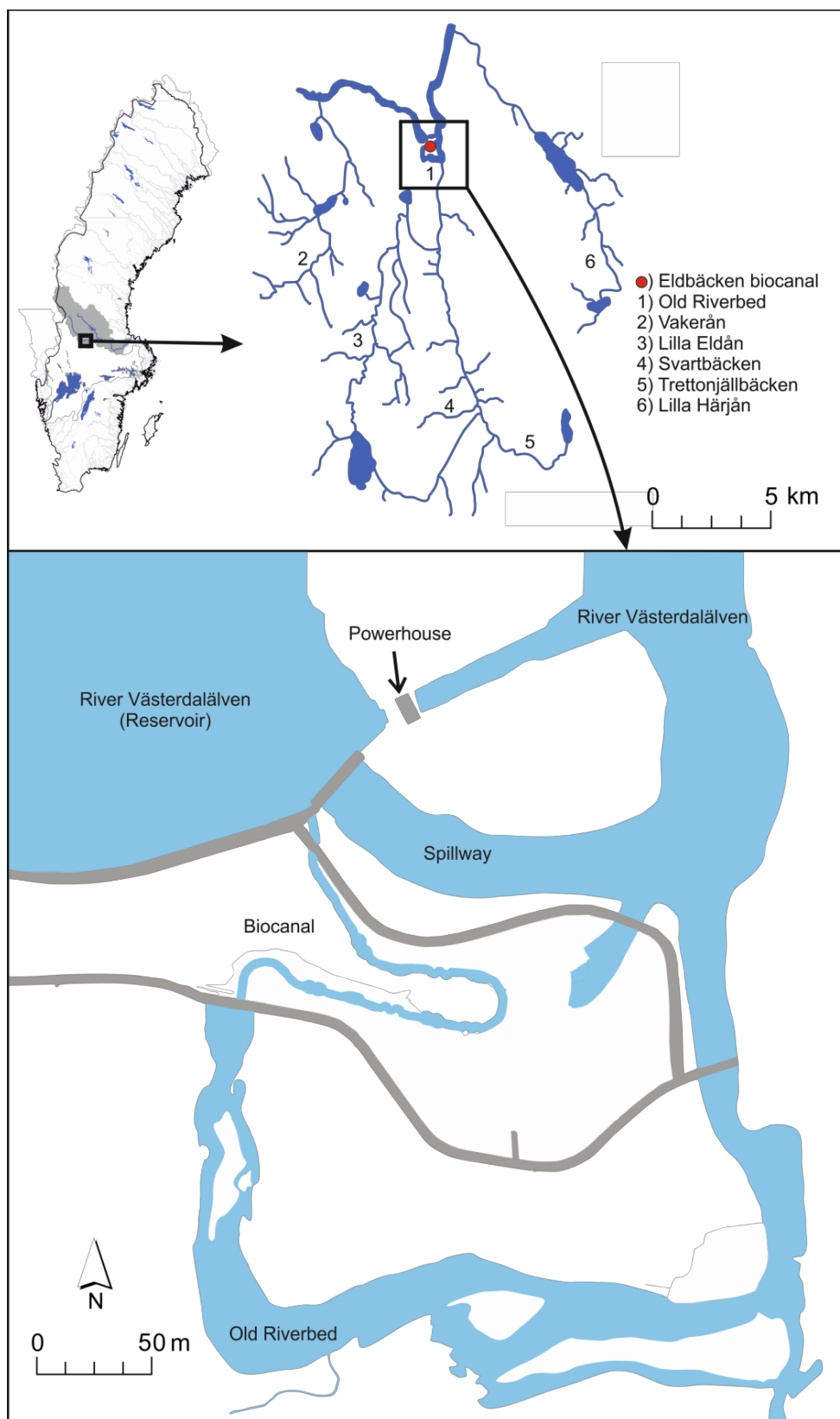


Figure 2. Map and location of the study area.

Prior to the studies conducted for **Paper IV** the biocanal was modified to better accommodate FPM and juvenile brown trout. Large woody debris (LWD) was added to the different habitat types and it was distributed in different concentrations according to a randomized block design (Fig. 3). The LWD concentrations were:

- 1) No LWD
- 2) Low concentration of LWD, ( $24.8 \text{ m}^3/\text{ha}$ ) representing the situation in forests affected by modern forestry in Scandinavia.
- 3) High concentration of LWD ( $98 \text{ m}^3/\text{ha}$ ) representing the situation in old growth forests in Scandinavia, i.e. before modern forestry (Dahlström 2005 and references therein)



Figure 3. The biocanal before modifications of the channel. Abbreviations; R = riffle, B = braided, P = pool, F = floodplain. – indicates habitats in which no LWD was added, one star indicates habitats in which a low density of LWD later was added and two stars indicates habitats in which a high density of LWD later was added. Photo: Anders Bruks

The fishway was also broadened and large boulders as well as fine grain material was added during the summer 2014 (Fig. 4).



Figure 4. Modifications of the biocanal, including widening of the channel and addition of boulders, fine grain material and LWD. Photo: Anders Bruks and Stina Gustafsson

### ***Benthos***

Macroinvertebrates used in study **I** and **II** were collected in the biocanal using a 0.04 m<sup>2</sup> Surber sampler fitted with 500 µm net, following standard procedure. For **Paper I** macroinvertebrates were also collected in six streams in the River Västerdalälven system, located within a 20 km radius of the biocanal. Five were small forest streams and one consisted of the old riverbed downstream of the biocanal (Fig. 2). At each sampling, four random samples were collected from one riffle and one pool in the reference streams and/or from each habitat in the biocanal. All samples were immediately preserved in 70% ethanol before transport to Karlstad University. For study **I** macroinvertebrates were identified to family level and for study **II** macroinvertebrates were identified to at least family



level, but further if needed to assign FFG properties to the given individual. Members of the family Chironomidae were identified as Tanypodinae and non-Tanypodinae. For the study in **Paper III** FPMs were collected from the river Tansån. Adult freshwater pearl mussels were monitored for gravidity in the field and when considered mature, ten mussels were taken to the aquaria facility at Karlstad University. After glochidia release, the mussels were returned to their native stream.

### ***Fish***

The fish used in assessing their suitability as hosts for FPM glochidia (**Paper III**), were YOY trout from 1) the FPMs local sympatric wild trout strain (Tansån), 2) a local allopatric wild trout strain (Trettonjällbäcken), 3) a local allopatric hatchery strain (Siljan) and 4) a foreign allopatric hatchery strain (Gullspång). Wild trout were caught by means of electrofishing (LUGAB, L1000, Sweden), and hatchery trout were provided by the Sävenfors hatchery. Fish used in study **IV** were 1+ trout from the Siljan strain, provided by the Särna hatchery. In study **III** fish were infected with FPM glochidia and later euthanized by exposure to an overdose of Benzocaine 1, 3 and 40 days post infestation (dpi). Sacrificed fish were weighed, measured and all gill arches on the right side were removed for inspection of glochidia encystment. If no glochidia were found, gill arches on the left side were also examined. To compare glochidia growth on the different fish strains the diameter of encapsulated larvae at 1 and 40 dpi were measured (+/- 1µm). In study **IV** the fish were individually tagged with 12 mm HDX passive integrated transponder tags (PIT-tag; Texas instruments, Texas, USA) placed in their body cavities. Ten fish were released in each habitat in the biocanal in four intervals (N=120 at each interval). To study the brown trout habitat choice, fish were caught by means of electrofishing (LUGAB, L1000, Sweden). Prior to the last two electrofishing events, the position of the tagged trout was also recorded using a portable PIT-tag antenna (LF HDX RFID backpack reader with pole antenna; Oregon RFID, Portland, USA).

To examine the impact that the Eldbäcken biocanal had on the connectivity of the stream, electrofishing was performed in autumn

2010-2012 (LUGAB, L1000, Sweden). Additional electrofishing data for 2013 and 2014 was acquired from the Swedish Electrofishing RegiSter (SERS).

### ***Habitat characteristics***

Conductivity, pH and oxygen were measured using an HQ40d multimeter (HACH LANGE AB, Sweden) (**Paper I**). Substrate composition was estimated visually using a 0.64 m<sup>2</sup> square grid, sectioned into 16 smaller cells where the dominating substrate size in each cell was noted. Water depth was measured using a rigid meter ruler and water velocity was measured using a Model 801 electromagnetic flow meter (Valeport Ltd., England) (**Paper I and IV**). Structural heterogeneity of the stream bed was measured in using a contour tracing device as described in Lepori et al. (2005) (**Paper I**) and access to shelter (number of interstitial spaces > 10 cm deep) was measured in a similar fashion to the method described in Finstad et al. (2007) (**Paper IV**). All habitat measurements were taken at six (**Paper I**) or ten (**Paper IV**) random positions in each habitat in the biocanal, as well as in the buffer stretches (**Paper IV**) or the reference streams (**Paper I**). In **Paper IV** depth, substrate composition and access to shelter were also measured at fish positions detected by the PIT-tag antenna.



## **Summary of results**

### ***Paper I and II***

These papers focus on the physical structure of the biocanal and its macroinvertebrate community colonization. Comparisons of the biocanal and the natural streams showed that the biocanal had a rougher and more uniform substrate of a larger size compared to the reference streams. Comparisons of the benthic fauna community composition in the biocanal and in the natural streams showed a partial convergence over time. Families found in the natural streams, but not in the biocanal, mainly belonged to taxa known for their poor dispersal abilities or linkages to the riparian vegetation, which in this stage of succession was scarce. Comparisons of the different habitat types in the biocanal showed that the pools were deeper than the other habitat types. The floodplain habitats had a low substrate roughness and high substrate diversity, whereas riffle and braided habitats had high water velocities, a large mean substrate size and low substrate heterogeneity and high substrate roughness. The taxonomic composition differed between the habitat types. The lowest number of families of benthic fauna was found in the riffle habitats, whereas the highest number of families was found in the pool and floodplain habitats, at all sampling dates, except the first. During the first two years, the total number of macroinvertebrate families in the fishway increased from ten to 26. After this initial increase, the family number leveled out at around 25-27 families during 2012-2014 (Fig. 5). The density of macroinvertebrates did however continue to increase during the study period and the highest density was found in the last year of sampling (2014; Fig. 6). Investigations of the functional feeding group composition showed that the densities of functional feeding groups changed over time and among habitats. Collectors, both gathering and filtering, dominated in the biocanal and the ratio of scrapers to shredders and total collectors indicated that the biocanal was a heterotrophic system.

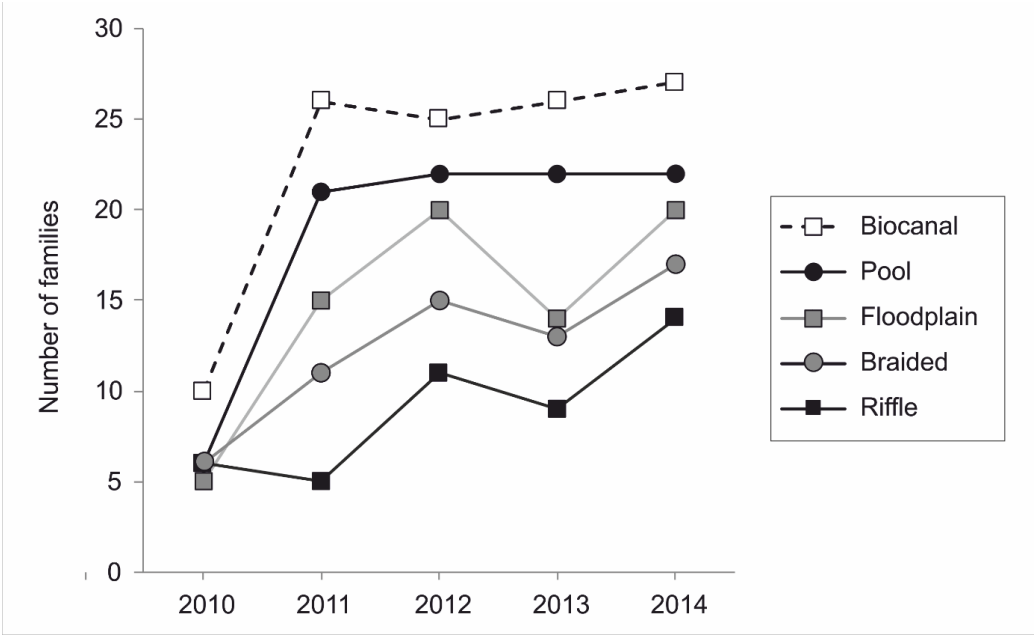


Figure 5. The total number of macroinvertebrate families present in the different habitat types in the biocanal during 2010-2014.

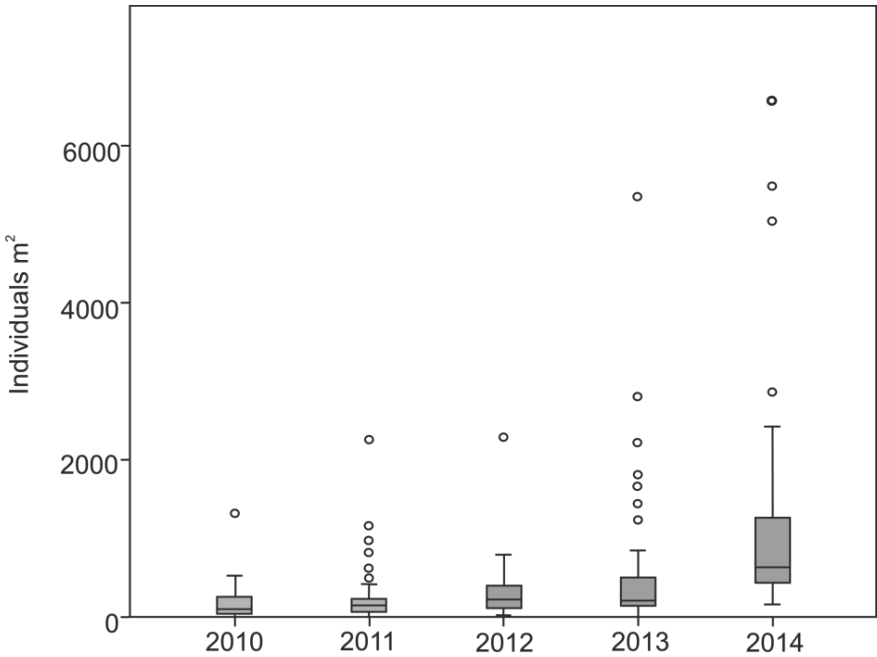


Figure 6. The increase in average density of macroinvertebrates in the biocanal during 2010-2014.

### ***Paper III***

Fish from four trout strains were tested in order to assess their suitability for hosting FPM glochidia. All fish strains in the study were successfully infested with glochidia 1 dpi. Wild fish from the local sympatric strain (Tansån) were only used for analyses of early infestation, as their survivability in laboratory conditions was low. During the first days post infestation a trend could be seen where large fish had a high number of glochidia per fish. This relationship was however no longer seen at 40 dpi and no significant difference in the number of glochidia per fish could be found between the three remaining fish strains. Fish from the local allopatric hatchery strain (Siljan) did however carry significantly larger glochidia 40 dpi compared to fish from the other strains.

### ***Paper IV***

The aim of this study was to investigate whether habitat type and/or the amount of LWD had any effect on the habitat choice of brown trout in the biocanal. In this study, the addition of high densities of LWD had a positive effect on the density of brown trout, as well as the fish's choice to stay in the habitat it was released in. The trout were quite evenly distributed among the riffle, braided and floodplain habitats, whereas almost no fish were found in the pool habitats. On average, fish occupied areas with  $11.2 \pm 7.7$  shelters/m<sup>2</sup>, a mean velocity of  $0.57 \pm 0.25$  m/s and a mean depth of  $42.3 \pm 15.6$  cm.

### ***Connectivity***

Electrofishing of the Eldbäcken biocanal 2010-2014 resulted in a total catch of 1222 fish belonging to nine species (Table 1). The fish fauna in the biocanal was dominated by a few opportunistic species and the two most common species were the European minnow (*Phoxinus phoxinus*) (N=1071) and the burbot (*Lota lota*) (N=121) (Fig. 7).

Table 1. Fish species present in the biocanal 2010-2014.

	2010	2011	2012	2013	2014
Brown trout					*
Burbot		*	*	*	*
Common dace	*				
Eurasian ruffe					*
European bullhead	*				*
European minnow	*	*	*	*	*
European perch	*				*
Grayling		*		*	*
Northern pike	*				



Figure 7. A burbot caught in the biocanal is eating a minnow while being measured.

## **Discussion and concluding remarks**

Nature-like bypass channels have become the most common fishway type constructed in Sweden during the last 15 years (Nöbelin 2014), and it is likely that the construction of nature-like fishways will remain an important remedial measure as river rehabilitation and connectivity issues are addressed. Consequently, it is important to investigate how to optimize these structures and such studies will be helpful in the design of future fishways to be used in stream conservation efforts. Nature-like fishways have mainly been constructed, as well as evaluated, for fish passage, whereas the habitat function in such structures largely has been overlooked. In this thesis, it is shown that nature-like fishways can be designed to achieve multiple species restoration goals when constructed to contain a wide range of habitats, hence both accommodating a specific species as well as increasing biodiversity, thereby creating a fish passage with added value.

The relationship between habitat heterogeneity and increased biodiversity has been accepted as one of the key elements of ecology (Ricklefs and Schluter 1993), and observations of this relationship have been seen in many ecological systems (Taniguchi et al. 2003; Tews et al. 2004; Weibull et al. 2000). The results presented in this thesis support this relationship as the highest number of macroinvertebrate families was found in the most heterogeneous habitats of the biocanal (**Paper I**). As the lowest number of macroinvertebrate families was found in the homogenous riffle habitat, designed to resemble a conventional nature-like fishway it also suggests that a nature-like fishway with added habitat heterogeneity has the potential to support a higher biodiversity than a conventional nature-like fishway constructed in the same area (**Paper I**). The restoration approach of constructing habitat structure in an attempt to restore ecosystems is called the Field of dream hypothesis (Palmer et al. 1997), named after the movie with the same title starring Kevin Costner. The catch phrase of the movie is – 'If you build it they will come'. Nevertheless, even though high habitat heterogeneity may constitute a template for high biodiversity, the result of habitat construction or restoration is not only dependent on the physical structure. Other factors,

such as overall catchment effects, climate, longitudinal connectivity, the distance between source populations and the restored or newly constructed area, dispersal abilities of different organisms and food availability in the new habitat will affect colonization patterns as well. Colonization of newly constructed habitats by macroinvertebrates has in some cases been seen to take decades, and in the study by Jones et al. (2008) it was believed that the low temperature limited the dispersal of macroinvertebrates. In comparison, the colonization processes of the biocanal was quite fast. Two years after its construction 63% of the benthic fauna families found in the surrounding streams had colonized the fishway (**Paper I**), and family number stabilized around 25-27 families during the subsequent years (**Paper II**). The fast colonization process may be attributable to high nutrient loads from the impoundment in the main river, creating a lake outlet effect in the fishway, as well as the ability for colonization from a range of nearby sources. The high habitat heterogeneity, with slow flowing pools creating deposition areas with higher organic matter retention as well as more fine grain substrate probably also gives opportunities for colonization by macroinvertebrates that normally are rare in channelized reaches. The density of macroinvertebrates did however continue to increase during the period, indicating that even though the family number seemed to have evened out, stabilization of the system is still under progress.

Colonization of naturally occurring fish species was slow, probably since the biocanal is connected to the old riverbed, formed by a much higher discharge. Fish must therefore pass 1 km of mainly slow flowing stretches on their upstream migration to reach the biocanal (Fig. 2). The dominant species in the biocanal were the European minnow, which is an opportunistic species, and the burbot. The burbot spawn both in lakes and rivers. Their eggs are semi-buoyant, their larvae are planktonic (McPhail and Paragamian 2000), and thus they may have drifted into the fishway from the upstream reservoir. The burbots may also originate from a spawning event within the fishway. All burbots seemed to belong to the same age class. The burbots were not tagged, so recapture rate between the years is unknown. The burbots caught in the biocanal were, however, of a uniform size, which did increase for each consecutive year. Other fish found in the biocanal were few in number. As there are no

diadromous species in this area of the river, and as upstream reaches contain few stream habitats, the biocanal was foremost constructed as a habitat and not for fish passage. The quality of the habitat in the biocanal is nevertheless irrelevant if fish will not find their way to the fishway.

As the design philosophy of nature-like fishways is to imitate the characteristics of natural streams, a study was conducted to find out whether a fishway that resembles a small stream in terms of its physical properties also possesses the trophic state of a small stream. According to the River continuum concept (*sensu*: Vannote et al. 1980), stream size should have an impact on ecosystem structure and function. Small streams generally receive a majority of their carbon from leaf litter (coarse particulate organic matter/CPOM) and are heterotrophic systems dominated by shredders and gathering collectors. Midsized rivers with high primary production are autotrophic and dominated by scrapers and collectors. Finally, large rivers are often heterotrophic with an increasing dominance of collectors with increasing stream size. This is due to impeded light penetration caused by turbid and deep waters as well as the downstream transport of fine particulate organic matter (FPOM). The ratio between scrapers to shredders and total collectors was used as to determine if the biocanal was likely an autotrophic or heterotrophic system. The ratio suggested that the biocanal, like most small-sized streams, was a heterotrophic system. The macroinvertebrate community in the biocanal was however dominated by gathering and filtering collectors, which suggest that FPOM was the primary energy source. The biocanal is therefore most likely more functionally similar to the main river, from which it receives its water, rather than to the small stream, which it was created to resemble (**Paper II**).

Achieving high biodiversity may not always be the primary goal of aquatic rehabilitation measures and in some cases, it may be more important to compensate for the damage human activity has had on a given species. The Eldbäcken biocanal contained habitat constructed for the FPM, and mussels from a nearby stream are planned to be introduced to the area. When constructing habitat for a specific species, not only the habitat requirements need to be taken into account, but also the effect that other

species have on the target species. In the case of the endangered FPMs, they are dependent on their host fish to complete their life cycle, and there is a possibility of FPMs being adapted to their local host fish strain. As previously mentioned, the colonization of fish in the biocanal was slow, hence in addition to mussel introduction, plans were made to release brown trout in the area to enable the mussels to complete their life cycle. A laboratory experiment to find a suitable host fish strain for the FPMs planned to be moved to the biocanal was therefore conducted. The results of the study showed that all tested fish strains, both wild and hatchery-reared, were successfully infested with FPM glochidia at 1 dpi. Furthermore, there was no difference in encystment abundance at 40 dpi between the local allopatric wild fish from the area that the mussels were to be moved to, and the two hatchery strains (**Paper III**). This suggests that FPMs from viable populations may be moved to suitable newly constructed stream habitats, and still maintain a functional reproductive cycle. It also implies that trout from foreign hatchery strains can be used as supplement in FPM streams where sympatric trout populations have disappeared. We suggest however, that infestation tests are performed prior to all relocation-projects as FPMs from different streams may show different responses. Shell length has been suggested as a good indicator of over winter survival for juvenile mussels (Denic et al. 2015). Hence, the number of juvenile recruits is likely to be highest from fish carrying large glochidia. In our study, glochidia grew better on fish from the local allopatric hatchery strain, indicating that these fish are good hosts, at least under laboratory conditions. However, as release of hatchery fish may have a negative effect on wild stocks due to displacement, increased predation and genetic contamination (Araki et al. 2007; Hansen and Loeschcke 1994; Kostow 2009; McMichael et al. 1999; Reisenbichler and Rubin 1999) and as the survival of hatchery fish often is low (Einum and Fleming 2001), using local allopatric wild fish for FPM infestation may still be a better option (**Paper III**).

The FPM glochidia only have the capacity to drift a few hundred meters after release (Jansen et al. 2001), and it is therefore essential that their host fish are present nearby for the FPM to complete their life cycle. In addition, recruitment of juvenile FPM has been seen to increase with trout densities up to 10 trout/100m<sup>2</sup> (Arvidsson et al. 2012). Knowledge



about optimal brown trout habitat is hence of fundamental importance when planning FPM introduction projects. Our results indicate that high densities of LWD have a positive effect on the abundance of brown trout, as well as the probability of release-site fidelity, whereas variation in channel morphology seems subordinate. The fish that were caught during electrofishing were distributed quite evenly among the habitat types riffle, braided and floodplain, whereas the deep and slow flowing pool habitats seemed to constitute inferior habitats. When constructing nature-like fishways containing 1+ brown trout habitat it seems sufficient to create riffle like-stretches with the addition of LWD. However, habitat preferences during winter conditions as well as of other age classes needs to be taken into consideration. For the FPM, YOY trout have been seen to be the most suitable hosts as older trout may have an acquired immunity to the glochidia infection (Hastie and Young 2001, and references therein). Instream structures, such as woody debris, providing complex habitat and shelter are beneficial for salmonids of this age class as well (Armstrong et al. 2003; Culp et al. 1996). As the FPM glochida will drift downstream, the mussels will be placed in the upstream part of the fishway, probably near the preferred habitats of the brown trout. If, after thorough investigation, other parts of the fishway are deemed more suitable for the mussel, areas downstream of these sites may be enhanced with high concentrations of LWD.

## ***Conclusions***

Nature-like fishways may constitute important lotic habitats, as these are the ones most often in need of compensation in areas affected by hydro-power development. Fishways may be designed both to contain diverse habitats with the potential to increase biodiversity and include habitats for a preferred target species, making them an important restoration tool. The placement of the Eldbäcken biocanal was a compromise between fish passage and continued water supply to the old riverbed, creating a fishway with low attraction efficiency. Even though the fish fauna in the biocanal was dominated by a few species, it is surely possible to exploit the habitat potential in nature-like fishways without adversely affecting the passage efficiency for fish. For conventional nature-like fishways with

a uniform channel design, the option of adding LWD to enhance habitat diversity exists. This may be an easy and relatively cheap way of improving habitat function for both brown trout and macroinvertebrates. In conclusion, it is possible to create a fish passage with added value through high habitat function, and nature-like fishways can be designed to reach multiple species restoration goals. Therefore, the habitat compensation aspect of nature-like fishway design should be taken into account to a greater extent than hitherto.

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## References

- Aarestrup, K., M. C. Lucas & J. A. Hansen, 2003. Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecology of Freshwater Fish* 12:160-168.
- Allan, J. D., 1975. The distributional ecology and diversity of benthic insects in Cement Creek. Colorado. *Ecology* 56:1040-1053.
- Almeida, P., B. Quintella & N. Dias, 2002. Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal) *Aquatic Telemetry*. Springer, 1-8.
- Almodóvar, A. & G. G. Nicola, 1999. Effects of a Small Hydropower Station Upon Brown Trout *Salmo trutta* L in the River Hoz Seca (Tagus Basin, Spain) One Year After Regulation. *Regulated Rivers: Research & Management* 15:477-484.
- Araki, H., B. Cooper & M. S. Blouin, 2007. Genetic Effects of Captive Breeding Cause a Rapid, Cumulative Fitness Decline in the Wild. *Science* 318:100-103.
- Armstrong, J. D., P. S. Kemp, G. J. A. Kennedy, M. Ladle & N. J. Milner, 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* 62:143-170.
- Arvidsson, B. L., J. Karlsson & M. E. Osterling, 2012. Recruitment of the threatened mussel *Margaritifera margaritifera* in relation to mussel population size, mussel density and host density. *Aquatic Conservation-Marine and Freshwater Ecosystems* 22:526-532.
- Bauer, G., 2001a. Characterization of the Unionoida (= Naiads) Ecology and Evolution of the Freshwater Mussels Unionoida. Springer, 3-4.
- Bauer, G., 2001b. Life-history variation on different taxonomic levels of naiads. *Ecology and Evolution of the Freshwater Mussels Unionoida*:83-91.
- Bednarek, A. T., 2001. Undamming rivers: a review of the ecological impacts of dam removal. *Environmental Management* 27:803-814.
- Bratrich, C., B. Truffer, K. Jorde, J. Markard, W. Meier, A. Peter, M. Schneider & B. Wehrli, 2004. Green hydropower: a new assessment procedure for river management. *River Research and Applications* 20:865-882.
- Brisbane Declaration, 2007. 10th international river Symposium and international environmental flows conference, held in Brisbane, australia. September.

- Bunn, S. E. & A. H. Arthington, 2002. Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. *Environmental Management* 30:492-507.
- Cairns, J. & J. R. Pratt, 1993. A history of biological monitoring using benthic macroinvertebrates. *Freshwater biomonitoring and benthic macroinvertebrates* 10:27.
- Calles, E. & L. Greenberg, 2007. The use of two nature-like fishways by some fish species in the Swedish River Emån. *Ecology of Freshwater Fish* 16:183-190.
- Cowx, I. G. & R. L. Welcomme, 1998. Rehabilitation of rivers for fish : a study undertaken by the European Inland Fisheries Advisory Commission of FAO. Fishing News Books, Oxford.
- Culp, J. M., G. J. Scrimgeour & G. D. Townsend, 1996. Simulated Fine Woody Debris Accumulations in a Stream Increase Rainbow Trout Fry Abundance. *Transactions of the American Fisheries Society* 125:472-479.
- Cummins, K. W., 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* 18:183-206.
- Dahlström, N., 2005. Function and dynamics of woody debris in boreal forest streams. *Ekologi och geovetenskap*.
- Denic, M., J.-E. Taeubert, M. Lange, F. Thielen, C. Scheder, C. Gumpinger & J. Geist, 2015. Influence of stock origin and environmental conditions on the survival and growth of juvenile freshwater pearl mussels (*Margaritifera margaritifera*) in a cross-exposure experiment. *Limnologica-Ecology and Management of Inland Waters* 50:67-74.
- Eberstaller, J., M. Hinterhofer & P. Parasiewicz, 1998. The effectiveness of two nature like bypass channels in an upland Austrian river. In Jungwirth, M., S. Schmutz & S. Weiss (eds) *Migration and fish bypasses* Fishing News Books, Oxford, 363-383.
- Einum, S. & I. Fleming, 2001. Implications of stocking: ecological interactions between wild and released salmonids. *Nordic Journal of Freshwater Research* 75:56-70.
- Elliott, J. M., 1994. Quantitative ecology and the brown trout. Oxford University Press.
- Enders, E. C., K. E. Smokorowski, C. J. Pennell, K. D. Clarke, B. Sellars & D. A. Scruton, 2007. Habitat use and fish activity of landlocked Atlantic salmon and brook charr in a newly developed habitat compensation facility. *Hydrobiologia* 582:133-142.
- Essington, T. E., T. P. Quinn & V. E. Ewert, 2000. Intra-and inter-specific competition and the reproductive success of sympatric Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 57:205-213.

- Finstad, A., S. Einum, T. Forseth & O. Ugedal, 2007. Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon. *Freshwater Biology* 52:1710-1718.
- Geist, J. & K. Auerswald, 2007. Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). *Freshwater Biology* 52:2299-2316.
- Hansen, M. & V. Loeschcke, 1994. Effects of releasing hatchery-reared brown trout to wild trout populations *Conservation genetics*. Springer, 273-289.
- Hastie, L. C. & M. R. Young, 2001. Freshwater pearl mussel (*Margaritifera margaritifera*) glochidiosis in wild and farmed salmonid stocks in Scotland. *Hydrobiologia* 445:109-119.
- Hastie, L. C. & M. R. Young, 2003. Timing of spawning and glochidial release in Scottish freshwater pearl mussel (*Margaritifera margaritifera*) populations. *Freshwater Biology* 48:2107-2117.
- Jansen, W., G. Bauer & E. Zahner-Meike, 2001. Glochidial Mortality in Freshwater Mussels. In Bauer, G. & K. Wächtler (eds) *Ecology and Evolution of the Freshwater Mussels Unionoida*. Springer Berlin Heidelberg, Berlin, Heidelberg, 185-211.
- Jansen, W., B. Kappus, J. Böhmer & T. Beiter, 1999. Fish communities and migrations in the vicinity of fishways in a regulated river (Enz, Baden-Württemberg, Germany). *Limnologica - Ecology and Management of Inland Waters* 29:425-435.
- Jones, F. O., 1954. Tukiangyien: China's Ancient Irrigation System. *Geographical Review* 44:543-559.
- Jones, N. E., G. J. Scrimgeour & W. M. Tonn, 2008. Assessing the effectiveness of a constructed arctic stream using multiple biological attributes. *Environmental Management* 42:1064-1076.
- Jungwirth, M., 1996. Bypass channels at weirs as appropriate aids for fish migration in rhithral rivers. *Regulated Rivers-Research & Management* 12:483-492.
- Katopodis, C., J. A. Kells & M. Acharya, 2001. Nature-Like and Conventional Fishways: Alternative Concepts? *Canadian Water Resources Journal / Revue canadienne des ressources hydriques* 26:211-232.
- Kellogg, L. P., 1922. The Electric Light System at Appleton. *The Wisconsin Magazine of History* 6:189-194.
- Kostow, K., 2009. Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. *Reviews in Fish Biology and Fisheries* 19:9-31.
- Lepori, F., D. Palm, E. Brannas & B. Malmqvist, 2005. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications* 15:2060-2071.

- Lucas, M. C., D. H. Bubb, M. H. JANG, K. Ha & J. E. Masters, 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwater Biology* 54:621-634.
- Mader, H., G. Unfer & S. Schmutz, 1998. The effectiveness of nature-like bypass channels in a lowland river, the Marchfeldkanal. In M. Jungwirth, S. S. & S. Weiss (eds) *Migration and fish bypasses*. Fishing News Books, Oxford, 384-402.
- Malmqvist, B., S. Rundle, C. Bronmark & A. Erlandsson, 1991. Invertebrate colonization of a new, man-made stream in southern Sweden. *Freshwater Biology* 26:307-324.
- McMichael, G. A., T. N. Pearsons & S. A. Leider, 1999. Behavioral Interactions among Hatchery-Reared Steelhead Smolts and Wild *Oncorhynchus mykiss* in Natural Streams. *North American Journal of Fisheries Management* 19:948-956.
- McPhail, J. D. & V. L. Paragamian, 2000. Burbot biology and life history. Burbot: biology, ecology, and management American Fisheries Society, Fisheries Management Section, Publication 1:11-23.
- Merritt, R. W., J. R. Wallace, M. J. Higgings, M. K. Alexander, M. B. Berg, W. T. Morgan, K. W. Cummins & B. Vandeneeden, 1996. Procedures for the functional analysis of invertebrate communities of the Kissimmee river-floodplain ecosystem, vol 59.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*, World Resources Institute, Washington, DC.
- Northcote, T., 1998. Migratory behaviour of fish and its significance to movement through riverine fish passage facilities. *Fish migration and fish bypasses*:3.
- Nöbelin, F., 2014. Naturliknande fiskvägar i södra Sverige (Nature-like fishways in southern Sweden). vol 2014:11. Swedish Agency for Marine and Water Management, 126.
- Osterling, M. & J. O. Hogberg, 2014. The impact of land use on the mussel *Margaritifera margaritifera* and its host fish *Salmo trutta*. *Hydrobiologia* 735:213-220.
- Palmer, M. A., R. F. Ambrose & N. L. Poff, 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5:291-300.
- Palmer, M. A., K. L. Hondula & B. J. Koch, 2014. Ecological Restoration of Streams and Rivers: Shifting Strategies and Shifting Goals. *Annual Review of Ecology, Evolution, and Systematics* 45:247-269.
- Pavlov, D. S., 1989. Structures assisting the migrations of non-salmonid fish: USSR. Food & Agriculture Org.

- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks & J. C. Stromberg, 1997. The natural flow regime. *Bioscience* 47:769-784.
- Reisenbichler, R. & S. Rubin, 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *ICES Journal of Marine Science* 56:459-466.
- Ricklefs, R. E. & D. Schluter, 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press.
- Rosberg, G., K. Scott & R. Rithaler, 1986. Review of the International Pacific Salmon Fisheries Commission sockeye and pink salmon enhancement facilities on the Fraser River. Salmonid Enhancement Program, Dept Fish and Oceans, Vancouver, BC V6E 2P1.
- Sanchez-Hernandez, J., R. Vieira-Lanero, M. J. Servia & F. Cobo, 2011. Feeding habits of four sympatric fish species in the Iberian Peninsula: keys to understanding coexistence using prey traits. *Hydrobiologia* 667:119-132.
- Skoglund, H. & B. T. Barlaup, 2006. Feeding pattern and diet of first feeding brown trout fry under natural conditions. *Journal of Fish Biology* 68:507-521.
- Spedicato, M., G. Lembo & G. Marmulla, Effect of hydropeaking on migrations and home range of adult Barbel (*Barbus barbus*) in the river Meuse. In: *Aquatic Telemetry: Advances and Applications: Proceedings of the Fifth Conference on Fish Telemetry Held in Europe, Ustica, Italy, 9-13 June 2003*, 2005. Food & Agriculture Org., p 35.
- Statistics Sweden, 2016. Aquaculture in Sweden in 2015 Jordbruk, skogsbruk och fiske. Stefan Lundgren, Statistics Sweden, 20.
- Taniguchi, H., S. Nakano & M. Tokeshi, 2003. Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. *Freshwater Biology* 48:718-728.
- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. Wichmann, M. Schwager & F. Jeltsch, 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of biogeography* 31:79-92.
- Thorstad, E. B., F. Økland, K. Aarestrup & T. G. Heggberget, 2008. Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries* 18:345-371.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.



- Webster, J. R. & E. F. Benfield, 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematic* 17:567-594.
- Weibull, A. C., J. Bengtsson & E. Nohlgren, 2000. Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography* 23:743-750.
- Welcome, R., 2001. *Inland Fisheries. Ecology and Management* Blackwell Science Ltd London.
- Wohl, E., S. N. Lane & A. C. Wilcox, 2015. The science and practice of river restoration. *Water Resources Research* 51:5974-5997.
- Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan & C. R. Liermann, 2010. Global threats to human water security and river biodiversity. *Nature* 467:555-561.
- Yoshimura, C., K. Tockner, T. Omura & O. Moog, 2006. Species diversity and functional assessment of macroinvertebrate communities in Austrian rivers. *Limnology* 7:63-74.
- Young, M. & J. Williams, 1984. The reproductive biology of the freshwater pearl mussel *Margaritifera margaritifera* (Linn.) in Scotland. I: Field studies. *Archiv Fur Hydrobiologie* 99:405-422.
- Young, M. R., P. J. Cosgrove & L. C. Hastie, 2001. The extent of, and causes for, the decline of a highly threatened naiad: *Margaritifera margaritifera*. *Ecology and Evolution of the Freshwater Mussels Unionoida*:337-357.
- Österling, E. M. & H. Söderberg, 2015. Sea-trout habitat fragmentation affects threatened freshwater pearl mussel. *Biological Conservation* 186:197-203.

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34. Stina Gustafsson. Habitat compensation in nature-like fishways: effects on benthos and fish. Doctoral thesis, 15 December.



# Habitat compensation in nature-like fishways

The construction of nature-like fishways has become an increasingly common measure to restore longitudinal connectivity in streams, but these fishways also have the potential to compensate for habitat degradation and loss associated with hydropower. The habitat potential of fishways has largely been overlooked, and therefore the aim of this dissertation was to examine the potential of nature-like fishways for habitat compensation, with special focus on the effect of added habitat heterogeneity.

I examined the effects of added habitat heterogeneity in a nature-like fishway on macroinvertebrate family composition and functional organization as well as on brown trout habitat choice. In addition, I studied the suitability of different strains of brown trout as hosts for the freshwater pearl mussel, one of the target species for this study.

I found that by relatively simple modifications to increase habitat diversity, including the addition of large woody debris, that one could not only accommodate specific target species, but also increase biodiversity in general. These results show that it is possible to build nature-like fishways with high habitat functionality that also include multiple species restoration goals.

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