Habitat compensation in nature-like fishways

effects on benthos and fish

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Abstract

The construction of nature-like fisways 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. Habitatpotentialen 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 naturlik 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 habitattyperna i biokanalen, samt mängden död ved hade på öringens habitatval.

Resultaten av denna avhandling visar att habitatheterogeniteten i biokanalen bidrog till en ökad familjediversitet 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 vandringavägar, något som bör beaktas när framtida naturlika fiskvägar designas.

Contents

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*

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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; Welcome 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).
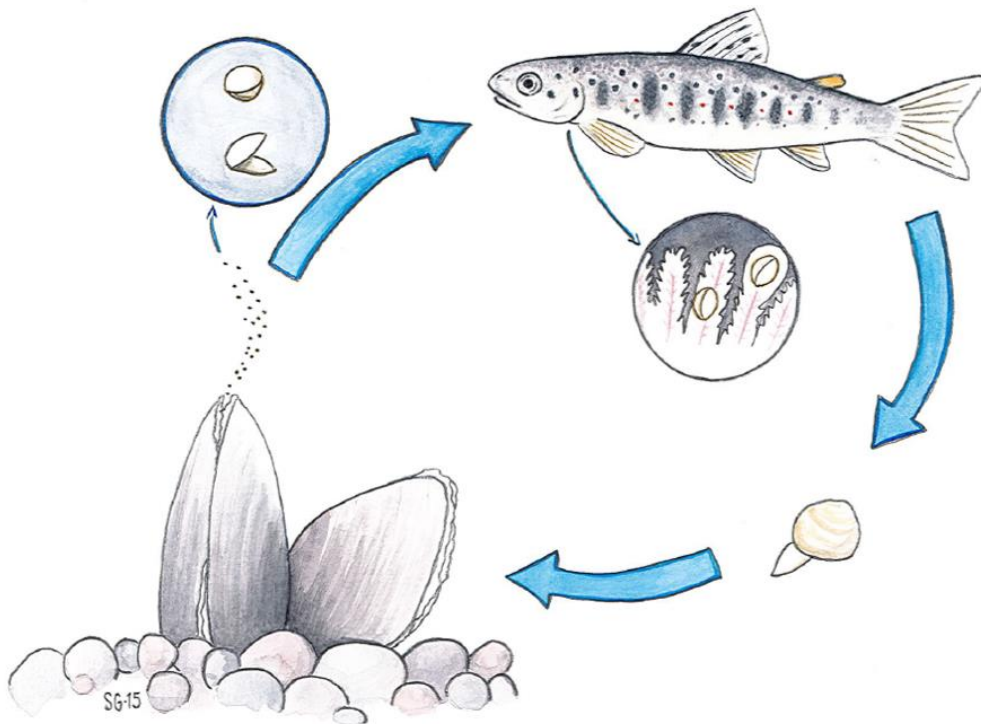

Figure 1. Life cycle of the Freshwater pearl mussel

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.

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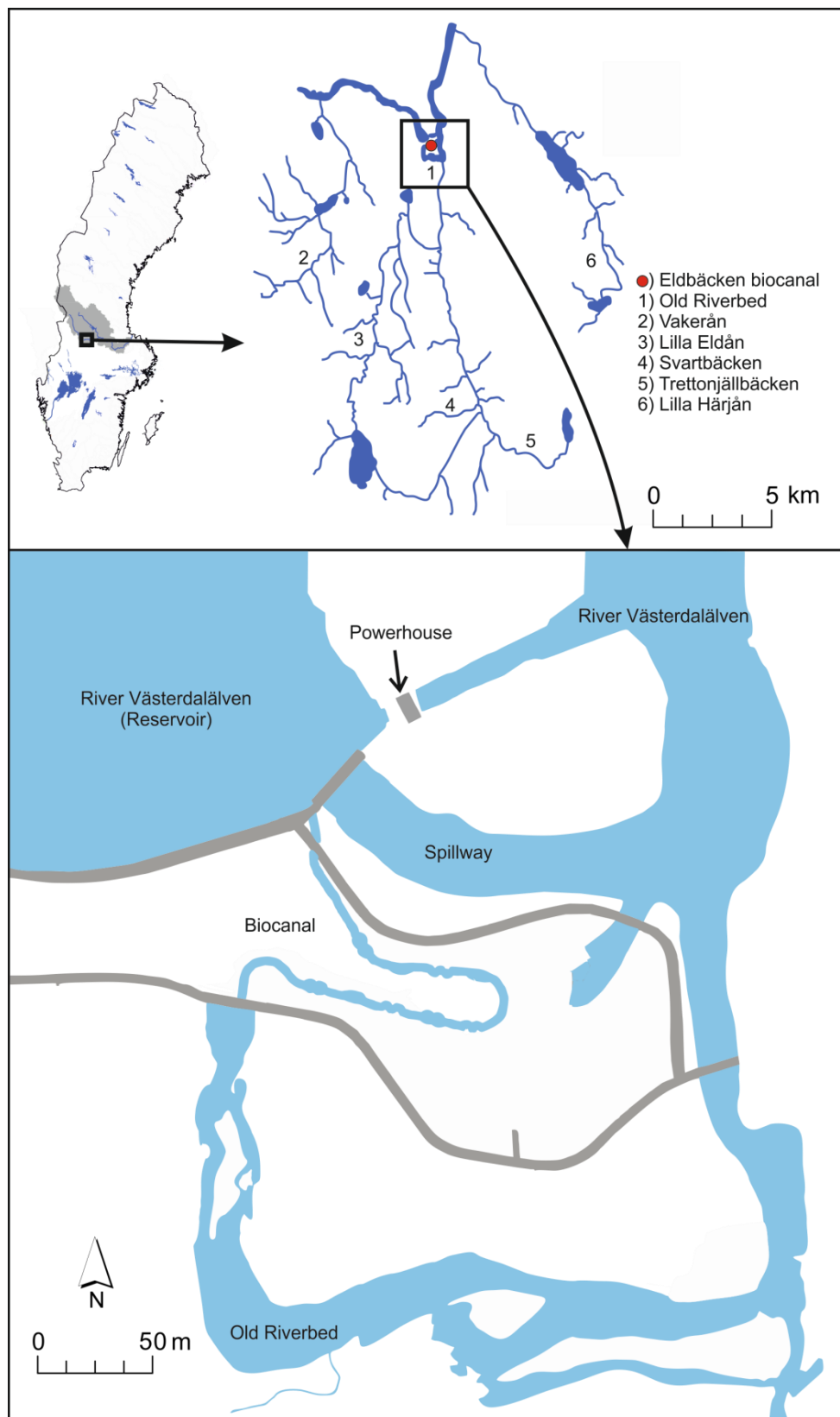
Figure 2. Map and location of the study area.

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 m³/ha) representing the situation in forests affected by modern forestry in Scandinavia.

3) High concentration of LWD (98 m³/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 m² 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 elecrofishing 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^2 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.
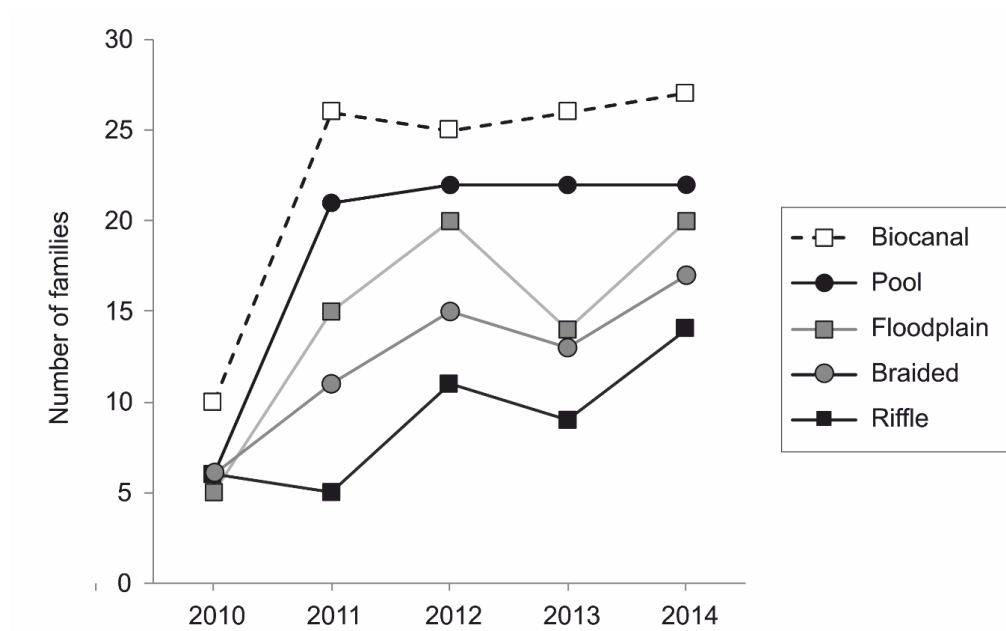
Figure 5. The total number of macroinvertebrate families present in the different habitat types in the biocanal during 2010-2014.
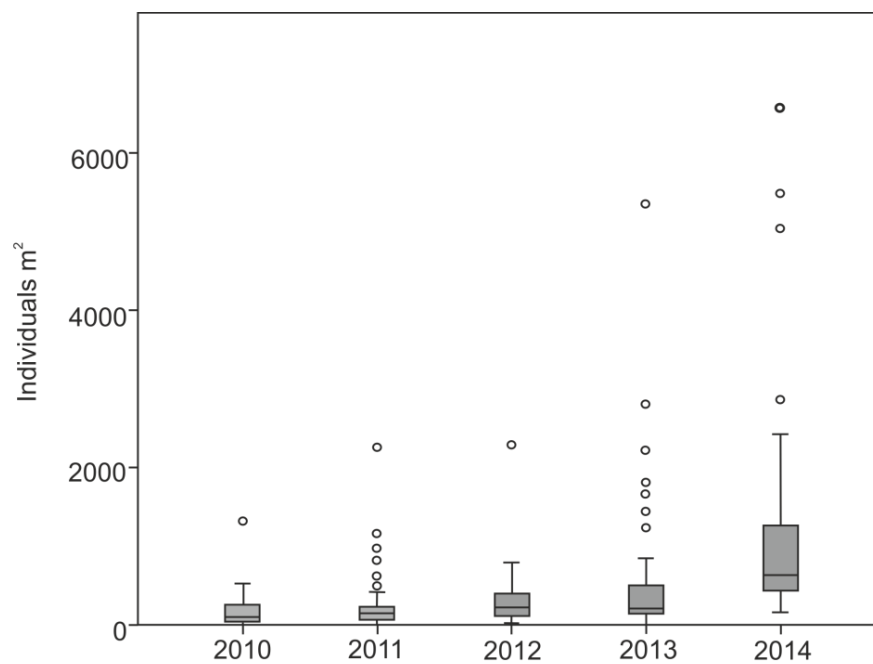
Figure 6. The increase in average density of macroinvertebrates in the biocanal during 2010-2014.

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 ± 7.7 shelters/m², a mean velocity of 0.57 ± 0.25 m/s and a mean depth of 42.3 ± 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,

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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 nuber. 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/100m² (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.

Acknowledgements

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Paper 1
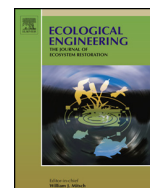
Macroinvertebrate colonization of a nature-like fishway: The effects of adding habitat heterogeneity

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A R T I C L E   I N F O

A B S T R A C T

Nature-like fishways are designed to imitate the characteristics of natural streams, thereby providing both fish passage and habitat for a variety of aquatic organisms. To date, however, the potential for habitat rehabilitation of nature-like fishways has not been fully realized. To develop the concept of how to design a nature-like fishway, a 500-m long nature-like fishway, termed the biocanal, was constructed at the Eldforsen hydroelectric facility, Sweden. It included four habitat types: riffle, pool, floodplain and braided (i.e. with islands), each replicated three times. The riffle sections were considered controls for typical Swedish nature-like fishways. Thus the biocanal had a more varied in-stream environment than those of conventional fishways. To test the prediction that the biocanal had a positive effect on biodiversity, we compared the physical habitat and benthic fauna composition of the more diverse habitat types in the biocanal to the riffle habitats. We also made comparisons between the biocanal and six natural reference streams in the area. After two years, 63% of the benthic fauna families found in the reference streams had colonized the biocanal. Families present in the reference streams, but not in the biocanal, were predominantly slow colonizers or taxa linked to riparian vegetation, which was scarce and in an early successional stage along the biocanal. In the biocanal, pool and floodplain habitats contained the highest number of families, the highest family diversity (Shannon–Weaver) and the highest densities of Ephemeroptera, Plecoptera and Trichoptera. Since these habitats contained more families and had higher diversities than the riffle habitats which are typical of conventional nature-like fishways, we suggest that the construction of biocanals indeed possesses the potential for high biodiversity.

1. Introduction

Hydropower development degrades river ecosystems, disrupting longitudinal connectivity and reducing available habitat for lotic organisms (Reyes-Gavilan et al., 1996; Rosenberg et al., 1997). This negatively impacts many stream fish species and can lead to the extinction of migratory fish populations (Northcote, 1998). To mitigate the effects of hydropower development, fishways are constructed in an attempt to restore connectivity (Clay, 1994). Historically, most fishways were modified wood or concrete canals constructed to mainly facilitate upstream migration of commercially important salmonids (Katopodis, 2002). During the last decades, however, the importance of designing passages suitable for other fish species and aquatic organisms of different life stages has been recognized (Eberstaller et al., 1998), resulting in

a new generation of more nature-like fishways (Parasiewicz et al., 1998).

Nature-like fishways have the potential to both facilitate fish passage and to provide habitat for loctic organisms (Pander et al., 2011), increasing the ecological integrity of regulated rivers. The design philosophy of nature-like fishways is to resemble similar-sized natural streams in the vicinity (Katopodis, 2002). The habitat quality aspect of nature-like design, however, is often overlooked, hence a potential benefit of habitat mitigation is generally not realized. In Sweden, for example, these fishways often have a static flow regime, a steep slope, coarse uniform substrate, and high water velocities (Calles et al., 2012); these do not constitute a template for a high biodiversity (Allan, 1975; Allan and Castillo, 2007; Gorman and Karr, 1978; Richter et al., 1997; Vinson and Hawkins, 1998). The hypothesis that habitat heterogeneity increases biodiversity is one of the key elements of ecology (Ricklefs and Schluter, 1993), and this has been shown across taxa on ecological scales, from macroinvertebrates on submerged plants (Taniguchi et al., 2003) to butterflies in agricultural landscapes (Weibull et al., 2000). A nature-like fishway with more habitat heterogeneity, therefore,

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should have the potential to increase species diversity, acting as a rehabilitation measure with added value.

The function of most nature-like fishways has mainly been evaluated for fish (Aarestrup et al., 2003; Calles and Greenberg, 2005, 2009; Eberstaller et al., 1998; Jansen et al., 1999; Jungwirth, 1996; Mader et al., 1998; Santos et al., 2005; but see Jansen et al., 2000). Yet, for a nature-like fishway to mimic a natural watercourse, the presence of other aquatic organisms is important. Macroinvertebrates are key components of freshwater systems, as they represent a main food source for fishes (Sanchez-Hernandez et al., 2011; Skoglund and Barlaup, 2006), and also play an important role in the decomposition of organic material (Webster and Benfield, 1986). Furthermore, macroinvertebrates act as a link between the stream and the terrestrial environment, since the emergent adults constitute an important food source for many terrestrial insectivores (Fukui et al., 2006; Jackson and Fisher, 1986; Sabo and Power, 2002). Benthic faunal assemblages, in fact, have long been used as indicators of habitat quality (Cairns and Pratt, 1993) and they could be used to assess whether habitat modifications in nature-like fishways are successful in mitigating for lost habitat.

To develop the concept of how to create a nature-like fishway with focus on the potential of habitat function and rehabilitation, a more diverse version of a nature-like fishway (termed the "biocanal"), was constructed at the Eldforsen hydroelectric facility, Sweden. The biocanal was created to resemble a natural stream in terms of hydraulics, gradient, flow regime and substrate and also to provide a range of habitats to increase the potential for high biodiversity. Four habitat types were created: pool, floodplain, braided habitats and riffles, each replicated three times. The riffles were designed to resemble a conventional nature-like fishway, acting as an in-stream control, and were used to assess how the benthic community in a typical nature-like fishway would develop over time. We predicted that the family-level composition of the benthic fauna would differ among the different habitat types. If true, the biocanal would thereby hold potential for a higher biodiversity compared to a conventional nature-like fishway. To assess the success of the habitat mitigation, the biocanal was compared to natural reference streams of equal size in the area. We assumed that the reference streams would exhibit a natural within- and between-year variation in benthic fauna composition, and that these streams would act as a species pool for colonization of the biocanal. These would also provide a baseline for family diversity against which we could compare the temporal development of diversity within the biocanal.

We anticipated initial differences in benthic fauna composition between the biocanal and the family-pool provided by the reference streams, but we expected that these different fauna compositions would at least to some extent converge with time.

To test our hypotheses we assessed: (1) the degree to which the physiochemistry and benthic fauna assemblages of the biocanal resembled the combined diversity of six nearby natural streams, during the first two years after biocanal construction; (2) habitat heterogeneity in the biocanal versus that in a conventional nature-like fishway, through physical comparisons between the habitat types, using the riffle habitat type as a representative for conventional nature-like fishways and (3) whether the potentially increased habitat heterogeneity in the biocanal increased benthic fauna biodiversity.

2. Material and methods

2.1. Study area

The study area is located in the province of Dalarna in central Sweden (Fig. 1). The mean annual temperature in this area

is 3 °C (mean annual temperature for the WMO defined normal period 1961–1990 (SMHI, 2012)), with 700 mm precipitation annually (estimated mean annual precipitation for the WMO defined normal period 1961–1990 (SMHI, 2012)). The region is dominated by coniferous forest, mainly spruce, underlain by granite. The major watercourse in this area is the River Västerdalälven. The biocanal was constructed in 2009 in this river system, diverting water around the Eldforsen hydroelectric power plant and into the old river bed. The power plant in Eldforsen is small, with a drop of 10 m and a storage capability of 300 000 m^3 water. The biocanal was created to resemble a natural stream and has a head of 5 m and a length of 500 m, resulting in a gradient of 1%, which is within the range of the typical gradient for small forest streams in the area (0.5–2%). Natural substrate of different size-classes was added to the biocanal and to make the flow as nature-like as possible, the intake of the biocanal is constructed to allow a variable flow regime. The biocanal was put in operation in 2010. During the first year, however, it lacked a natural water supply and approximately 200 l s^{-1} was pumped into the channel from the hydropower plant reservoir. In February 2011, the hydroelectric dam was filled to a level which allowed for a continuous supply of water from the river Västerdalälven to the biocanal. To increase the potential for a high biodiversity, four different habitat types were created within the biocanal:

(1) Pools with deep and slow flowing water.
(2) Floodplains with a winding channel and shallow ponds.
(3) Braided habitats, where the canal has been diverted into narrow channels separated by islands. To increase the structural heterogeneity, the narrow channels were also fitted with woody debris, consisting of birch trees, in a nested design.
(4) Riffles with a straight channel and high water velocity, representing a conventional nature-like fishway.

Each habitat type was replicated three times within the canal using a randomized block design. All habitat units were 18 m long and separated by 18 m long buffer zones, constructed according to the same design as a conventional nature-like fishway. Riparian vegetation along the biocanal was scarce; in September 2011 it consisted mainly of white clover (*Trifolium repens*), tufts of grasses (*Agrostis capillaris*, *Deschampsia cespitosa*, *Deschampsia flexuosa*) and small individuals of birch (*Betula* sp.), pine (*Pinus* sp.), alder (*Alnus* sp.) and willow (*Salix* sp.). The in-stream macrophyte vegetation was also largely absent two years after the construction of the biocanal. The dominant fish species within the biocanal was the European minnow (*Phoxinus phoxinus*) until June 2011, followed by the burbot (*Lota lota*) in September 2011 (unpublished electrofishing data).

Six streams in the River Västerdalälven system, located within a 20 km radius of the biocanal, were selected as reference streams (Fig. 1). These streams resembled the biocanal in size and they were regarded as potential sources of colonization of benthic fauna. Five of these were small forest streams and one was a narrow part of the old riverbed. The old riverbed was used as a reference since it was seen as one of the most important sources of colonization due to its location close to the biocanal.

One pool and one riffle, each 18 m long, were sampled in the reference streams. The riparian vegetation along the reference streams mainly consisted of *Vaccinium myrtillus*, grasses, mosses (*Sphagnum* sp., *Pleurozium schreberi*) and *Carex* species, whereas the in-stream macrophyte vegetation was mostly represented by *Fontinalis* sp., *Sparganium* sp., *Utricularia* sp. and *Myriophyllum* sp. The most common fish species within the reference streams 2010–2011 were the European minnow (*P. phoxinus*), brown trout
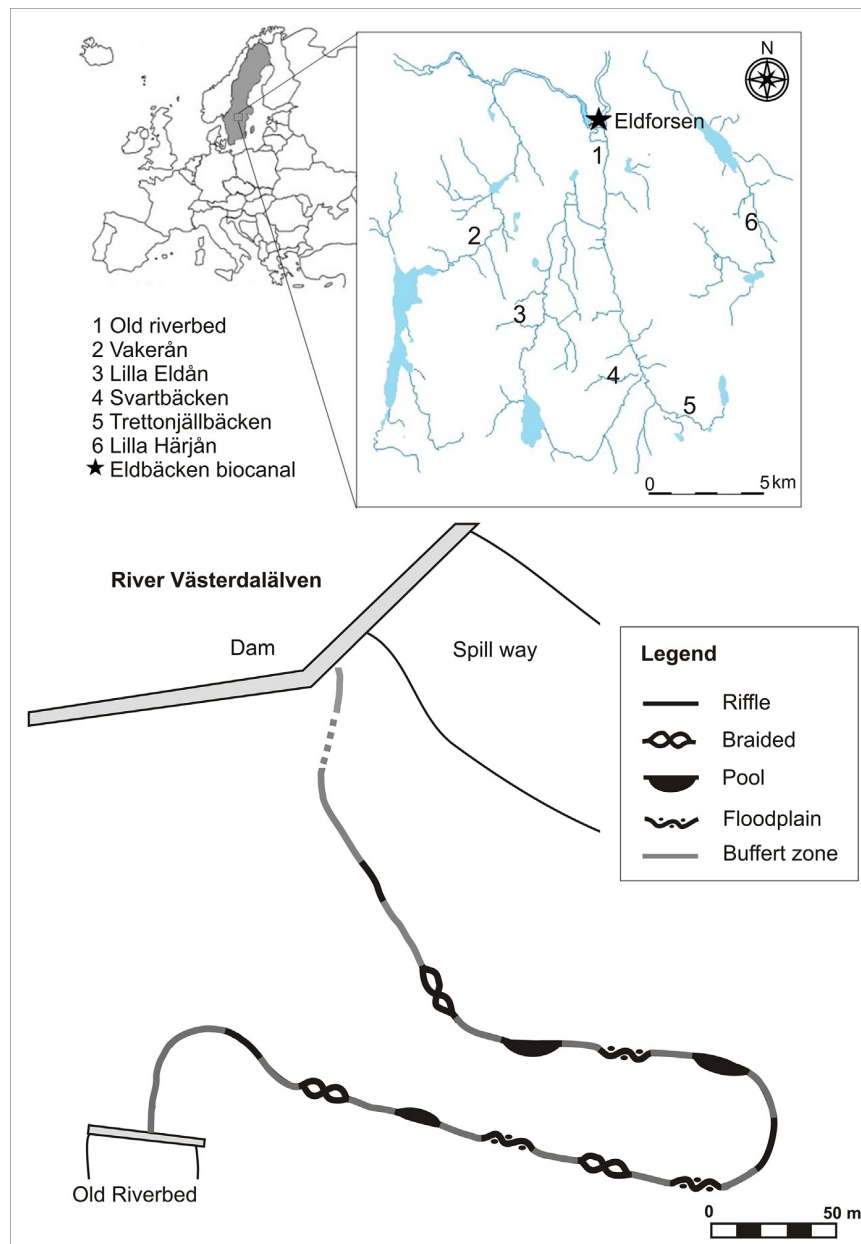
Fig. 1. The geographic location of the reference streams and the biocanal with its habitat types.

(*Salmo trutta*) and European bullhead (*Cottus gobio*) (unpublished electrofishing data).

2.2. Physiochemical parameters

Water depth and velocity were recorded at all sampling occasions at six points in each habitat unit. The velocity was measured using a Model 801 electromagnetic flow meter (Valeport Ltd., England). Conductivity, pH and oxygen were measured in free flowing water in May and September 2011, using an HQ40d multimeter (HACH LANGE AB, Sweden). Substrate composition was estimated visually at six points in each habitat unit in July 2011 and to ensure consistency in the collected data, all estimates were performed by the same person. The substrate was classified according to the Wentworth scale, modified by Cummins (Cummins and Lauff,

1969). In addition a category for coarse particulate organic matter (CPOM) was added. A 0.64 m^2 square grid, sectioned into 16 smaller cells, was used to estimate the percentage of the different substrate sizes. The dominant substrate was visually estimated within each cell, after which the percentage cover for each substrate category was calculated as:

$$\frac{\text{Number of cells dominated by a specific substrate size}}{\text{Total number of cells}} \times 100$$

Mean particle size was calculated using the weighted mean.

Structural heterogeneity of the stream bed was measured at six points in each habitat unit, using a contour tracing device consisting of 17 movable rods, with a total length of 90 cm and a diameter of 8 mm, positioned 4 cm apart on a metal frame, similar to that described in Lepori et al. (2005). At each point the contour tracing device was placed perpendicular to the flow and pressed

against the stream bottom. The length of the rods below water and the water depth was measured, after which the structural heterogeneity, also defined as substrate roughness, was calculated as the standard deviation of the rod length below water level.

2.3. Benthic fauna

Benthic fauna samplings were performed on six occasions in the biocanal (spring, summer and autumn, in 2010 and 2011) and on four occasions in the reference streams (spring and autumn 2010 and 2011). The benthic samples were collected from four randomly selected points within each habitat unit in the biocanal ($N = 48$, for each sampling date) and from each of the pool and riffle areas in the reference streams ($N = 48$, for each sampling date). Samples were collected using a $0.04\,m^2$ Surber sampler fitted with $500\,\mu m$ net, following standard procedure. All samples were immediately preserved in 70% ethanol. In the laboratory, invertebrates were sorted from organic matter after which all individuals were identified to family, with the exception of Nematoda, which were identified to order. Identifications were based on taxonomic keys (Lechthaler, 2007; Nilsson, 1996, 1997; Waringer and Graf, 1997).

2.4. Data analysis

All data were tested for normality with the Shapiro–Wilk test and the homogeneity of variances was tested using the Levene's test. As all data were non-normally distributed univariate testing was carried out with non-parametric Kruskal Wallis tests (alpha < 0.05), and in case of significance followed by Mann–Whitney U post hoc tests. To reduce the risk of making a type I error a Bonferroni correction was applied for multiple testing (Rice, 1989). All univariate analyses were done in the open-source statistical software R version 2.14.1 (R Development Core Team, 2011).

2.4.1. Habitat characteristics

The substrate roughness in each habitat type was calculated as the mean of the heterogeneity measurements of the habitat units, and the substrate heterogeneity was calculated using the percentage cover of all substrate classes, by means of the Shannon diversity index (Shannon, 1997) for each study site and habitat type. Differences in water chemistry, depth, velocity, habitat heterogeneity, mean grain size and substrate roughness were compared using Kruskal Wallis (alpha < 0.05).

To summarize patterns in physical traits of the habitats in the biocanal and the pools and riffles in the reference streams, a Principal Components Analysis (PCA) was performed using the CANOCO program for Windows, version 4.5 (ter Braak and Smilauer, 2002). The physical vectors used were; depth, velocity, substrate roughness and substrate diversity and since the variables were measured in different units the option "center and standardize by species" was applied in the CANOCO program.

2.4.2. Benthic fauna

Overall macroinvertebrate abundance and abundance of Ephemeroptera, Plecoptera and Tricoptera (EPT) were standardized by conversion to macroinvertebrate densities (individuals m^{-2}) prior to non-parametric analysis of habitat preferences. To get an estimate of the biodiversity in the different habitats the Shannon–Weaver diversity (H) was used. To assess the taxonomic richness in samples from the braided habitat types with and without woody debris, a rarefaction of samples to a common number across sample types was needed (Gotelli and Colwell, 2001). Rarefaction curves were generated using resampling without replacement and were carried out with the function specaccum
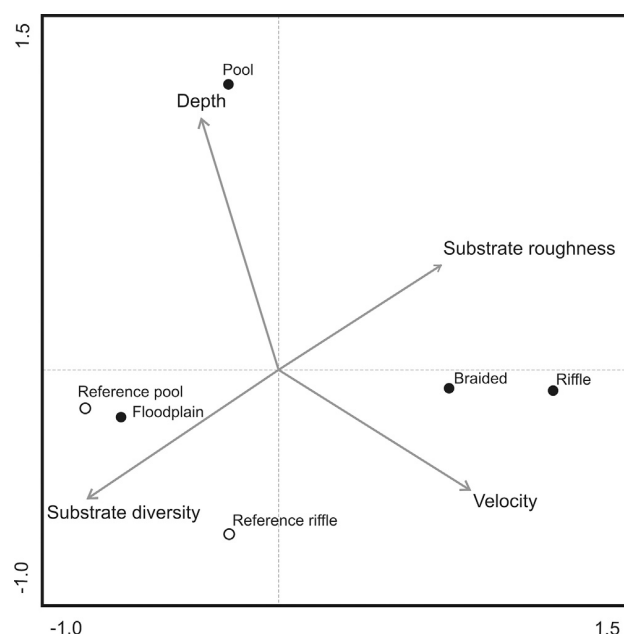
Fig. 2. Principal Components Analysis (PCA) for four physical traits in the habitats in the biocanal and the reference streams. The first axis explains 51.3% of the variance and the second axis explains 34%. Black circles represent samples from the biocanal and empty circles represent samples from the reference streams. Vectors point in the direction of increasing value, with length indicating the strength of the relationship.

using the package vegan (Oksanen et al., 2011) in the software R version 2.14.1. Taxa composition in the biocanal and the reference streams was compared using Sorensens index (Sorensen, 1948), ranging from 0–1, where 1 is the maximum, indicating total similarity. This index was also used when comparing similarities between the different habitat types in the biocanal.

The average score per taxon index (ASPT) (Armitage et al., 1983) was used to determine if colonization of more sensitive families could be identified in the biocanal. Calculations of the ASPT index were based on information from the Swedish Environmental Protection Agency (1999).

3. Results

3.1. Habitat characteristics

The physiochemical measurements in the biocanal and in the reference streams showed few significant differences. Because they belong to the same watershed, and since the hydroelectric dam has a limited amount of storage, there were few significant differences in the chemical measurements. In terms of physical structure, the biocanal was generally deeper than the reference streams, and it had a higher water velocity, but the difference was not significant. The main feature that separated the biocanal from the reference streams was the substrate. The biocanal had a larger mean substrate size ($p < 0.001$) compared to the reference streams. The substrate in the biocanal was also rougher ($p < 0.01$) as well as more monotonous (significantly lower substrate diversity $p < 0.01$) and CPOM, which occurred in the reference streams, was not present in the biocanal.

A PCA analysis of the different habitat types in the biocanal and the reference streams revealed that some habitat types were more similar than others. Habitat types with similar physical traits are positioned closer to each other in the PCA ordination, which led to a division of the habitats into three distinct groups (Fig. 2). The

Table 1
List of taxa found during the study.

Class/Order	Family	Ref	Bio	Class/Order	Family	Ref	Bio
Bivalvia	Sphaeriidae	p r			Pulmonata	p	
Coleoptera	Dryopidae	p r			Valvatidae	p	
	Dytiscidae	r	R B P F	Megaloptera	Sialidae	p	
	Elmidae	p r	B P	Odonata	Aeshnidae	p	
	Gyrinidae	p r	B		Calopterygidae	p	
	Hydrophilidae	r			Cordulegastridae	p r	F
Clitellata	Lumbriculidae	p r	B F		Corduliidae	p	
	Naididae	p r	R B P F		Gomphidae	p r	
	Tubificidae	p r	B P F		Platycnemididae	p	
Diptera	Athericidae	p r		Plecoptera	Nemouridae	p r	R B P F
	Ceratopogonidae	p r	R B P F		Perlodidae	p r	B P F
	Chironomidae	p r	R B P F		Taeniopterygidae	p r	R B F
	Empididae	p r	B P F	Trichoptera	Glossosomatidae	p r	F
	Limoniidae	p r	R B P F		Goeridae	p r	
	Muscidae	p	F		Hydropsychidae	p r	R B P F
	Pediciidae	p r	P		Hydroptilidae	p r	R B P F
	Simuliidae	p r	R B P F		Lepidostomatidae	p r	B P F
	Tabanidae	p r	B P F		Leptoceridae	p r	R B P F
	Tipulidae		P F		Molannidae	p	
Ephemeroptera	Baetidae	p r	R B P F		Philopotamidae	r	
	Caenidae	r	R P F		Leuctridae	p r	F
	Ephemerellidae	p r	R B P F		Limnephilidae	p r	F
	Ephemeridae	p r	P		Polycentropodidae	p r	R B P F
	Heptageniidae	p r	R B P F		Psychomyiidae	p r	R B P F
	Leptophlebiidae	p r	B P F		Rhyacophilidae	p r	R B P F
	Siphlonuridae	p r	P		Sericostomatidae	p r	
Gastropoda	Lymnaeidae	p		Other	Nematoda	p r	R B P F
	Planorbidae	p r			Total	54	37

Abbreviations: p, reference pool; r, reference riffle; R, riffle; B, braided; P, pool; F, floodplain.

pools in the biocanal, being deeper than all other habitats, did not group with any other habitat types. One group consisted of the floodplain habitats in the biocanal and the riffles and pools in the reference streams. These habitats were all characterized by low substrate roughness and high substrate diversity, highest in the reference pools, albeit not significantly so compared to the floodplains. The floodplain habitats had the lowest mean grain size in the biocanal, not significantly different from what was found in the pool and riffles in the reference streams. The last group included the braided habitats and the riffle habitats in the biocanal. These two habitat types represented areas with low substrate heterogeneity and higher water velocities and substrate roughness. The riffle habitats and the braided habitats also had significantly larger mean grain size compared to all other habitats, both natural and constructed ($p < 0.001$).

3.2. Benthic fauna

3.2.1. Biocanal and reference stream comparisons

During the entire study period a total of 22 900 benthic organisms were identified, comprising a total of 55 families, of which 37 were found in the biocanal and 54 in the reference streams (Table 1). The total family number for the different reference streams ranged from 23 to 45. When comparing the family composition in spring and autumn 2010 and 2011 (equal sampling effort), the family number in the biocanal was 35, compared to 54 in the reference streams. Only one family, the Tipulidae, was found exclusively in the biocanal, and 18 families were found only in the reference streams. 63% of the families found in the reference streams were also found in the biocanal. In the biocanal, a gradual increase in the number of families was observed over time (Fig. 3.), while no such trends were evident in the reference streams. In general, dipterans were early colonizers in the biocanal, as were the

ephemeropterans, for which all occurring taxa in the biocanal had been found during the first months. The Odonata were among the slowest colonizers, and only one out of the seven Odonata families found in the reference streams was found in the biocanal at the end of the study. Another group that was missing from the biocanal was the mollusks, both clams and snails.

The similarities in family composition between the biocanal and the reference streams, expressed as the Sorensen index, showed an increasing similarity with time (Fig. 4). The gradual change in benthic fauna community in the biocanal and increased similarity between the reference streams and the biocanal was also illustrated by the ASPT index. The index values were at a constantly high level of about 7.0 at all sampling dates in the reference streams, whereas it increased gradually from 5.2 in June 2010 to 6.8 in September the same year in the biocanal, indicating a colonization of more sensitive families.
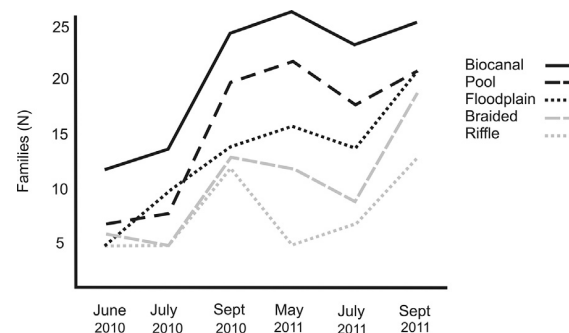

Fig. 3. The number of macroinvertebrate families found in the different habitats in the biocanal during the different sampling dates.
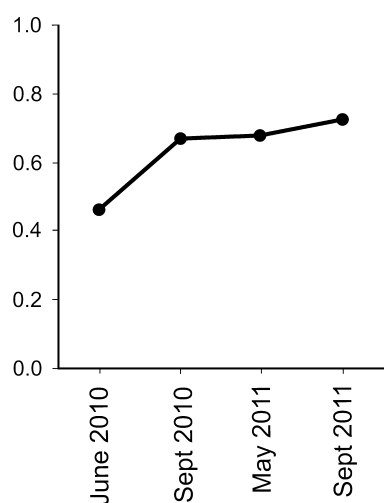
Fig. 4. Sorensens similarity index for the family-level between the biocanal and the reference streams.

The converging similarities between the biocanal and the reference streams were also shown by the Shannon–Weaver diversity and the EPT densities, of which both were significantly higher in the reference streams than in the biocanal at all dates ($p < 0.001$), except for the last sampling date in September 2011 ($p > 0.50$). The high EPT found in the biocanal during the last sampling date was mainly due to an increase in the number of ephemeropterans.

3.2.2. Within biocanal comparisons

The lowest number of families of benthic fauna in the biocanal 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 (Fig. 3). The total number of families in the different habitats added up to 32 in the floodplain habitats, 29 in the pool habitats, 28 in the braided habitats and 20 in the riffle habitats. The riffle habitats did not contain any families that did not occur in one or more of the other habitat types.

The Sorensen similarity index applied to the biocanal habitat types showed that the riffle habitat had the lowest similarity values, whereas the habitat types pool, floodplain and braided had a more similar benthic fauna composition, the pool and braided habitats having the highest similarities (Table 2).

The pool habitat types had the highest mean EPT densities at all sampling dates. High EPT densities were also found in the floodplain habitat types during the last sampling date, whereas EPT densities generally were low in the riffle habitats (Table 3).

There were no significant differences in the Shannon–Weaver diversities among habitats in the biocanal during 2010. In 2011, however, the diversity was highest in the pool and floodplain habitat types and lowest in the riffle habitat types (Table 4), a pattern which mirrors the EPT densities. Comparisons of samples taken in

Table 2
Sorensens similarity index for the different habitats in the biocanal, all sampling dates combined.

	R	P	F	B
R	–			
P	0.75	–		
F	0.75	0.82	–	
B	0.77	0.88	0.83	–

Abbreviations: R, riffle; P, pool; F, floodplain; B, braided.

areas with and without woody debris in the braided habitat types indicated that the added woody debris probably had a positive effect on the biodiversity in these habitat types. After rarefaction to 28 samples (i.e. the maximum number of samples in the treatment with lowest sampling effort), the taxonomic richness summed up to 24 families in samples with woody debris and 18 in samples without woody debris.

4. Discussion

The two-year investigation of the benthic fauna assemblage in the biocanal showed that the taxonomic composition differed among habitat types. This implies that a nature-like fishway with a more heterogeneous habitat structure has the potential to promote a higher biodiversity than a conventional nature-like fishway. This was further supported by the fact that the lowest number of families was found in the riffle habitat in the biocanal, the habitat type designed to resemble the typically homogenous design of a conventional Swedish nature-like fishway, whereas the highest number of families was found in the most heterogeneous habitats, i.e. the pool and floodplains. These results suggests that the biodiversity in the biocanal is probably higher than would have been the case if a conventional nature-like fishway had been built. Furthermore, the macroinvertebrate community composition in the biocanal and the reference streams showed partial convergence, i.e. an increasing resemblance over time. After two years, the biodiversity in the biocanal remained lower than the combined diversity of the reference streams, but colonization of the biocanal appears to be ongoing and the community composition will likely continue to converge.

A prerequisite for colonization success are means of colonization and the suitability of the area as habitat. Since the biocanal belongs to the same watershed as the reference streams and since the hydroelectric dam in Eldforsen has a limited amount of storage, there were small differences in chemical properties both within the biocanal and between the biocanal and the reference streams. As a result, the benthic fauna composition is probably determined by other factors such as the physical characteristics of the different habitats, food availability, and dispersal mechanisms.

The physical parameters used to describe the different habitats in this study were substrate roughness and substrate diversity, water velocity, and depth. Substrate roughness has previously been used to quantify structural heterogeneity (Lepori et al., 2005; Muotka and Laasonen, 2002; Tikkanen et al., 1994), providing an

Table 3
Comparisons of EPT density between the habitat types in the biocanal. All *p* values are Bonferroni corrected to avoid bias caused by multiple testing.

Month	2010		2011	
	Difference	*p*	Difference	*p*
May/June	Pool > floodplain	<0.05	Pool > riffle	<0.01
			Braided > riffle	<0.05
July	–	No sig. diff.	Pool > Braided	<0.05
September	Pool > Riffle	<0.05	Floodplain > Riffle	<0.01
	Pool > Braided	<0.05	Floodplain > Braided	<0.05
	Braided > Riffle	<0.05		

Table 4
Comparisons of Shannon–Weaver diversity between the habitat types in the biocanal. All p-values are Bonferroni corrected to avoid bias caused by multiple testing.

Month	2010		2011	
	Difference	p	Difference	p
May/June	–	No sig. diff.	Braided > Riffle	<0.05
July	–	No sig. diff.	Pool > Riffle	<0.001
			Pool > Floodplain	<0.01
			Pool > Braided	<0.01
September	–	No sig. diff.	Floodplain > Riffle	<0.01
			Floodplain > Braided	<0.05

estimate of available habitats. In the biocanal, the braided and riffle habitat types had the highest substrate roughness, but the lowest benthic fauna diversity, so this did not seem to be the most important factor in explaining the biodiversity patters in the biocanal. In a study of streams restored after timber floating Lepori et al. (2005) found that the restored sites had higher substrate roughness than natural sites. They proposed that the increased heterogeneity could be explained by a lack of fine material embedding the larger cobbles and boulders, creating large gaps. This explanation can be applied to the situation in the biocanal as well, since no fine substrate was found in the habitats with the highest substrate roughness.

Another way of quantifying structural heterogeneity is by means of substrate diversity (Beisel et al., 1998; Boyero, 2003), which in the biocanal was highest in the pool and floodplain habitat types. These were the habitat types in the biocanal in which the highest benthic fauna diversity and EPT densities were found. The low water velocities in such habitats often lead to deposition of fine material, like sand and silt. This deposition, in combination with an already diverse substrate in the pool and floodplain habitat types, gives a wide range of particle sizes, something that has been shown to benefit many taxa (Allan and Castillo, 2007). The low water velocity in the pool and floodplain in the biocanal may also explain the high EPT densities in these habitats, since these orders have been seen to prefer low velocities in the range of 0.1–0.4 m s^{-1} (Gore et al., 2001).

Recreating physical structures in an attempt to restore biodiversity in degraded ecosystems is sometimes termed the "Field of dreams hypothesis" (Bond and Lake, 2003). The theory states that "if you build it, they will come". However, even though the design morphology is of great importance for the species composition in a particular location, there are several other factors that affect the species composition. The organisms ability to recolonize the area and the availability of appropriate food sources will influence to what extent the community composition in the biocanal will resemble that of the natural streams in the area. The time span for which colonization takes place is largely dependent on the life history and dispersal capabilities of the colonizing organisms (Wallace, 1990; Yount and Niemi, 1990), which may explain much of the colonization patterns observed for the biocanal. For example the Dipterans, in particular individuals of the family Chironomidae, have been shown to be early colonizers of new areas (Jones et al., 2008; Malmqvist et al., 1991), and were also among the first colonizers of the biocanal. Taxa with poor dispersal capabilities like the Gastropoda or Bivalvia (Kappes and Haase, 2012) and families with life stages associated to the riparian vegetation, like the Sialidae (Evans and Neunzig, 1996) represented the slowest colonizers and were only found in the reference streams. Still, new families of Trichoptera and Coleoptera were found during the last sampling in September 2011, indicating that the colonization is still in progress. It has been proposed that colonization processes, such as the one in the biocanal, may take from as little as one year under favorable conditions (Malmqvist et al., 1991) up to a decade or more in extreme climate (Jones et al., 2008). It appears likely, therefore,

that over time the benthic fauna community in the biocanal will continue to converge with those of nearby natural streams.

However, these results may not have been as evident if species level identifications had been used, and even though there is a colonization of new families with time, many of these families are represented by few individuals. The major increase in EPT abundance in September 2011 was, for example, largely attributable to high densities of a few families, predominantly Baetidae and Lepidostomatidae. The patchy distribution of macroinvertebrates might also have affected the results.

Another factor influencing the rate of colonization is the distance from the source of colonization (Gore, 1982). Most adult aquatic insects seem to reside in the stream corridor and the riparian zone, moving within this narrow area (Petersen et al., 2004), but adults have been found dispersing upstream between 1.6 and 1.9 km for *Baetis* (Hershey et al., 1993) and 16 km for Hydropsychidae (Coutant, 1982). This should be sufficient to allow colonization of the biocanal from numerous streams in the area. Of the sampled reference streams, the old riverbed, which is connected to the biocanal, contained the highest number of families, constituting an excellent source of colonization. This stream might also be the main species pool for colonization of mollusks. Even though their active movement is limited they may still disperse with the aid of other animals, such as birds, fish or insects (Kappes and Haase, 2012). The old riverbed contained three families of mollusks, Pulmonata, Sphaeriidae and Valvatidae, and even though none of these families were found in the biocanal during this study, colonization is still possible in the future since they hypothetically could colonize new areas as far as 3 km away within in a time span of 3–10 years (Kappes and Haase, 2012).

The colonization of macroinvertebrates also depends on food availability in the new habitats. Allochthonous input of CPOM is an important basal resource to food webs in small streams, a food resource which many macroinvertebrate taxa exploit. The rate of CPOM in a stream is largely dependent on downfall of leaves and other plant parts from the riparian vegetation, something which in this early stage of succession is scarce along the biocanal. A plant colonization of the riparian zone may therefore facilitate the colonization of new families of benthic fauna in the future.

5. Conclusions

After only two years of colonization we observed differences in benthic fauna compositions between habitat types in the biocanal. The riffle habitat, created to resemble a conventional Swedish nature-like fishway, contained the lowest number of families of benthic fauna. The riffle habitat type also exhibited the lowest family diversity and EPT abundance. We therefore recommend constructions of more diverse, nature-like fishways with a multitude of habitat types to increase biodiversity. The overall macroinvertebrate community composition in the biocanal showed convergence to that of the natural reference streams in the area during the two year study. However, a more developed

riparian zone would probably increase the suitability of the bio-canal as macroinvertebrate habitat through its contribution of allochthonous CPOM. Riparian vegetation is also known to increase shading, resulting in reduced water temperatures (Welsch, 1991) and reduced algal growth (Quinn et al., 1997). Later in the succession, large woody debris is often added from the riparian zone, increasing the complexity of the habitat and providing additional substrate (Benke and Wallace, 2003). A more developed riparian zone would thereby increase the potential for an even more nature-like benthic fauna composition and thus a higher biodiversity.

Further suggestions for future projects include the following:

(1) A more nature-like and variable substrate in the fast flowing areas could be achieved by adding pebbles, cobbles and a few large boulders to create a variable flow regime and favorable areas for fish.
(2) Planting of riparian vegetation to facilitate detritus-based energy pathways.
(3) Addition of supplementary woody debris to increase structural complexity and create additional habitats.

However, a high biodiversity may not always be the desired goal of the rehabilitation measures; in some cases it may instead be more important to compensate for the damage human activity has had on a given species. In such cases it might be necessary to design habitat especially for this species.

Acknowledgements

Appendix A.

Mean densities (individuals m^{-2}) of benthic fauna, mean densities of EPT and Shannon–Weaver diversity of benthic fauna in the biocanal and the reference streams.

Date	Stream	Treatment	Density	EPT	Diversity
June 2010	Biocanal	Total	1517 ± 1226	7 ± 15	0.47 ± 0.35
		B	1525 ± 775	2 ± 7	0.59 ± 0.42
		F	642 ± 388	0 ± 0	0.29 ± 0.28
		P	1792 ± 1250	21 ± 21	0.49 ± 0.29
		R	2108 ± 2041	6 ± 16	0.48 ± 0.35
	References	Total	4671 ± 4892	260 ± 374	1.11 ± 0.49
		r	5908 ± 6206	355 ± 445	1.18 ± 0.47
		p	3433 ± 3234	152 ± 235	1.03 ± 0.51
July 2010	Biocanal	Total	10 463 ± 13 300	12 ± 25	0.67 ± 0.31
		B	3783 ± 2999	2 ± 7	0.72 ± 0.30
		F	10 675 ± 6785	17 ± 37	0.60 ± 0.40
		P	22 483 ± 23 839	21 ± 26	0.57 ± 0.28
		R	4908 ± 4421	8 ± 16	0.78 ± 0.20
Sept 2010	Biocanal	Total	2552 ± 2082	69 ± 99	0.88 ± 0.56
		B	3350 ± 4021	40 ± 58	0.65 ± 0.60
		F	2375 ± 641	40 ± 42	0.67 ± 0.53
		P	3608 ± 478	156 ± 152	1.36 ± 0.30
		R	875 ± 363	42 ± 49	0.84 ± 0.51
	References	Total	5217 ± 3322	486 ± 727	1.62 ± 0.51
		r	4533 ± 3725	583 ± 946	1.65 ± 0.54
		p	5900 ± 3047	389 ± 408	1.59 ± 0.49
May 2011	Biocanal	Total	3698 ± 3633	39 ± 64	0.69 ± 0.37
		B	5975 ± 6284	73 ± 108	0.84 ± 0.35
		F	3067 ± 435	27 ± 43	0.74 ± 0.25
		P	2492 ± 1425	48 ± 36	0.74 ± 0.42
		R	3258 ± 4477	6 ± 16	0.43 ± 0.34
	References	Total	4910 ± 4389	241 ± 226	1.37 ± 0.41
		r	3996 ± 1790	269 ± 227	1.43 ± 0.40
		p	5825 ± 6097	214 ± 226	1.31 ± 0.43
July 2011	Biocanal	Total	8683 ± 10 770	46 ± 58	0.83 ± 0.40
		B	10 100 ± 10 611	19 ± 39	0.63 ± 0.40
		F	2792 ± 674	56 ± 88	0.84 ± 0.37
		P	3450 ± 1491	73 ± 38	1.26 ± 0.12
		R	18 392 ± 16 887	35 ± 43	0.60 ± 0.27
Sept 2011	Biocanal	Total	2652 ± 2112	304 ± 462	1.27 ± 0.67
		B	2292 ± 1901	160 ± 255	1.07 ± 0.57
		F	3092 ± 1465	384 ± 413	1.70 ± 0.23
		P	4642 ± 2426	573 ± 691	1.49 ± 0.77
		R	583 ± 225	83 ± 72	0.83 ± 0.63
	References	Total	2213 ± 2399	330 ± 488	1.24 ± 0.66
		r	1329 ± 1021	244 ± 302	1.16 ± 0.61
		p	3096 ± 3122	421 ± 621	1.33 ± 0.72

Abbreviations: p, reference pool; r, reference riffle; R, riffle; B, braided; P, pool; F, floodplain.

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Paper 2

Functional organization and colonization of macroinvertebrates in a nature-like fishway with added habitat heterogeneity

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Abstract

Stream habitat lost due to hydroelectric development can be partly mitigated through the construction of nature-like fishways that facilitate passage and provide habitat. Such habitats will become increasingly important as river rehabilitation and connectivity issues are addressed, and information concerning trophic levels and habitat functions brings important knowledge for conservation incentives. In 2009, a nature-like fishway, termed the biocanal, with added habitat heterogeneity in the form of four habitat types ('pools', 'floodplains', 'braided habitats' and 'riffles'), was constructed in River Västerdalälven, Sweden. The trophic state and colonization by macroinvertebrates in the biocanal was studied

during five years. Densities of functional feeding groups changed over time and among habitats, and functional feeding group ratios indicated that the biocanal is a heterotrophic system, probably caused by influx of nutrient rich water from the main river. Most macroinvertebrate families were found in the pools and fewest were found in the riffles, showing that the added habitat heterogeneity influenced both function and biodiversity. The total number of macroinvertebrate families increased initially to level out two years after the biocanal was constructed. The densities of macroinvertebrates did however depict a constant increase during the period, indicating that stabilization of the system is still under progress.

Introduction

Stream rehabilitation efforts are increasing worldwide (Bae 2011; Bernhardt et al. 2005; Castillo et al. 2016; Del Tánago et al. 2012; Morandi et al. 2014; Suding 2011). In areas where important habitats have been degraded or destroyed by human activities, habitat can be rehabilitated or even created to compensate for these losses (Enders et al. 2007; Parasiewicz et al. 2013; Scruton 1996; Scruton et al. 2005). One rehabilitative measure which holds the potential to simultaneously provide habitat and re-establish connectivity in fragmented streams is the construction of nature-like fishways, built using natural materials with the intent of mimicking natural stream characteristics, such as slope, morphology and hydraulic condition (Katopodis 2012). Many studies have focused on the fish passage function of nature-like fishways (Aarestrup et al. 2003; Calles and Greenberg 2005; Calles and Greenberg 2009; Eberstaller et al. 1998; Jansen et al. 1999; Jungwirth 1996; Mader et al. 1998; Santos et al. 2005) and fish are the target organisms of many habitat compensation measures (Enders et al. 2007; Jones et al. 2003; Scruton 1996). However, the potential effects of habitat rehabilitation in nature-like fishways for other organisms have hitherto not been fully realized and only a few studies have focused on the benthic fauna composition in artificial habitats (Goeller and Wolter 2015; Jansen et al. 2000).

As the connection between increased habitat heterogeneity and increased biodiversity has been accepted as a fundamental element of ecology (Ricklefs and Schluter, 1993), the main efforts in stream restorations have been aimed at restoring habitat heterogeneity (Palmer et al. 2014). When a nature-like fishway of bypass-type was built in 2009, at an existing HEP dam on River Västerdalälven in Eldforsen, Sweden, it was fitted with three replicates of four habitat types, referred as to 'pools', 'floodplains', 'braided habitats' and 'riffles' to achieve increased habitat heterogeneity. To emphasize the morphological differences between this construction and the more homogenous design of conventional nature-like fishways, the investigated fishway type was referred to as a 'biocanal'. To find out if the high habitat heterogeneity in the biocanal had a positive effect on the biodiversity, we assessed the effectiveness of the biocanal as habitat for macroinvertebrates during its first two years after completion (2010-2012), leading to the conclusion that the biocanal possessed a higher family diversity than a conventional nature-like fishway (Gustafsson et al. 2013). However, in many stream restoration studies species richness has not increased as a result of improved habitat heterogeneity (Palmer et al. 2010). Therefore, a more holistic view of stream restorations has been proposed, and it has been suggested that, in addition of focusing on biodiversity and the presence of individual species, the functional properties of the ecosystem should be a main goal of restorations (Palmer et al. 1997).

In a functioning ecosystem, it is essential that the capacity to uphold nutrient and energy cycling is maintained and macroinvertebrates are an important part of these processes (Covich et al. 1999; Cummins and Klug 1979; Wallace and Webster 1996). Different taxa in the benthic community have different functions in the ecosystem and one way of studying this is to divide them 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, a shift in energy input should be reflected in the macroinvertebrate community and small heterotrophic streams that receive much of their carbon from leaf litter should be dominated by shredders and gathering collectors, whereas midsized autotrophic rivers with high primary production should be dominated by scrapers and collectors. Finally, in large rivers,

where high turbidity and water depth often impede light penetration, there should be an increasing dominance of collectors with increasing stream size (Vannote et al. 1980). Information on FFG composition can thereby provide indirect information on stream ecosystem attributes, such as indicating if the system is autotrophic or heterotrophic (Cummins et al. 2005; Merritt et al. 1996; Yoshimura et al. 2006).

In the present study, the functional organization and colonization of macroinvertebrates in the biocanal was followed along a five-year period from 2010 to 2014. An FFG approach was used to give an insight of the trophic state of this new system and whether this state changes over time. As the biocanal was designed following the philosophy of physiomimesi (Katopodis et al. 2001), i.e. mimicking the properties of an equal-sized natural stream in the area, we wanted to find out if the functional organization in the biocanal reflected that of a small stream. We did believe that the lack of riparian vegetation during the early colonization phase, in combination with a high insolation would promote algal growth, causing the biocanal to be an autothrophic system with an abundant community of scrapers. However, we also believed that the biocanal might become more similar to the small natural streams in the area with increasing canopy cover leading to a possible shift to heterotrophy. The study also encompassed comparisons of the family composition, diversity and density of macroinvertebrates between the four biocanal habitat types. We predicted that the added habitat heterogeneity should have a positive influence on family diversity and density in the biocanal, and that this pattern would stabilize over the five-year study period.

Materials and methods

Study area

The biocanal, situated in Eldforsen, Sweden, has a total length of 500 m and was designed to resemble a similar-sized natural stream with the aim of ameliorating loss of lotic habitat and longitudinal connectivity inflicted by the hydroelectric facility in the area. Four different habitat types,

referred as to 'pools', 'floodplains', 'braided habitats' and 'riffles', were included along the biocanal to increase heterogeneity of substrate composition, water depth and water velocity. 'Pools' resemble deeper habitats with slow flowing water. 'Floodplains' have a winding channel and a diverse substrate. In 'braided habitats', the canal has been diverted into narrow channels separated by islands and 'riffles' hold a relative uniform substrate and a high water velocity, reflecting the homogenous structure of conventional nature-like fishways. Each habitat type, whose main physical characteristics (width, depth, flow velocity) are reported in Table 1, is replicated three times within the biocanal. The habitats are separated by 18 m long riffles acting as buffer zones (Fig. 1). The flow-regime in the biocanal was set to resemble the natural hydrograph for the area and the biocanal was constructed with a relatively low gradient (1%) compared to conventional fishways. The discharge ranges from 200 L s^{-1} (in 2010, when water was pumped into the biocanal due to a delayed startup of the hydroelectric facilities), to 1200 L s^{-1} at high flow. The biocanal was designed not only to allow fish passage and to supply the former main stem of the river with a residual flow, but also to compensate for lost habitat for the Red Listed freshwater pearl mussel (*Margaritifera margaritifera*) occurring in Västerdalälven.

Natural recolonization of the riparian vegetation was slow along the biocanal and the vegetation was sparse the first years after its construction. It mainly consisted of white clover (*Trifolium repens,* L.), grass and small trees (*Betula* sp., *Pinus* sp., *Alnus* sp. and *Salix* sp.), with an increase in coverage of mainly alder (*Alnus* sp.) with time. The most common fish species that recolonized the biocanal were the European minnow (*Phoxinus phoxinus,* L.) and the burbot (*Lota lota,* L.) (mean length 109 mm in 2012 and 181 mm in 2013*).* Other fish species found in the fishway, although represented by few individuals, were brown trout (*Salmo trutta,* L.), grayling (*Thymallus thymallus,* L.), northern pike (*Esox lucius,* L.), European perch (*Perca fluviatilis,* L.), European brook lamprey (*Lampetra planeri,* Bloch), Eurasian ruffe (*Gymnocephalus cernua,* L.), Eurasian dace (*Leuciscus leuciscus,* L.) and European bullhead (*Cottus gobio,* L.) (unpublished electrofishing data).

Table 1. Physical characteristics (average ± standard deviation; length, width, depth and flow velocity) of the habitat types in the biocanal. Mean values are based on 18 measurements in each habitat type in 2010, 2011 and 2014.

	Lenght (m)	Width ± SD (m)	Depth ± SD (m)	Velocity ± SD (m s-1)
Pool	18	7.2 ± 0.6	0.56 ± 0.21	0.129 ± 0.142
Floodplain	18	8.1 ± 0.8	0.32 ± 0.11	0.246 ± 0.214
Braided	18	9.0 ± 0.4	0.31 ± 0.17	0.384 ± 0.232
Riffle	18	4.5 ± 0.5	0.28 ± 0.11	0.453 ± 0.222
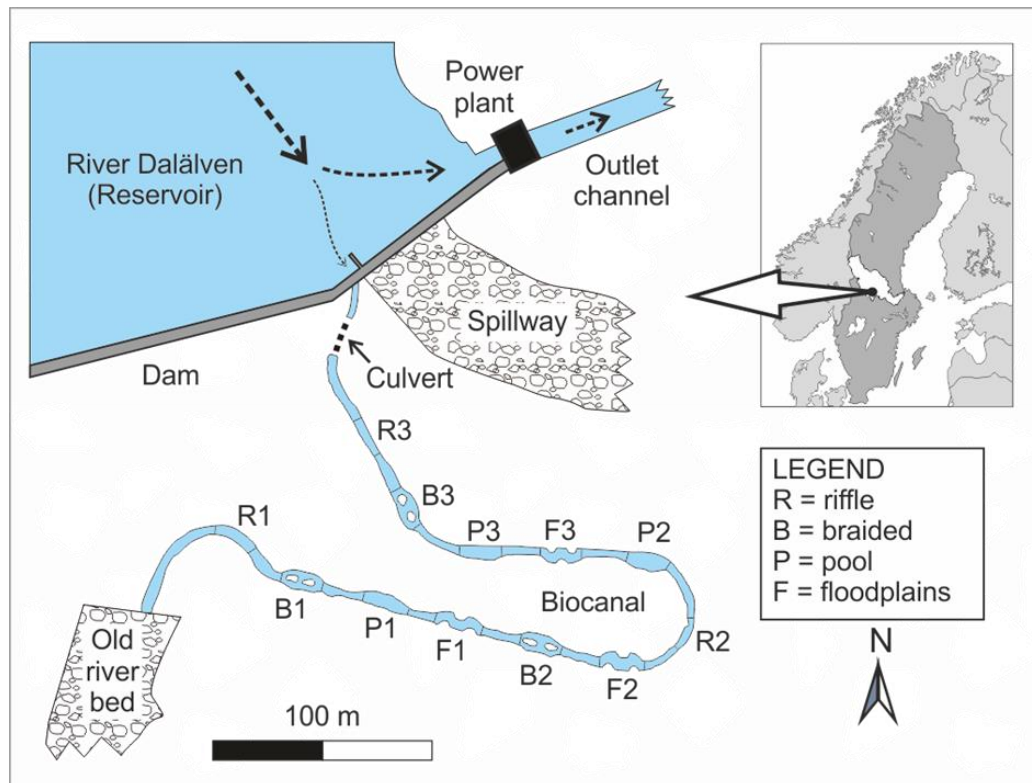
Figure 1. Location of the biocanal with its four habitat types (riffles, braided habitats, pools and floodplains). The map of the biocanal illustrates the wet area at minimum flow (200 **L s-1**).

Macroinvertebrate sampling

In each habitat type of the biocanal, macroinvertebrates were collected using a 0.04 m^2 Surber sampler fitted with 500 μm net. Samples were collected in spring over a five-year period (2010-2014) and additional samples used for FFG assessment were collected in autumn over a three-year period (2010-2012). The Surber sampler was placed at a randomly selected location on the streambed and the substrate within the samplers frame was scrubbed with a brush. Twelve samples from each habitat type were collected on each sampling date. Samples were preserved in 70% ethanol in the field before being transported to the laboratory for analysis. Individual invertebrates were identified to family- or the taxonomic-level needed to assign FFG properties to the given individual. Members of the family Chironomidae were identified as Tanypodinae and non-Tanypodinae. The FFGs used were; gathering collectors, filtering collectors, scrapers, predators, shredders, xylophagous, other and unknown. Identifications were made using microscope binoculars and taxonomic keys (Lechthaler 2007; Nilsson 1996; Nilsson 1997; Waringer and Graf 1997). Many taxa are generalists (Mihuc 1997), and thus a weighted FFG list according to Moog (2002) was used to account for potential use of different food sources by taxa. Tanypodinae and non-Tanypodinae were however classified as predators and gathering collectors, respectively (Ely and Wallace 2010; Stone and Wallace 1998; Wallace et al. 1997). Each individual was assigned a total of 10 points which then were divided among the preferred feeding modes (Table 2).

Data analysis

The FFG density was calculated as the density of individual taxa multiplied by 1-10 points for each feeding mode according to the weighted list (Table 2) after which the value for each FFG was divided by ten. The ratio of scrapers to shredders and total collectors were used as an indicator for autotrophy or heterotrophy. Here values below 0.75 indicate a heterotrophic system dependent on allochthonous organic matter (Merritt and Cummins, 2006). Moreover, macroinvertebrate density (individuals m^{-2}) was calculated for every sampling occasion and biocanal habitat type, as was the number of macroinvertebrate families.

The community composition was estimated for macroinvertebrate families using Shannon-Weaver-Index (H) (Shannon and Weaver, 1949). Repeated-measures ANOVA, referred to as 'RMA', were used to compare the 'FFG density', the 'macroinvertebrate density' and the 'Shannon Index' between the biocanal habitat types over time. An ANOVA was also performed to compare the density of simuliids for the different years. Prior to analyses, dependent variables were tested for normality using a Kolmogorov–Smirnov test and were log transformed if normality assumptions were not met. Sphericity was tested using Mauchly's test, with Greenhouse-Geisser correction used if assumptions were violated. Tukey test was used when significant differences were found. All statistical analyses were performed in IBM SPSS statistics version 22.0.0.1.

Results

A total of 26 257 macroinvertebrate individuals belonging to 38 families were found in the biocanal in spring 2010-2014 (Appendix A). The number of individuals collected increased gradually over time with an average annual increase of approximately 200%, moving from 728 individuals collected in 2010 to 12 478 individuals in 2014 (total increase of more than 1 600%).

Functional Feeding Groups

Of the eight feeding modes used in the classification in this study, gathering collectors, filtering collectors, scrapers and predators were most common, whereas the groups shredders, xylophagous, other and unknown each contributed to 1.5% or less of the FFG composition the consecutive years. Disregarding taxa identified as unknown, the gathering collectors and filtering collectors combined constituted 97, 92, 75, 88 and 93% of the FFG composition in the biocanal the consecutive years (Fig. 2). During the first three years of the study the gathering collectors were the most common FFG as they represented > 60% of the

Table 2. Taxa found during the study, and their corresponding functional feeding groups. Each taxon is assigned 10 points distributed among its preferred feeding modes. Abbreviations: SHR: shredder, SCR: scraper, A.FIL: active filter feeder, P.FIL: passive filter feeder, GATH: gathering collector, MIN: miner, XYL: xylophagous, piercer, PRE: predator, PIE: piercer, OTH: other, UNK: unknown.

Order	Family	Subfamily/Genus	SHR	SCR	A.FIL	P.FIL	GATH	MIN	XYL	PRE	PIE	OTH	UNK
Diptera	Athericidae									10			
	Ceratopogonidae									10			
	Chironomidae	Non-Tanypodinae					10						
		Tanypodinae								10			
	Limoniidae	Antocha					10						
	Pediciidae	Dicranota								10			
	Simuliidae	Simulium				10							
	Tabanidae	Chrysops					10						
	Tipulidae		7				3						
	Empididae									10			
Ephemeroptera	Baetidae			5			5						
	Caenidae						10						
	Ephemerellidae			5			5						
	Heptageniidae	Heptagenia		5			5						
	Leptophlebiidae	Leptophlebia					10						
Odonata	Aeshnidae									10			
	Cordulegastridae									10			
	Gomphidae									10			
Plecoptera	Nemouridae	Amphinemura	2	5			3						
		Nemoura	7				3						
		Nemurella	2	3			5						
		Protonemura	5	3			2						
	Perlodidae	Isoperla	1	1			1			7			
		Diura								10			
	Leuctridae		3	3			4						
	Taeniopterygidae	Taeniopteryx	2	3			5						

Table 2. Continued

Order	Family	Genus	1	2	3	4	5	6
Coleoptera	Dytiscidae					10		
	Elmidae			10				
	Gyrinidae				10			10
Trichoptera	Brachycentridae	*Micrasema*	5					
	Glossosomatidae	*Agapetus*	5	8		2	3	
	Hydropsychidae			2	5			
	Hydroptilidae	*Hydroptila*				3		10
		Orthotrichia						10
		Oxyethira						10
		Ithytrichia		10				
	Lepidostomatidae	*Lepidostoma*	2	5			3	
	Leptoceridae	*Athripsodes*	5		3	3	2	
		Mystacides	2		5	5	1	
	Limnephilidae		5	2	1	2		
	Polycentropodidae				1	1	9	
	Psychomyiidae	*Psychomyia*	7		1	1	1	
		Tinodes	8		1	1	1	
	Rhyacophilidae						10	
Megaloptera	Sialidae						10	
Non-Insects	Lymnaeidae	*Lymnaea*	4	4				2
	Planorbidae	*Gyraulus*	2	6				2
	Sphaeriidae	*Pisidium*			10			
	Naididae	*Naidinae*	5	5		5		
		Tubificinae			10	10		
	Nematoda							10

total FFG composition. The density of both, gathering collectors, scrapers and predators increased from 2010 to 2012, after which the densities seemed to level out. The densities of filtering collectors did however increase in 2013 and 2014, and they constituted 59% and 69% of the FFG composition these years.
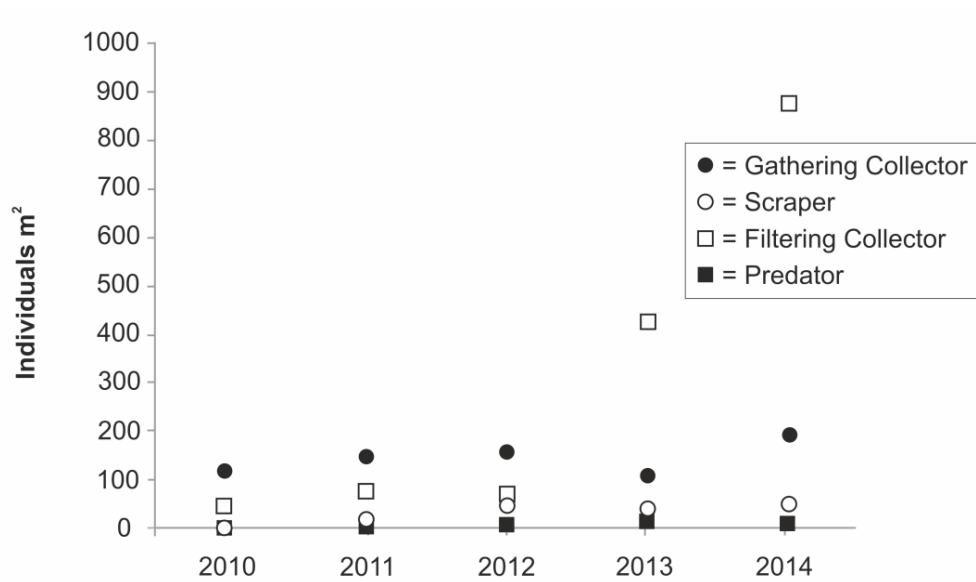
Figure 2. Average density (ind m^{-2}) of the most common FFGs in the biocanal in spring 2010-2014.

There was a significant interaction between time and habitat type for the density of scrapers (RMA: $F_{10.14,154.89}$ = 2.32, p < 0.05) and gathering collectors (RMA: $F_{10.14,148.71}$ = 2.32, p < 0.05). The density of scrapers developed differently over time in the floodplain (ANOVA: $F_{4,55}$ = 6.45, p < 0.0001), pool (ANOVA: $F_{4,55}$ = 2.83, p < 0.005) and riffle habitats (ANOVA: $F_{4,55}$ = 3.84, p < 0.05). In the floodplains scrapers were found in lower densities in 2010 (Tukey, p < 0.05) and 2013 (Tukey, p < 0.005) compared to 2014, in 2011 compared to 2013 (Tukey, p < 0.05) and in 2013 compared to 2012 (Tukey, p < 0.0001). In the pool habitats they were found in lower densities in 2011 than in 2014 (Tukey, p < 0.05). In the riffles the density of scapers was lower in 2013 compared to 2014 (Tukey, p < 0.005). Comparisons of the density of scapers beween the habitat types revealed a significantly higher density in the floodplain (ANOVA: $F_{3,44}$ = 3.95, p < 0.05, Tukey, p < 0.05) and pool habitats (Tukey, p < 0.05) than the riffle habitats in 2012 and in the pool habitats than the

floodplain (ANOVA: $F_{3,44}$ = 3.44, p < 0.05, Tukey, p < 0.05) and riffle habitats (Tukey, p < 0.05) in 2013 (Table 3).

The density of gathering collectors developed differently over time among the braided (ANOVA: $F_{4,55}$ = 8.25, p < 0.0001) and riffle habitats (ANOVA: $F_{4,55}$ = 4.15, p < 0.005). In the braided habitats they were found in lower densities in 2013 compared to 2010 (Tukey, p < 0.05), 2011 (Tukey, p < 0.005) and 2014 (Tukey, p < 0.0001). The densities were also lower in 2012 compared to 2014 (Tukey, p < 0.005). In the riffle habitats the densities of gathering collectors were lower in 2010 (Tukey, p < 0.05) and 2013 (Tukey, p < 0.0001) than 2014. Comparisons between the habitat types revealed that there was a significantly higher density in pool habitats compared to braided habitats in 2012 (ANOVA: $F_{4,55}$ = 8.25, p < 0.0001, Tukey, p < 0.005) and 2013 (Tukey, p < 0.05). The densities were also lower in riffle habitats compared to braided habitats in 2012 (ANOVA: $F_{4,55}$ = 4.15, p < 0.005, Tukey, p < 0.05) and pool habitats in 2013 (Tukey, p < 0.05).

The densities of the filtering collectors (RMA: $F_{4,176}$ = 92.8, p < 0.0001) and predators (RMA: $F_{2.56,112.66}$ = 12.97, p < 0.0001) differed among the sampling occasions, and among the biocanal habitat types, but there was no significant interaction between the factors. There were significantly more filtering collectors in the biocanal in 2012 than in 2013 (ANOVA: $F_{4,235}$ = 8.83, p < 0.0001; Tukey, p = 0.008) and in 2014 compared to 2010 (Tukey, p < 0.0001), 2011 (Tukey, p < 0.05) and 2013 (Tukey, p < 0.0001). Significantly more filtering collectors were found in the riffle and braided habitats compared to the pool and floodplain habitats (Tukey, p < 0.05). There were significantly more predators in the biocanal in 2011 than in 2013 (ANOVA: $F_{4,235}$ = 13.62, p < 0.0001; Tukey, p < 0.001), in 2012 than in 2010 (Tukey, p < 0.05) and in 2014 than in 2010 (Tukey, p < 0.0001), 2011 (Tukey, p < 0.05) and 2013 (Tukey, p < 0.0001). The density of predators was significantly higher in the pool habitats compared to the riffle and braided habitats (Tukey, p < 0.05) (Table 3).

Table 3) Density (ind m^{-2}) of the most common FFGs in the biocanal habitats.

FFG / Habitat	2010		2011		2012		2013		2014	
Scraper										
Riffle	1	+/- 4	4	+/- 8	16	+/- 12	12	+/- 11	13	+/- 11
Braided	4	+/- 3	21	+/- 22	47	+/- 40	53	+/- 61	37	+/- 46
Pool	5	+/- 5	10	+/- 8	76	+/- 59	71	+/- 63	78	+/- 56
Floodplain	2	+/- 3	14	+/- 13	49	+/- 40	32	+/- 30	63	+/- 46
Gathering Collector										
Riffle	111	+/- 98	225	+/- 408	79	+/- 71	41	+/- 28	181	+/- 101
Braided	122	+/- 146	137	+/- 86	162	+/- 120	91	+/- 92	143	+/- 76
Pool	137	+/- 121	85	+/- 78	211	+/- 172	243	+/- 402	210	+/- 95
Floodplain	89	+/- 84	155	+/- 95	168	+/- 102	55	+/- 42	240	+/- 126
Predator										
Riffle	1	+/- 3	1	+/- 4	3	+/- 3	8	+/- 10	4	+/- 6
Braided	0	+/- 0	3	+/- 4	7	+/- 11	11	+/- 11	4	+/- 4
Pool	1	+/- 2	4	+/- 5	15	+/- 14	17	+/- 18	9	+/- 9
Floodplain	0	+/- 0	7	+/- 11	9	+/- 5	9	+/- 6	10	+/- 6
Filtering Collector										
Riffle	139	+/- 329	171	+/- 310	54	+/- 67	700	+/- 900	2067	+/- 1868
Braided	49	+/- 91	132	+/- 290	211	+/- 526	917	+/- 1438	979	+/- 1428
Pool	3	+/- 6	0	+/- 0	7	+/- 10	26	+/- 22	209	+/- 284
Floodplain	6	+/- 13	3	+/- 4	3	+/- 3	69	+/- 86	244	+/- 316

Autotrophy or heterotrophy

The ratio reflects the high number of gathering collectors and filtering collectors in the biocanal and indicates that the biocanal is a heterotrophic system (< 0.75 for all years, Table 4).

Table 4) Ratio of functional feeding groups, scrapers to shredders and total collectors, and the stream ecosystem parameter for which it can serve as a surrogate (modified from Merritt and Cummins (2006). Autotrophy is defined as a ratio > 0.75.

Year	Ratio of functional feeding groups	
	Spring	Fall
2010	0.02	0.15
2011	0.06	0.60
2012	0.26	0.27
2013	0.11	-
2014	0.07	-

Macroinvertebrate families

The total number of macroinvertebrate families in the biocanal initially increased, from ten in 2010 to 26 in 2011, after which it leveled out at around 25-27 families the consecutive years (Fig. 3). Every family was not found each year, but a total of 19 families were found in the riffle habitats during the study, 23 in the braided habitats, 27 in the floodplain habitats and 35 in the pool habitats. Early colonizers were dipterans such as chironomids and simuliids, but also annelid worms of the family Naididae and ephemeropterans of the family Baetidae (Appendix A.). The family diversity (H) differed between the sampling dates (RMA: $F_{4,3} = 23.95$, $p < 0.0001$) and varied between the biocanal habitat types over time (RMA: $F_{12,0.53} = 4.4$, $p < 0.0001$). The family diversity was significantly higher in the braided habitats than the riffle habitats in 2011 (ANOVA: $F_{3,44} = 3.25$,

p < 0.05; Tukey, p < 0.05) and in the floodplain habitats in 2014 (ANOVA: $F_{3,44}$ = 3.14, p < 0.05; Tukey, p < 0.05). The diversity was also higher in the pool habitats than the braided habitats (ANOVA: $F_{3,44}$ = 9.41, p p < 0.0001; Tukey, p = 0.002) and the riffle habitats (Tukey, p < 0.0001) in 2013. Finally, the diversity was higher in the floodplain habitats than in the riffle habitats in 2013 (Tukey, p < 0.05).
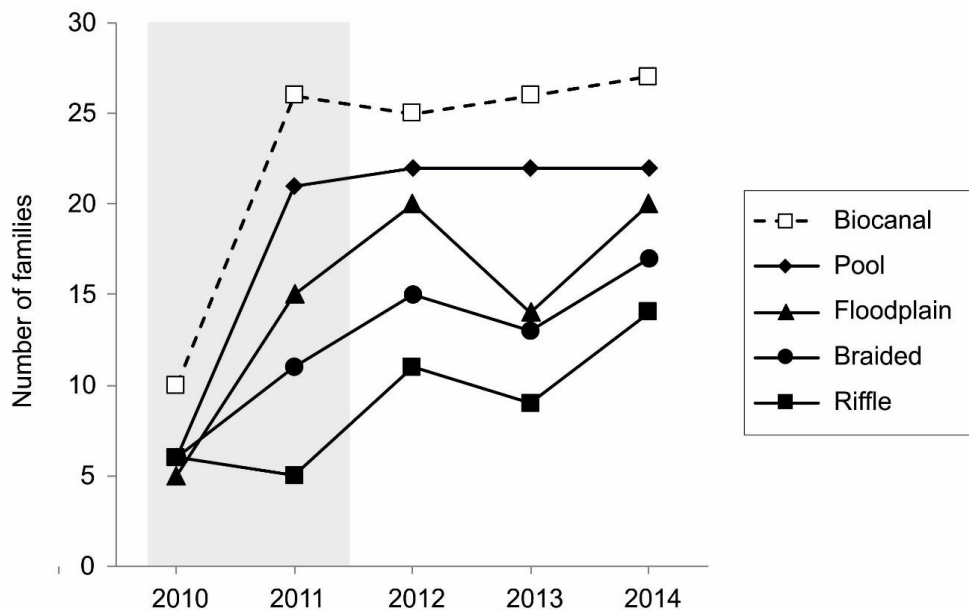
Figure 3. The total number of macroinvertebrate families present in the different habitats in the biocanal during the study period 2010-2014. Data from 2010 and 2011 (shaded area) have previously been published in Gustafsson et al. (2013).

The total macroinvertebrate density differed significantly between the sampling occasions (RMA: $F_{2.8,19}$ = 39.6, p < 0.001) and it was significantly higher in 2014 compared to all other sampling dates (Tukey, p < 0.005), highlighting a marked increase trend over time. No significant differences in total macroinvertebrate density could be found between the habitat types (Tukey, p > 0.5). In 2014, Simuliidae was the most common family in the biocanal as they accounted for > 69% of the total density. Comparisons of the density of simuliids between the years showed that there was a significant difference between the years (ANOVA : $F_{4,69645083}$ = 15,7, p < 0.001) and that the density was significantly higher in 2014 compared to all other years, even after removal of the four highest density samples in 2014 (Tukey, p < 0.05).
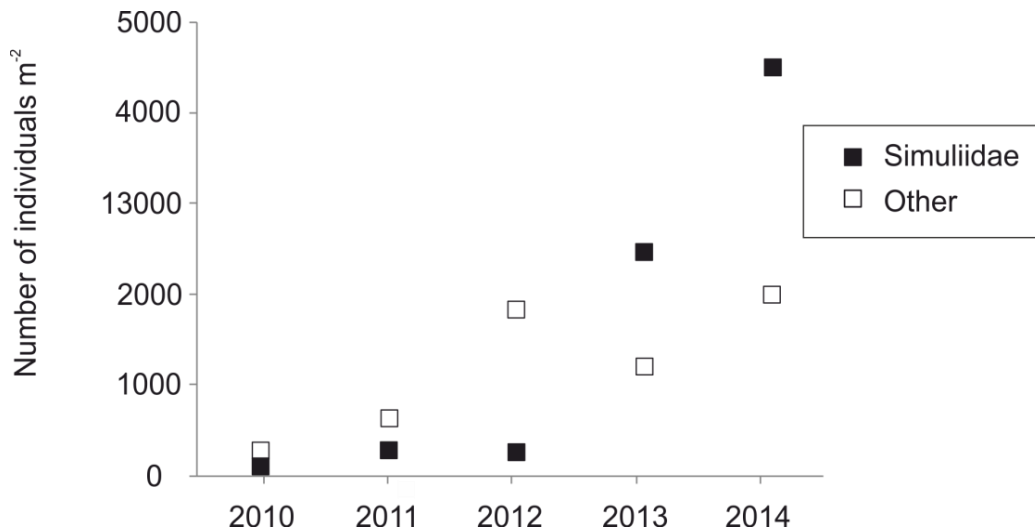
Figure 4. Mean densities (ind. m^{-2}) of Simuliidae and all other families combined in the biocanal during spring 2010-2014.

Discussion

The design philosophy of nature-like fishways is to imitate the characteristics of natural streams. However, the aim should not only be a construction that resembles similar-sized streams in terms of physical properties, but also their trophic state and biodiversity. A newly constructed habitat may neither have the vegetation in the riparian zone needed to fuel the stream with necessary allochtonous carbon, nor possess the fauna of a fully developed natural stream. Previous studies have shown that colonization processes of macroinvertebrates may occur over extended periods of time (Jones et al. 2008; Milner et al. 2008; Winking et al. 2014). To monitor colonization, investigating effects of added habitat complexity on function and diversity for longer periods is therefore needed. The results from this five-year study of the macro-invertebrate colonization of the biocanal showed that it is a heterotrophic system. Due to the lack of riparian vegetation and the influx of nutrient rich water from the main river, it is however likely that it is more functionally similar to the main river than to the small nearby streams that it is created to resemble. We could also see that the biocanal constituted habitats for a variety of macroinvertebrate families, and that

most families were found in the pools and fewest were found in the riffles, showing that the added habitat heterogeneity influenced the biodiversity. The total number of families increased initially and leveled out two years after the biocanals construction. The macroinvertebrate densities did however continue to increase during the whole study period, leading us to believe that stabilization of the system is still in progress.

Collectors, both gathering and filtering, dominated in the biocanal, which suggests that fine particulate organic matter (FPOM) both on the substrate and in suspension was the primary energy source for the macroinvertebrate community. The ratio of scrapers to shredders and total numbers of collectors indicated that the biocanal was heterotrophic and thereby dependent on input of allochthonous organic material (Merritt and Cummins 2006). This was not in accordance with our hypothesis, as we believed that the lack of riparian vegetation and the high insolation would make the biocanal an autothrophic system, at least during the first years. The supplementary samplings done in September 2010-2012 showed that there was no difference in trophic state in the biocanal between spring and autumn. Nevertheless, there was a large proportion of scrapers in the biocanal in September 2011, which indicates that a proportion of the carbon in the biocanal is derived from autochthonous sources. However, though the scrapers were abundant during this sampling, they were not common enough for the biocanal to be classified as an autotrophic system (Merritt and Cummins 2006). Even though the ratio indicates that the biocanal is a heterotrophic system, it does however not take into account whether the allochtonous carbon derivers from coarse particular organic matter (CPOM), thereby leading to high numbers of shredders, or from FPOM, fueling a community of collectors. The organic input in high order streams such as the River Västerdalälven often originates from FPOM from upstream areas (Cummins 1975), and judging by the dominance of collectors in the biocanal it is likely that the biocanal through its connection to the River Västerdalälven also receives much of its organic material from the same source. Therefore, even though the biocanal morphologically resembles a small stream and is heterotrophic, the source of carbon is probably different from that found in small forest streams and the biocanal may be more functionally similar to the main river.

The density of shredders was low in the biocanal during the study, probably since the riparian vegetation still was scarce and the associated input of CPOM therefore likely was low. None of the taxa in the study were obligate shredders and the most common taxa with shredder-abilities in the biocanal could also function as scrapers, predators and gathering collectors (e.g. *Lepidostoma hirtum* and *Athripsodes cinererus*) and were thus probably exploiting other energy sources in the absence of CPOM. As the riparian vegetation develops along the biocanal, it may lead to higher densities of shredders (Vannote et al. 1980). An increase in leaf input may also have a positive effect on gatherers benefiting from increased food availability after leaves have been processed by shredders, as well as a positive effect on predators as there is potential for more prey (Flory and Milner 1999). It is however also possible that the effect of the main river will overshadow future potential effects of the developing riparian vegetation.

The density of predators in the biocanal seemed to stabilize during the third year of the study. The first predators to colonize the biocanal were ceratopogonids and chironomids belonging to the subfamily Tanypodinae, as well as trichopterans of the family Polycentropodidae. The latter were likely feeding on the highly abundant chronoimids and simuliids. Predators of families such as Sialidae, Dytiscidae, Aeshnidae, Cordulegastridae and Gomphidae were absent or represented by few individuals. There was a lack of macrophytes in the biocanal, which may explain the low abundance of odonatans, as they are linked to the presence of such vegetation (Buchwald, 1992; Hofmann and Mason, 2005a; Hofmann and Mason, 2005b). Perhaps these large predators need more time to establish in the biocanal or maybe they are not adequately sampled by the surber sampler, as other sampling methods have been seen to be more effective for mobile taxa (Ghani et al. 2016; Taylor et al. 2001).

We found a rapid increase in family number in the biocanal during the first years and the family number leveled out at around 25-27 families during the study. The first colonizers of the biocanal were families predominantly characterized by their high dispersal abilities, of which

Chironomidae, Simuliidae and Baetidae have been described as early colonizers in several other studies (Mackay 1992) and references therein). Even though the number of families stabilized during the study period, the density of macroinvertebrates continued to increase. In 2013 and 2014 the predominant increase in density was caused by simuliids. The patchy distribution of macroinvertebrates (Downes et al. 1993) might to some extent explain these results, especially in 2013 when over 30% of the simuliids were found in a single sample. The increase in simuliid density was however not only an artefact of the patchy distribution, as the densities of simuliids were significantly higher in 2014 compared to all other years even after the four highest density samples (comprising 40% of the simuliid density this year) were excluded from statistical testing. It is however not uncommon to find high densities of simuliids in lake or reservoir outlets and densities as high as 120-140 individuals cm^2 have been found (Malmqvist 1994; Wotton 1987), to be compared to the highest density sample in our study with approximately four simuliids cm^2. The density of all other families combined also increased during the study period, but with a slight drop in 2013, perhaps caused by a cold spring (SMHI 2015).

Something that may have influenced the macroinvertebrate community in the biocanal is the local fish fauna (Gilliam et al. 1989) but see: (Flecker and Allan 1984). During the first two years it chiefly consisted of European minnows, which mainly feed of macroinvertebrates and terrestrial drift (Frost 1943). In 2012, the burbot became the dominant fish species. Young burbots mainly feed of macroinvertebrates, but will shift towards a piscivorous diet as they grow (McPhail and Paragamian 2000), thereby probably relieving some predator pressure on the macroinvertebrates as the minnow population is decimated, perhaps contributing to the increase in macroinvertebrate density. The aforementioned lack of riparian vegetation at the beginning of the study may also have had an effect on the density and composition of the macroinvertebrate community in the biocanal. It may for example have affected the establishment of different families of Trichoptera as the availability of plant material for some case building taxa may have been limited (Flory and Milner 1999). This was further supported by the fact that most trichopterans in the biocanal were either free-living, net

spinning or constructed their cases of sand. Early instar larvae of the family Lepidostomatidae, living in cases made of sand, were abundant in the study, but it was not until 2014 that a Lepidostomatidae larvae with a case made of plant material was found. In 2014, the first Limnephilidae larvae in the biocanal was also encountered, this with a case constructed of plant materials as well.

In stream restorations, the habitat most often in need of compensation is riffle habitats and rheophilic species are often those that are limited. The riffles in this study were constructed to resemble the homogenous design of conventional nature-like fishways and they had a significantly lower family diversity compared to the braided habitats in 2011 and the floodplain and pool habitats in 2013. The densities of predators was lower in the riffles than the pool habitats. The density of scrapers was also lower in the riffles compared to in the floodplains in 2012, as well as in the pools in 2012 and 2013. In addition, the densities of gathering collectors was lower in the riffles than in the braided habitats in 2012 and than in the pools in 2013. A previous study showed that the floodplain habitats were the habitats in the biocanal that resembled natural streams the most (Gustafsson et al. 2013) and they probably constitute a better compensation for natural stream habitats than the more uniform riffle habitats. In streams with little or no free flowing water, such artificial stream habitats can be very important for the function and diversity, and by constructing fishways with as nature-like and variable habitats as possible, we can, to some extent, mitigate habitat fragmentation and habitat loss in freshwater ecosystems.

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Appendix A. Densities of macroinvertebrate families in the biocanal 2010-2014.

Family	2010 Stream	2010 Pool	2010 Floodplain	2010 Braided	2011 Stream	2011 Pool	2011 Floodplain	2011 Braided	2012 Stream	2012 Pool	2012 Floodplain	2012 Braided
Baetidae	8 +/-14			8 +/-14	8 +/-14	32 +/-6	33 +/-14	36 +/-13	8 +/-26	104 +/-29	63 +/-22	127 +/-88
Beraeidae						25 +/0						
Caenidae						13 +/-18	25 +/0					
Ceratopogonidae		8 +/-14					25 +/-35		25 +/0	100 +/-66	50 +/0	25 +/0
Chironomidae	219 +/-76	453 +/-403	154 +/-60	206 +/-44	465 +/-463	572 +/-463	594 +/-119	460 +/-167	353 +/-222	1616 +/-735	833 +/-100	835 +/-461
Dytiscidae						25 +/0						
Elmidae	25 +/0			25 +/0		13 +/-18						
Empididae						17 +/-29	17 +/-29			50 +/-35	25 +/-25	
Ephemerellidae						13 +/-18		8 +/-14	13 +/-18	17 +/-29	11 +/-19	8 +/-14
Ephermeridae						17 +/-29				8 +/-14		
Glossosomatidae											25 +/0	
Gomphidae												
Gyrinidae												
Heptageniidae						17 +/-14	13 +/-18		25 +/0	54 +/-51	25 +/0	
Hydropsychidae						8 +/-14	8 +/-14	75 +/-71		25 +/-25	25 +/0	13 +/-18
Hydroptilidae						8 +/-14				33 +/-7	25 +/-25	
Lepidostomatidae						8 +/-14				136 +/-24	67 +/-52	33 +/-38
Leptoceridae						8 +/-14	25 +/-25	13 +/-18		113 +/-76	54 +/-31	63 +/-88
Leptophlebiidae						8 +/-14				17 +/-14		
Leuctridae												
Limnephilidae											25 +/0	
Limoniidae		17 +/-29	8 +/-14		25 +/-43	8 +/-14	13 +/-22	25 +/0	25 +/-25	50 +/-14	25 +/-25	8 +/-14
Lumbriculidae							13 +/-18			13 +/-18	25 +/-35	
Naididae	8 +/-14	53 +/-5	17 +/-14	22 +/-19		92 +/-22	135 +/-4	140 +/-42	142 +/-138	1173 +/-190	662 +/-246	449 +/-233
Nematoda			8 +/-14	8 +/-14		50 +/0	25 +/-25				14 +/-29	17 +/-29
Nematomorpha										8 +/-14		
Nemouridae					17 +/-29			131 +/-133		25 +/0		33 +/-47
Pedicidae						25 +/0						
Perlodidae						50 +/0	13 +/-18	25 +/0		13 +/-18	13 +/-18	
Planorbidae						13 +/-18						
Polycentropodidae	25 +/0								13 +/-18	78 +/-35	13 +/-18	38 +/-53
Psychomyiidae									38 +/0	54 +/-19		33 +/-14
Rhyacophilidae								25 +/0	33 +/-14	67 +/-38	40 +/-20	33 +/-14
Sericostomatidae						25 +/0						
Simuliidae	269 +/-348	17 +/-29	29 +/-31	306 +/-288	358 +/-577	18 +/-14	17 +/-14	835 +/-1340	290 +/-301	72 +/-38	29 +/-7	750 +/-1064
Siphlonuridae		39 +/-13					25 +/0					
Tabanidae												
Tipulidae												
Number of families	6	7	5	6	5	22	16	12	11	23	20	15
Mean Total Density	253 +/-356	154 +/-140	98 +/-90	176 +/-170	410 +/-648	112 +/-98	201 +/-136	295 +/-341	152 +/-98	339 +/-260	257 +/-171	443 +/-602
EPT Density	17 +/-12	31 +/-22	0 +/0	8 +/-12	17 +/-24	28 +/-2	31 +/-5	44 +/-15	62 +/-22	74 +/-10	43 +/-6	75 +/-13

Appendix A. Continued

	2013				2014			
	Stream	Pool	Floodplain	Braided	Stream	Pool	Floodplain	Braided
Baetidae	135 +/-66	267 +/-63	121 +/-69	261 +/-99	69 +/-23	98 +/-53	68 +/-37	11 +/-19
Beraeidae		13 +/-18						
Caenidae								
Ceratopogonidae	142 +/-101		13 +/-18			17 +/-29		
Chironomidae		817 +/-413	219 +/-128	294 +/-178	998 +/-712	1335 +/-840	1354 +/-612	627 +/-162
Dytiscidae		25 +/-0						
Elmidae				25 +/-0	25 +/-0			
Empididae			8 +/-14			13 +/-18	54 +/-40	22 +/-21
Ephemerellidae	63 +/-88	92 +/-52	42 +/-52	76 +/-79	50 +/-43	14 +/-24	13 +/-22	17 +/-14
Ephemeridae						17 +/-29	50 +/-0	25 +/-0
Glossosomatidae						75 +/-0		
Gomphidae		25 +/-0						
Gyrinidae		25 +/-0						
Heptageniidae		25 +/-25		13 +/-18	38 +/-18	25 +/-0	44 +/-62	
Hydropsychidae						50 +/-66	8 +/-14	
Hydroptilidae	25 +/-25	64 +/-77	8 +/-14	42 +/-19	25 +/-0	58 +/-80	38 +/-13	25 +/-0
Lepidostomatidae		104 +/-62	17 +/-14	42 +/-52	25 +/-0	83 +/-93	14 +/-14	38 +/-33
Leptoceridae		58 +/-52	42 +/-38	13 +/-18	25 +/-0	50 +/-45	54 +/-26	63 +/-18
Leptophlebiidae						58 +/-29		
Leuctridae		25 +/-0						
Limnephilidae	8 +/-14					25 +/-0		
Limoniidae		113 +/-159				17 +/-14	33 +/-38	25 +/-0
Lumbriculidae		953 +/-687						
Naididae	36 +/-43	42 +/-12	406 +/-359	388 +/-300	199 +/-98	1214 +/-554	1086 +/-471	467 +/-354
Nematoda		25 +/-0			8 +/-14		8 +/-14	25 +/-25
Nematomorpha	33 +/-14			174 +/-247	17 +/-14			
Nemouridae			88 +/-71		50 +/-0	50 +/-0	25 +/-0	13 +/-18
Pedicidae								
Perlodidae						38 +/-18	19 +/-27	
Planorbidae		50 +/-0		25 +/-0		65 +/-38		
Polycentropodidae		85 +/-55	13 +/-18			65 +/-28	13 +/-18	13 +/-18
Psychomyiidae		17 +/-29	19 +/-27				25 +/-35	8 +/-14
Rhyacophilidae	58 +/-44	29 +/-26	38 +/-13	85 +/-36	17 +/-14	17 +/-14	39 +/-2	17 +/-14
Sericostomatidae		25 +/-0						25 +/-0
Simuliidae	3226 +/-4424	217 +/-41	329 +/-172	6322 +/-4604	10056 +/-2165	1369 +/-905	1496 +/-772	5106 +/-1498
Siphlonuridae								
Tabanidae								
Tipulidae							25 +/-14	
Number of families	9	22	14	13	14	22	20	17
Mean Total								
Density	735 +/-923	278 +/-219	183 +/-81	1054 +/-1486	2267 +/-1855	546 +/-271	590 +/-307	1174 +/-1428
EPT Density	94 +/-29	109 +/-8	60 +/-13	113 +/-10	44 +/-5	77 +/-12	50 +/-8	33 +/-6

Paper 3

A test for suitable fish hosts for the threatened freshwater pearl mussel *(Margaritifera margaritifera)* prior to reintroduction

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Abstract

Habitat restoration in areas where a species has gone extinct, followed by reintroduction of a strain from a different population can be a viable option to repopulate habitats. For species with a parasitic life stage, the suitability of potential host strains must be taken into account to ensure a functional parasite-host interaction. Prior to a planned introduction of the freshwater pearl mussel (*Margaritifera margaritifera*) to a newly built nature-like fishway, we tested the compatibility of different brown trout (*Salmo trutta*) strains from local and foreign drainages as hosts for mussels taken from a nearby river system. The trout strains that were tested were a) a local sympatric wild strain (i.e. from the local drainage and sympatric with the mussel strain), b) a local allopatric wild strain in the vicinity of the fishway, c) a local allopatric hatchery strain used for compensatory stocking within the local drainage and d) a foreign allopatric hatchery strain from a distant drainage. Excluding the local sympatric wild strain, for which there were few survivors, there was no significant difference in infestation between the remaining three strains at forty days post infestation, suggesting that at this stage all trout strains

could act as hosts for the mussel. Glochidia on the local allopatric hatchery strain grew faster than glochidia from the other strains, which leads us to believe that this strain was the most suitable host, at least under laboratory conditions. Hatchery strains often have negative effects on ecosystems however, why using local wild fish presents an option that does not involve continued introductions of hatchery fish. In conclusion, it seems important to investigate the compatibility between mussels and potential host fish strains before reintroduction and stocking of fish or mussels in pearl mussel streams.

Introduction

Habitat restoration is a common action taken when attempting to preserve threatened aquatic organisms. If a certain strain has gone extinct before such restoration efforts are put into practice, reintroduction of a different strain can be the only viable option to repopulate a habitat (Griffith et al., 1989). Identifying the most suitable source strain for a reintroduction program is often based on ecological and genetic aspects of the candidate strains. If no such information is available for the candidates, the source strain geographically closest to the extinct strain is often chosen. For threatened species with a parasitic life stage, conservationists not only have to consider which strain to re-introduce, but also take into account the suitability of the available host strain to ensure a functional parasite-host interaction.

Freshwater mussels of the order Unionoida are one of the most threatened organism groups on earth (Richter et al., 1997), sometimes related to their obligate parasitic stage on one or more host fish species. After the larval parasitic stage, unionoid mussels become benthic filter-feeders (Bauer, 2001). In high-density, and healthy populations of mussels, their filter-feeding has been shown to have a fundamental impact on ecosystem function (Strayer, 2008). Reestablishment of threatened mussels can therefore both contribute to mussel conservation and restore ecosystem functions in freshwaters.

The freshwater pearl mussel, *Margaritifera margaritifera L.* (FPM) is a host specialist on salmonids and in Europe the host fish species are brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) (Young and Williams, 1984a). The FPM is decreasing in abundance and viability throughout its distribution (Young et al., 2001), and one reason for this decline has been attributed to high sedimentation (Osterling et al., 2008; Reid et al., 2013). A lack of viable host fish populations has however also been proposed as a threat to FPM recruitment (Arvidsson et al., 2012; Hastie and Cosgrove, 2001; Popov, 2017; Salonen et al., 2017). In fact, salmonid densities are decreasing in several European countries (Burkhardt-Holm et al., 2002; Butler and Walker, 2006; Gargan et al., 2006; Parrish et al., 1998; Poulet et al., 2011), and this decline has been attributed to the presence of migration barriers (Parrish et al., 1998), overfishing (Popov, 2017), pollution (Parrish et al., 1998), and infection by salmon lice (Thorstad et al., 2015).

The release of hatchery-reared salmonids is a common course of action to compensate for loss of natural fish reproduction and to support recreational or commercial fisheries (Cowx, 1999). This measure is however problematic as hatchery-reared fish have been shown to negatively affect wild stocks due to displacement (McMichael et al., 1999) and genetic contamination (Araki et al., 2007; Hansen and Loeschcke, 1994). Release of hatchery fish also has the potential to affect FPM populations, because the performance of the FPM may differ between host fish strains (Osterling and Larsen, 2013; Taeubert et al., 2010).

In the River Dalälven catchment in south-central Sweden, FPM habitat was lost due to hydropower development. A nature-like fishway was built to compensate for the lost habitat, and the goal was to introduce FPM to the fishway, using mussels from a healthy population in a stream in the River Dalälven catchment. The natural colonization of brown trout in the fishway was slow due to low attraction efficiency. To create a self-sustaining FPM population in the artificial habitat therefore requires that one is able to identify a suitable host fish that can be introduced with the mussel. Several potential brown trout host strains have their origin in the River Dalälven catchment, but the most suitable trout strain has not been identified.

The aim of this study was to evaluate the host suitability of different brown trout strains for the FPM population selected for introduction to the nature-like fishway. Using wild trout for introduction programs could potentially have negative effects on the wild source populations, whereas using hatchery strains could, just as for foreign wild trout, result in a parasite-host mismatch. We thus wanted to compare the host suitability of wild and hatchery-reared trout strains from local and foreign catchments. The suitability of the wild host strain of brown trout living in sympatry with the mussels was compared to one wild allopatric trout strain living in the vicinity of the fishway and two allopatric hatchery trout strains from the local and a foreign catchment.

Materials and methods

Mussel and fish origin

In this study, we conducted an infestation experiment using FPM from the River Tansån, situated in the River Dalälven catchment, and three trout strains from this local catchment and one trout strain from a foreign catchment, the Göta älv catchment (Fig. 1). The trout strains that we used were:

1) a local sympatric wild strain (River Tansån)

2) a local allopatric wild strain (River Trettonjällbäcken from the River Dalälven catchment, situated near the fishway)

3) a local allopatric hatchery strain (Lake Siljan, used for compensatory stocking within the River Dalälven catchment)

4) a foreign allopatric hatchery strain from a different catchment (River Gullspång/Lake Vänern).
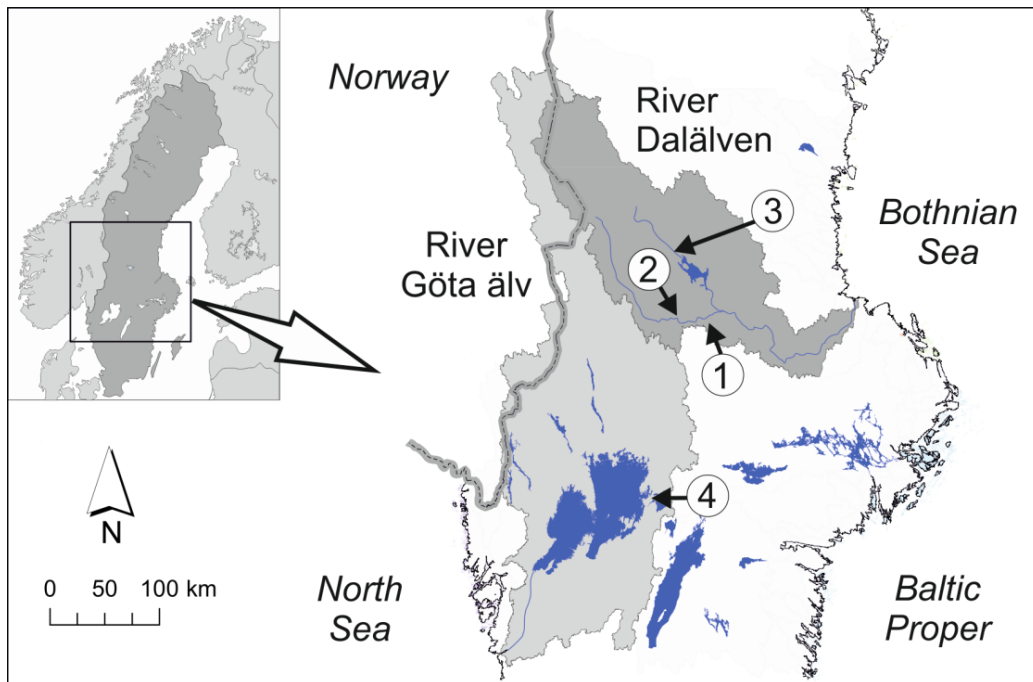
Figure 1. Fish origin. (1) River Tansån, (2) River Trettonjällbäcken, (3) Lake Siljan and (4) River Gullspång.

Adult FPMs were monitored for gravidity in River Tansån during July and August 2014. The mussels were carefully opened approximately 1 cm using specially manufactured tongs and their marsupiums were visually inspected for glochidia (Osterling et al., 2008). When the mussels were classified as mature, ten mussels were transported to the aquaria facility at Karlstad University, where they were placed in 10 L aerated containers. Once the glochidia had been released, the adult mussels were returned to their native stream.

Wild YOY brown trout were caught by electrofishing (LUGAB, L1000, Sweden) in August 2014. The two hatchery-strains (YOY) were provided by the Sävenfors hatchery. The trout were brought to the lab for testing, and after the experiments were completed the fish were euthanized according to the requirements of the ethical permits (Dnr 88-2013, approved by the ethical committee of Göteborg).

Study design and data anlysis

On 5 September, glochidia larvae from four mussels were collected. Larval viability, indicated by valve closure, was tested by adding a grain of salt to glochidia subsamples (Coker et al., 1921). A well-mixed suspension of glochidia from the four FPM individuals was used during the infestation on 5-6 September 2014. The glochidia were put in 10 L containers at a concentration of 25 000 larvae L^{-1}, whereupon fish were carefully put in the containers and were exposed to the suspension for 45 minutes. After infestation, trout were moved to 100 L aquaria (local sympatric wild strain and local allopatric wild strain, N = 4 aquaria; local allopatric hatchery strain and foreign allopatric hatchery strain, N = 8 aquaria). The water was constantly filtered (EHEIM 2215 filter) and approximately half of the water in the aquaria was replaced with fresh water twice a week. Fish were fed with commercial fish food pellets twice a week (2% of body weight) and with red chironomids once a week (10% of body weight). Water temperature was measured four times a week (except for one week when temperature was measured twice), and was 17.2 +/- 0.85 °C for the entire study period. The sum of degree days did not differ between the fish strains ($X2(3)$ = 2.51, p = 0.473). Dead fish were recorded and removed from the tanks. The low survival rate of the local sympatric wild strain could not be explained by any observed technical problems, whereas pump failure causing oxygen depletion in two aquaria was responsible for 35% (local allopatric wild strain, N = 6) and 17% (foreign allopatric hatchery strain, N = 9) of the mortalities in the hatchery strains.

Fish were removed from the tanks and exposed to an overdose of Benzocaine 1, 3 and 40 days post infestation (dpi). The sum of day degrees was 654 +/- 16 °C at 40 dpi, which places the larvae at a developmental stage between the early sloughing of glochidia by unsuitable hosts (Osterling and Larsen, 2013; Taeubert et al., 2010) and the excystment of juvenile mussels at 1300-3440 day degrees (Hruska, 1992; Taeubert et al., 2013). Statistical testing of fish from the local sympatric wild strain was only possible for the early sampling occasions, due to few fish surviving until the end of the study. The number of fish that were removed was N = 10 from each strain at 1dpi, N = 10 from each

strain at 3 dpi and N = 28 for the local allopatric wild strain, the local allopatric hatchery strain, and the foreign allopatric hatchery strain at 40 dpi. All fish were weighed (+/- 0.01g) and measured (+/- 1mm) and immediately stored in 70% ethanol prior to examination of the gills. The condition factor of the fish were calculated as $C = w*100/l\,{}^3$, where w = weight in gram and l = length in cm.

Fish from the local allopatric hatchery strain weighed significantly more ($X2(3) = 41.65$, $p < 0.0001$; Dunn test, $p < 0.0001$) than fish from the local sympatric wild strain, local allopatric wild strain (Dunn test, $p < 0.0001$) and foreign allopatric hatchery strain (Dunn test, $p = 0.007$). The foreign allopatric hatchery strain also weighed more than fish from the local allopatric wild strain (Dunn test, $p = 0.034$). Fish from the local allopatric hatchery strain had a significantly higher condition factor (ANOVA $F(3,79) = 37.69$, $p < 0.0001$; Tukey, $p < 0.0001$) than fish from the other strains. Fish from the foreign allopatric hatchery strain had a significantly higher condition factor than fish from the local sympatric wild strain (Tukey, $p = 0.033$).

The four gill arches on the right side of each fish were removed using tweezers and scissors and the number of glochidia were counted under a stereo microscope (Nikon, SMZ 745T, Tokyo, Japan). As an earlier study has shown that the number of glochidia does not differ significantly between gill arches on the left and right side (Taeubert et al., 2010), this number was multiplied by two to get the total number of glochidia per fish individual. However, if the number of glochidia on the right side of the fish was zero, the gill arches on the left side of the fish were also examined. The prevalence of glochidia infestation on each trout strain was calculated by dividing the number of infested fish by the total number of fish. A Generalized Linear Model (GLM) assuming a binomial error distribution and a logit link function was used to test if there was a difference in prevalence between the fish strains at 40 dpi. Due to differences in individual fish size, the weight normalized glochidia abundance, i.e. the number of glochidia larvae per gram fish, was calculated. Differences in the number of glochidia per fish and the weight normalized glochidia abundance between brown trout strains were analyzed with two-way ANOVAs with 'brown trout strain' and 'time' as

factors. The two sampling occasions 1 dpi and 3 dpi were pooled (hereafter referred to as 'early sampling occasion') to be compared to sampling at 40 dpi (hereafter referred to as 'late sampling occasion'). Mean values of glochidia abundance were calculated for each aquaria, and the data were therefore considered normally distributed (Underwood, 1991). The correlations between glochidia abundance and fish weight and condition factor were tested using Spearman's rank-order correlation coefficient.

To study the glochidia growth on the different fish strains, the diameter of encapsulated larvae was measured (+/- 1µm) at the early and the late sampling occasion. Glochidia were examined at 50 x magnification with a stereomicroscope (Nikon, SMZ 745T, Tokyo, Japan) connected to a computer using the software INFINITY ANALYZE (Lumenera Corporation, Ottawa, Canada). Gills from ten fish from each strain were examined at each sampling and the number of glochidia measured was N= 400 at the early sampling occasion and N= 288 at the late sampling occasion. Differences in initial mean glochidia size on individual fish between the fish strains was calculated using an ANOVA with mean glochidia size per fish as the dependent variable and 'brown trout strain' as the independent variable. The factor 'aquarium' was nested within the factor fish strain to account for fish being kept in different aquaria. Differences in glochidia size between the local allopatric wild strain, the local allopatric hatchery strain, and the foreign allopatric hatchery strain were analyzed with a two-way ANOVA with 'brown trout strain' and 'time' as factors. Mean values of glochidia size were calculated for each aquaria, and the data were therefore considered normally distributed (Underwood, 1991). The relationships between glochidia size at the late sampling occasion and fish weight were tested using Spearman rank correlation. To find out if there was a correlation between high glochidia abundance and glochidia growth, the mean glochidia size and the glochidia abundance at the late sampling occasion was tested using a Spearman rank-order correlation. IBM SPSS statistics version 22.0.0.1. was used for statistical tests and square root transformations were applied to improve normality and homogeneity of variances when required.

Results

Glochidia abundance

Every inspected brown trout individual was infested with glochidia during the early sampling occasion. Excluding fish removed as part of the experimental procedure, the survival during the study period was 6% for the local sympatric wild strain, 68% for the local allopatric wild strain, 83% for the local allopatric hatchery strain, and 61% for the foreign allopatric hatchery strain. The prevalence of glochidia infestation was 67% for the local sympatric wild strain, 64% for the local allopatric wild strain, 54% for the local allopatric hatchery strain and 79% for the foreign allopatric hatchery strain at the late sampling occasion. Excluding the local sympatric wild strain, for which there were few survivors, there was no effect of fish origin on prevalence of glochidia at the late sampling occasion (GLM: Wald X^2 = 3.76, df = 2, p = 0.153).

Due to low survival, the local sympatric wild strain was excluded from statistical testing of differences in glochidia abundance per fish and weight normalized glochidia abundance. Glochidia abundance per fish between the local allopatric wild strain, local allopatric hatchery strain and foreign allopatric hatchery strain changed over time, revealed by the significant interaction between 'time' and 'fish strain' (Two-way ANOVA F (2,25) = 5.54, p = 0.010) (Fig. 2). Fish from the local allopatric hatchery strain had significantly more glochidia per fish at the early sampling compared to the local allopatric wild strain (ANOVA F (2,13) = 18.32, p < 0.0001; Tukey, p = 0.001) and the foregin allopatric hatchery strain (Tukey, p = 0.001). There were however no significant differences in glochidia abundance per fish between the trout strains at the late sampling (ANOVA F (2,12) = 1.51, p = 0.261).

Weight normalized glochidia abundance was significantly higher at the early sampling compared to the late sampling (Two-way ANOVA F (1,25) = 105.62, p < 0.0001). There was however, no significant effect of fish strain (p = 0.412) or the interaction between time and fish strain (p = 0.228) on the weight normalized glochidia abundance (Fig 2).
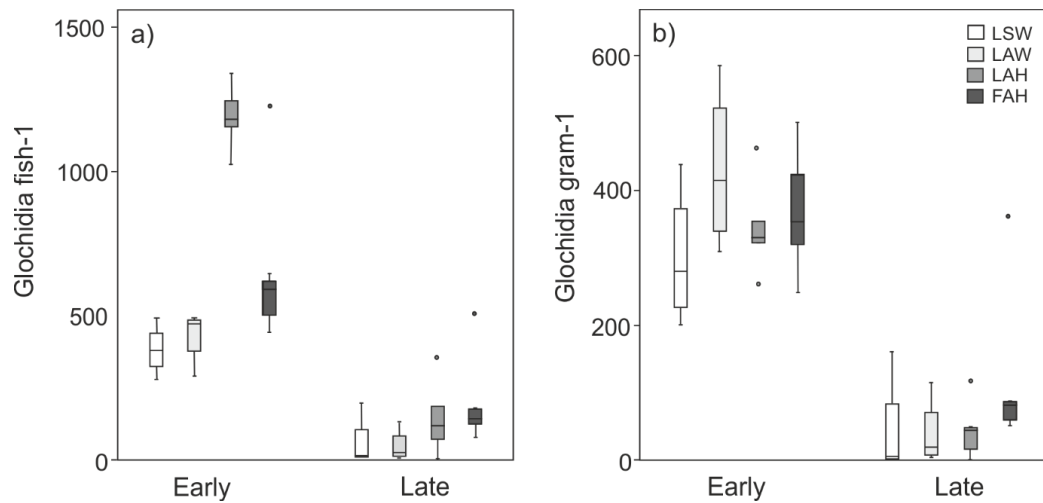
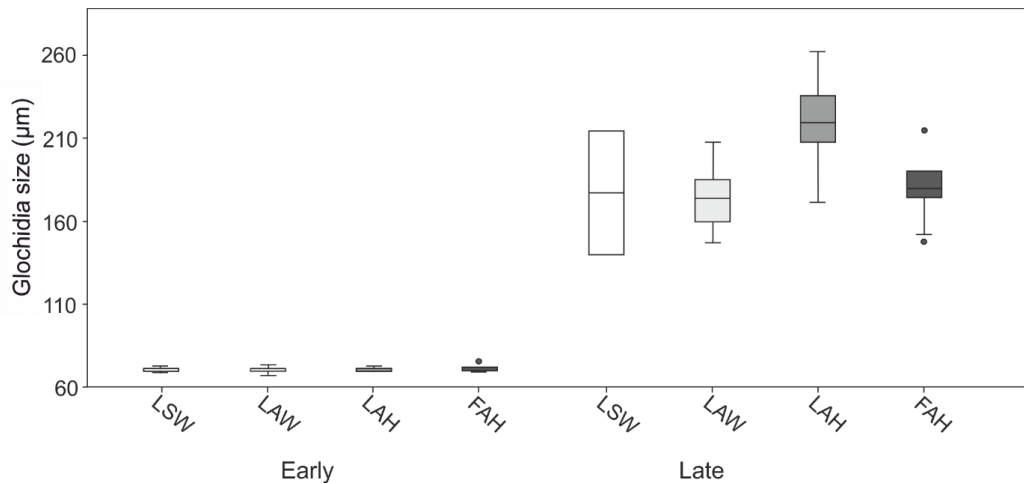Figure 2. a) Glochidia abundance per fish and b) weight normalized glochidia abundance at the early and the late sampling occasions. Boxes depict the 75 and 25 percentiles and the vertical lines within each box the medians. Abbreviations: LSW = local sympatric wild, LAW = local allopatric wild, LAH = local allopatric hatchery and FAH = foreign allopatric hatchery.

There was a positive association between the glochidia abundance per fish and fish weight ($r_s = 0.70$, $p < 0.0001$) and the glochidia abundance per fish and condition factor at the early sampling occasion ($r_s = 0.52$, $p < 0.0001$). There was no association between glochidia abundance per fish and fish weight ($r_s = 0.22$, $p = 0.216$) or fish condition factor ($r_s = 0.12$, $p = 0.497$; Fig 3) at the late sampling occasion.
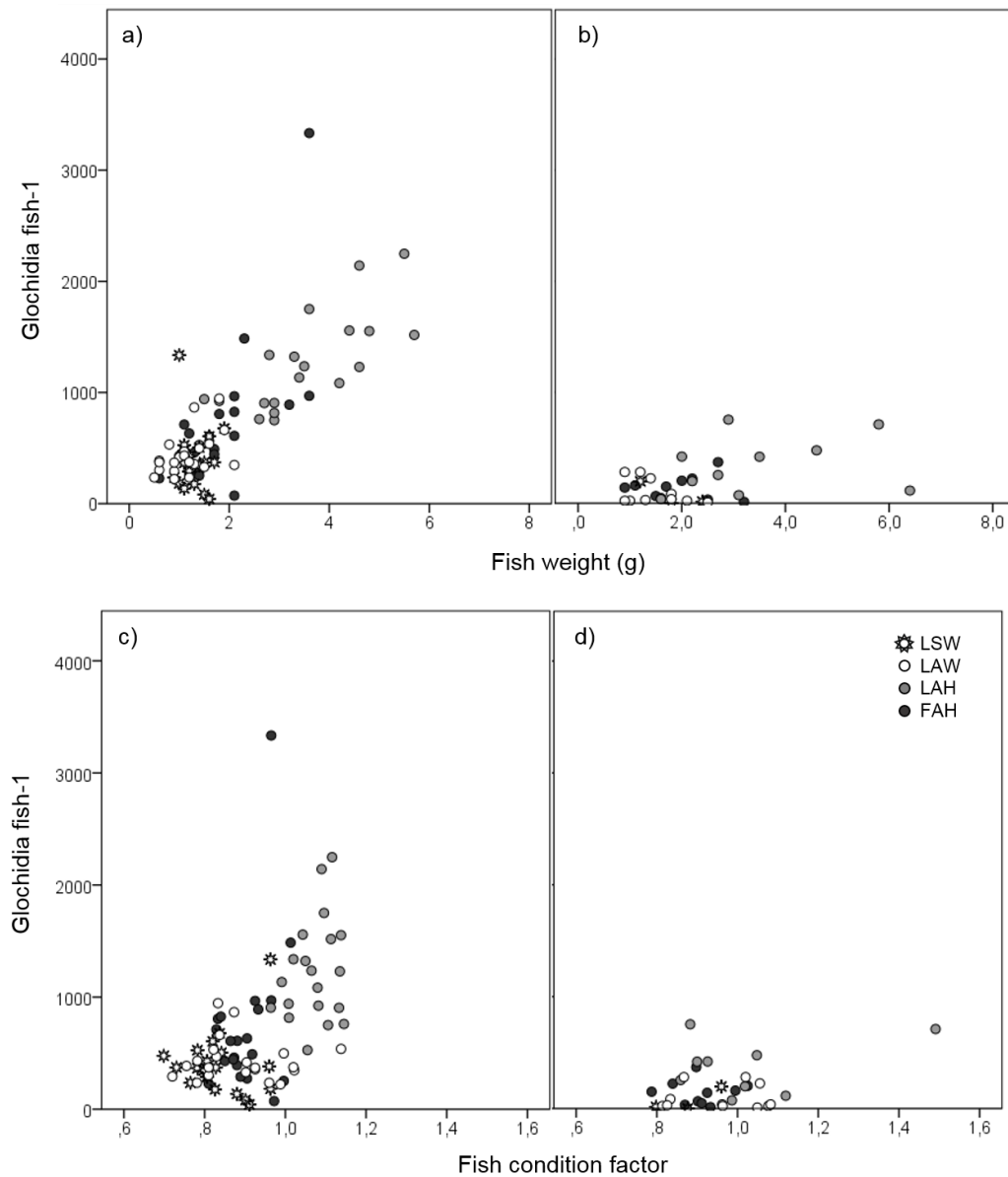
Figure 3. Scatter plot of glochidia abundance per fish and fish weight during the a) early sampling occasion and the b) late sampling occasion and number of glochidia per fish and fish condition factor during the c) early sampling occasion and the d) late sampling occasion. Abbreviations: LSW = local sympatric wild, LAW = local allopatric wild, LAH = local allopatric hatchery and FAH = foreign allopatric hatchery.

Glochidia size

The glochidia did not differ significantly in size between the four trout strains at the early occasion (ANOVA $F_{(3,20)} = 0.74$, $p = 0.538$). The size of the glochidia on fish from the local allopatric wild strain, the local allopatric hatchery strain, and the foreign allopatric hatchery strain

changed over time, revealed by a significant interaction between 'time' and 'fish strain' (Two-way ANOVA $F_{(2,22)}$ = 41.2, p < 0.0001). At the late sampling occasion, glochidia on the local allopatric hatchery strain were significantly larger than glochidia on the local allopatric wild strain and the foreign allopatric hatchery strain (ANOVA $F_{(2,9)}$ = 31.4, p < 0.0001; Tukey, (p < 0.0001; Fig 4).

Figure 4. Glochidia size on different fish strains at the early and the late sampling occasions. Boxes depict the 75 and 25 percentiles and the vertical lines within each box the medians. Abbreviations: LSW = local sympatric wild, LAW = local allopatric wild, LAH = local allopatric hatchery and FAH = foreign allopatric hatchery. The estimate of glochidia size for LSW at the late sampling is only based on two fish and was therefore excluded from statistical testing.

Overall, there was a positive relationship between mean glochidia size and glochidia abundance per fish for the local allopatric wild strain, the local allopatric hatchery strain, and the foreign allopatric hatchery strain at the late sampling occasion (r_s = 0.76, p < 0.0001). When testing the fish strains separately no relationship between glochidia size and glochidia abundance per fish could be found for the local allopatric wild strain (r_s = 0.36, p = 0.311), but there was a positive relationship between glochidia size and glochidia abundance per fish for the local allopatric hatchery strain (r_s = 0.69, p = 0.026) and the foreign allopatric hatchery strain (r_s = 0.867, p = 0.001). No overall relationship between mean glochidia size and fish weight could be seen (r_s = 0.77, p = 0.328). Separating the fish strains, there was a negative relationship between mean glochidia size

and fish weight for the local allopatric wild strain (rs = -0.73, p = 0.018), a positive relationship between glochidia size and fish weight for the local allopatric hatchery strain (rs = 0.72, p = 0.020), while there was no relationship between glochidia size and fish weight for the foreign allopatric hatchery strain (rs = -0.91, p =0.803) (Fig. 5).

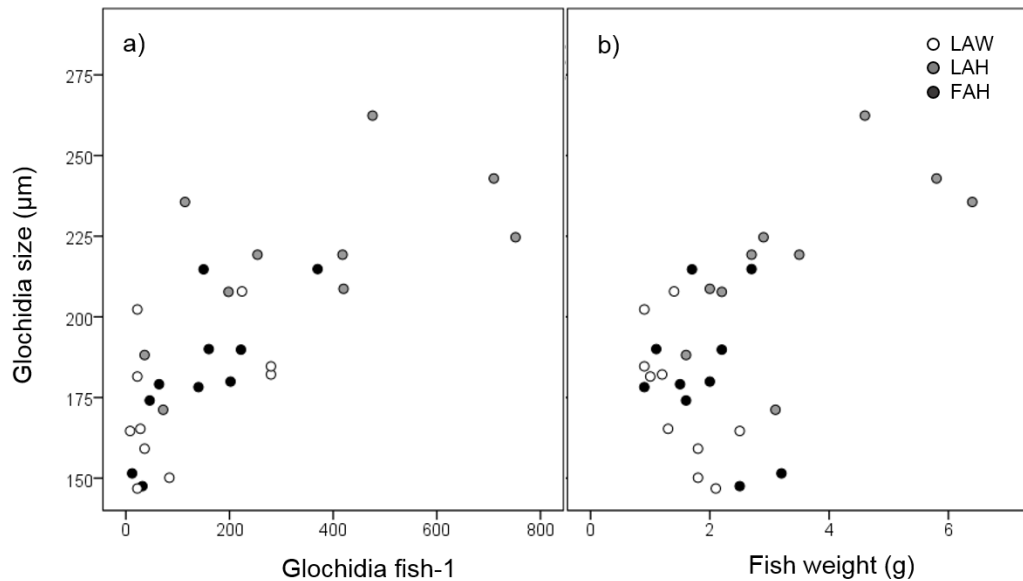Figure 5. Scatter plot of glochidia size at the late sampling and a) glochidia abundance per fish and b) fish weight.

Discussion

Our study provides information on the host suitability of four brown trout strains for FPM larvae, with implications for conservation. Both wild and hatchery trout strains were successfully infested with glochidia and no difference in prevalence of glochidia infestation could be seen at the early sampling occasion (1-3 days post infestation, dpi). The natural host of the studied mussel strain, i.e. the local sympatric wild trout strain, suffered high mortalities shortly after infestation, but no difference in glochidia abundance could be seen between the remaining three strains at the late sampling occasion (40 dpi). This suggests that local allopatric wild trout can support mussel introductions. Moreover, our results suggest that

local and foreign hatchery strains may be used to supplement FPM streams where local wild trout populations have disappeared. The largest glochidia were found on the local allopatric hatchery strain, indicating that this strain is the most suitable host. Hatchery fish with a high glochidia abundance at the late sampling occasion had the largest glochidia, which leads us to believe that suitable host fish have the potential to produce high numbers of large mussels with a high survival. Our results have implications for management strategies, such as when planning to introduce mussels or trout into streams and when culturing juvenile mussels for reintroduction.

Glochidia abundance

We found no differences in weight normalized glochidia abundance among the trout strains at the early or at the late sampling occasion, indicating that suitability did not differ among the strains. The local allopatric hatchery strain had however more glochidia per fish than the local allopatric wild strain and the foreign allopatric hatchery strain at the early sampling occasion. Fish from the local allopatric hatchery strain were significantly larger than fish from the other strains and a positive relationship between fish size and early glochidia abundance has been found in previous studies as well (Hastie and Young, 2001; Taeubert et al., 2010; Thomas et al., 2014). This has been suggested to be caused by the fact that large fish has larger gill surface area and higher ventilation rate, which result in higher glochidia attachments (Young and Williams, 1984b). Larval infestation decreased over time on all trout strains, as reported for suitable fish hosts in previous field (Hastie and Young, 2001) and laboratory-based studies (Osterling and Larsen, 2013). The positive relationship between host body size and glochidia abundance per fish was transitory as no significant effect of body size could be found at the late sampling, possibly caused by a stronger immune response by larger fish (Hastie and Young, 2001; Thomas et al., 2014).

Glochidia size

The glochidia grew significantly faster on the local allopatric hatchery strain than the other strains. This indicates that the numbers of juvenile

recruits will be highest from the local allopatric hatchery strain, at least under laboratory conditions, as shell length has been suggested to be a good indicator of overwinter survival for juvenile mussels (Denic et al., 2015). The higher growth rate may be a result of the higher condition factor of the local allopatric hatchery strain, where the glochidia larvae may benefit from a host with a high nutritional supply (Osterling and Larsen, 2013). There was also a positive relationship between fish weight and glochidia size for this strain, indicating that large fish from this strain represent better hosts.

Management implications

Our results show that FPM infestation was successful for all brown trout strains, including even the hatchery strain originating from a foreign catchment, indicating that non-local hatchery strains could be used as supplement in FPM streams where local trout populations have been depleted. This pattern could however also be strain-specific and should hence be interpreted with caution, especially since we tested only one foreign strain. Glochidia abundance was also in general independent of fish size for late glochidia infestation. Screening for large fish for artificial mussel infestation and propagation to attain a high number of juvenile mussels thus seems unnecessary. Glochidia did however grow faster on large fish of the local allopatric hatchery strain, potentially with higher chances of over-winter survival. The opposite trend was found for infested fish from the local allopatric wild strain in the vicinity of the fishway. It is therefore recommended that infestation tests using different fish strains is performed in an effort to find a suitable host before mussel propagation begins.

Fish from the hatchery strains with high glochidia abundance at the late sampling occasion were more likely to have larger glochidia, indicating that suitable host fish do not only carry more mussels, the mussels also grow faster on these fish. Using individuals from hatchery strains with many fast growing glochidia may thus be a cost-effective alternative for mussel propagation. Previous studies have, however, shown that high glochidia abundance might have deleterious effects on the host's respiratory performance (Thomas et al. 2014) and drift feeding efficiency

(Österling et al. 2014). Attaining a high number of glochidia per fish might therefore not always result in the highest juvenile mussel production. Finding an intermediate glochidia load suitable for both parasite and host should thus be the goal. Previous studies have reached different conclusions regarding patterns of local adaptation between the FPM and their sympatric host fish strain (Bauer and Vogel, 1987; Osterling and Larsen, 2013; Taeubert et al., 2010). Fish from the local sympatric wild strain in this study did not cope well in the laboratory environment, and as a result artificial infestation of fish from this strain cannot be recommended based on this single experiment. High numbers of trout from wild strains tolerant to artificial infestations in laboratory conditions are however needed to produce juvenile mussels. It may thus not be sustainable to use fish from FPM streams with weak stocks of trout, especially as only about 5-10% of the infested glochidia will metamorphose (Hastie and Young, 2003; Young and Williams, 1984a) and the survival of juvenile mussels is low (Reid et al., 2013; Young and Williams, 1984a).

The hatchery trout and one wild trout strain had a relatively high survival in the aquaria environment in this study. Hatchery-raised strains are often easy to attain in high numbers, while wild strains are often found in low numbers. If hatchery trout are normally used for compensatory stocking, one option is to infest them with FPM larvae before they are released into streams. Currently, fish from the local allopatric hatchery strain are used for compensatory stocking near the fishway, and as larvae grew fast on the fish from this strain they may de facto constitute a functioning host for FPM from Tansån. One potential problem that needs to be addressed in future studies is survival of these hatchery-raised fish in the field. This is because survival of released hatchery fish is generally low (Einum and Fleming, 2001), and since juvenile mussels are released from the host fish after ten to twelve months, low winter survival of the fish may result in low mussel recruitment. In addition, stocking of hatchery fish is problematic and several studies have shown negative effects on wild populations caused by displacement, competition, increased predation and genetic contamination (Kostow, 2009; McMichael et al., 1999; Reisenbichler and Rubin, 1999). As fish from the local wild allopatric trout strain in our study were also found to be

suitable hosts for the FPM, infesting this strain or letting them be naturally infested by introduced adult mussels, presents options that does not involve continued introductions of hatchery fish.

Acknowledgements

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Paper 4

Brown trout *(Salmo trutta)* habitat choice: relative importance of woody debris ad river morphology in nature-like fishways

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Abstract

Brown trout *(Salmo trutta)* habitat choice was studied in a nature-like, bypass fishway containing four different habitat types, namely pools, riffles, floodplains and braided habitats. Constructing a fishway with different habitats was done to enhance biodiversity as well as to create habitat for freshwater pearl mussels and brown trout. To each habitat type, large woody debris (LWD) was added at no, low or high densities, and the effects on brown trout habitat choice were evaluated. Our results showed that the addition of a high density of LWD had a positive effect on the abundance of brown trout, as well as the probability that fish remained in the experimental stream section into which it was released. Based on electrofishing, we found that the trout were distributed relatively evenly among the riffle, braided and floodplain habitat types, whereas use of the pool habitats was less common. Fish occupied areas with a mean velocity of 0.57 ± 0.25 m/s and a mean depth of 42.3 ± 15.6 cm. They also preferred areas with high shelter availability and large substrate sizes to a greater extent than expected based on availability in

the fishway. In conclusion, the addition of boulder substrate and high densities of LWD to nature-like fishways may be an easy and relatively inexpensive way of improving habitat function for brown trout.

Introduction

Habitat degradation and loss has been highlighted as one of the most serious threats to biodiversity in freshwater systems (Allan and Flecker 1993; Dudgeon et al. 2006). Humans have extensively manipulated rivers for transport, agriculture and power generation (Cowx and Welcomme 1998), and according to the Millennium Ecosystem Assessment (2005), between three to six times as much water is being stored behind large dams, compared to what is freely flowing in our rivers.

In an effort to mitigate some of the damage done, stream restoration has been widely practiced, and substantial amounts of money have been spent on improving habitat composition in streams and rivers (Bernhardt et al. 2005; Jähnig et al. 2011; Wohl et al. 2005; Wohl et al. 2015). A majority of stream restoration efforts consists of physical manipulations of the channel, such as re-meandering or improving in-stream structures, often with the goal of increasing biodiversity, stabilizing channels, and improving habitat and water quality (Palmer et al. 2014). Meta-studies of stream restoration efforts have, however, shown that habitat improvements do not necessarily lead to recovery of ecological communities (Jähnig et al. 2010; Leps et al. 2016; Nilsson et al. 2015; Palmer et al. 2010). Existing success stories (e.g. Baldigo et al. 2010; Langler and Smith 2001), coupled with increased knowledge about effective measures, the monetary gain to private actors, and the will of the public and government to continue making remedial measures in degraded streams, does nevertheless suggest that habitat restoration will remain an important restoration approach (Bernhardt et al. 2005; Nakamura et al. 2006; Palmer et al. 2005).

In areas where habitat restoration is no longer possible, for example following road construction, forestry and mining, and where there

consequently is no habitat left to restore, one remedial action may be the construction of new habitat (Jones et al. 2017). When constructing new habitat it can be created to meet the requirements of target species or of specific species' life stages. Examples of habitat compensation in freshwater systems can be found in Canada. Here spawning habitats, rearing habitats and habitats for older fish (Jones et al. 2003; Scruton 1996; Scruton et al. 2005) have been constructed to sustain fish production in an effort to meet the goal of 'no net loss of habitat productive capacity', an aim that has been active in Canada since 1986 (DFO 1986).

Nature-like fishways have become increasingly popular and represent the fishway type most constructed in Sweden during the last 15 years (Nöbelin 2014). The construction of nature-like fishways that mimic natural streams, opens the opportunity to combine new habitat with passage solutions to allow fish to pass dams. Most studies of nature-like fishways have focused on evaluating passage performance (Aarestrup et al. 2003; Eberstaller et al. 1998; Mader et al. 1998), and the use of nature-like fishways as spawning or rearing habitats by fish has not been the focus of much research (Calles and Greenberg 2007; Jansen et al. 1999; Jungwirth 1996).

In Eldforsen in South central Sweden, a 500 m long nature-like bypass channel with high habitat heterogeneity was constructed in 2009. The aim was to create a fishway that had the potential to promote high biodiversity (Gustafsson et al. 2013), and to contain habitats for the threatened freshwater pearl mussel (*Margaritifera margaritifera*) and their host fish, the brown trout (*Salmo trutta*), while facilitating passage past the Eldforsen hydroelectric dam. To achieve this multi-purpose functionality, the fishway was designed with four habitat types, namely 'pool', 'riffle', 'floodplain' and 'braided' habitats, providing a more diverse physical habitat and wider channel compared to what is found in many conventional nature-like fishways. Hence, construction costs, including workload and material costs, were higher in comparison to constructing a conventional nature-like fishway, and moreover more water must be taken from the dam due to the wide channel. A more cost-effective way of achieving increased habitat functionality may be through the addition of

large woody debris (LWD) to nature-like fishways. Several studies have shown that LWD has a positive effect on salmonid abundance as it provides shelter (Fausch and Northcote 1992) and leads to increased food availability (Benke and Wallace 2003; Gustafsson et al. 2014). Therefore, we added LWD in three different densities to the fishway, (one replicate of each habitat-LWD combination) and investigated its effects on brown trout in terms of habitat choice and abundance.

Materials and methods

Study area

The Eldbäcken biocanal (WGS84 (60.436013, 14.229297)) is a nature-like fishway, constructed in 2009 in the River Västerdalälven system, Sweden (Fig.1). It was built to compensate for habitat lost due to the construction of a hydroelectric dam at Eldforsen, and to allow fish to pass the dam. The biocanal was created according to the philosophy of physiomimesi (Katopodis et al., 2001), and thus resembles a natural stream. It has a total length of 500 m and a head of 5 m, resulting in a gradient of 1%. The bottom of the fishway contains natural substrate of various sizes and the intake of the biocanal is constructed to allow for a variable flow regime. During the study period the discharge was set to approximately 780 L s^{-1}. To compensate for lost habitat suitable for the freshwater pearl mussel and its host fish, the brown trout, as well as to improve aquatic biodiversity in general, four habitat types were constructed within the biocanal:

1) Pools with deep and slow-flowing water.
2) Floodplains with a winding channel and a diverse substrate.
3) Braided habitats, where the flow has been diverted into two channels separated by islands.
4) Riffles with a straight channel and high water velocity, constructed to resemble the often homogenous construction of conventional nature-like fishways.

Each habitat type is replicated three times, resulting in a total of twelve 18 m long experimental stream sections. These were separated by buffer zones identical in design to the riffles but hereafter referred to as 'buffers'. Prior to this study, large woody debris (LWD) was added at three different densities to the experimental stream sections according to a randomized block design. The LWD concentrations were:

1) No LWD
2) Low density of LWD, representing the situation in a stream running through a forest affected by modern Swedish forestry (24.8 m³/ha).
3) High density of LWD, representing the situation in a stream running through a forest in a nature reserve, or an area not affected by modern forestry (98 m³/ha).
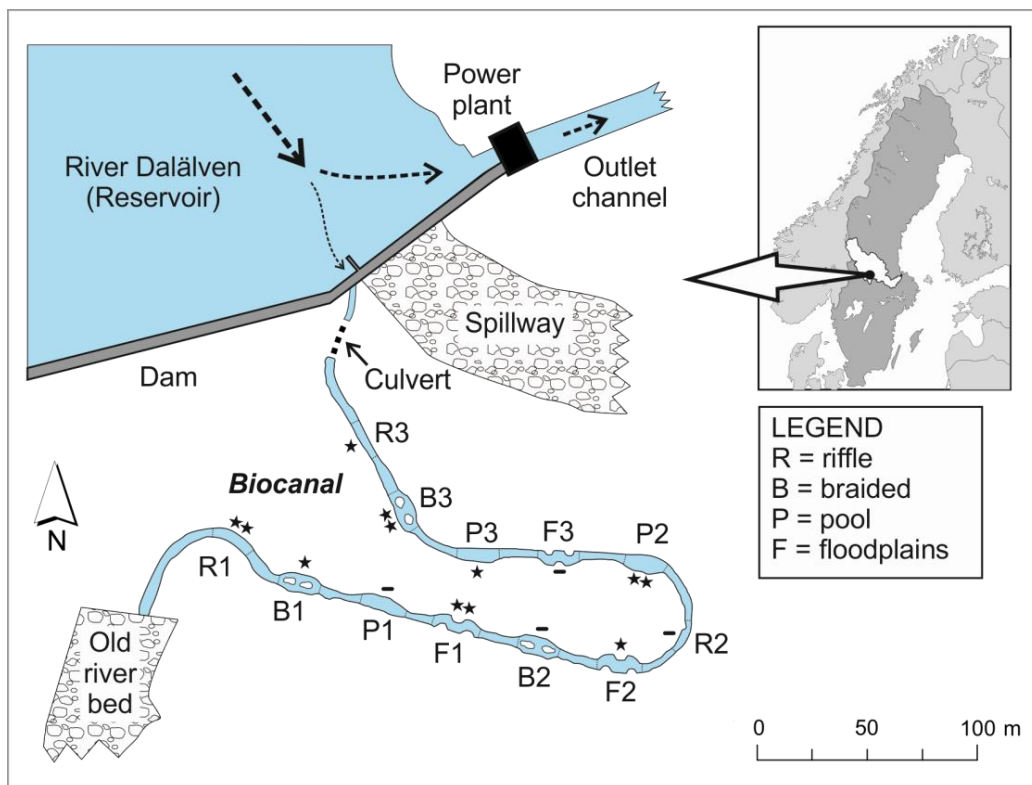
Figure 1. The biocanal with its habitat types (riffle, braided, pool and floodplain) and LWD treatments (**-** = no wood, one star = low density of wood (24.8 m3/ha) and two stars = high density of wood (98 m3/ha)).

Field studies

The biocanal was electrofished before the study to remove as many predators, mainly pike and burbot, as possible. The fish used in the experiment was 1+ trout from the Lake Siljan strain, provided by the Särna hatchery. This is the fish strain commonly used for compensatory stocking in the area. Fish were individually measured (average total length: 117 ± 12 mm), weighed (average weight: 19 ± 6 g) and tagged with 12 mm HDX passive integrated transponder tags (PIT-tag; Texas instruments, Texas, USA) in their body cavity. Ten fish were released in each experimental stream section on four occasions (August 11, August 20, September 1 and September 15 2015). After the first fish release, the densities of trout in the experimental stream sections were 10.8 ± 2.9 trout/100 m^2, on average, which is comparable to natural densities in the region (9 ± 3.4 trout/100 m^2, data obtained from the Swedish Electrofishing RegiSter, SERS). To prevent fish from escaping the study site, fyke-nets were placed at the upper- and lower part of the biocanal. Fish caught in the fyke-nets were considered having left the fishway and were removed from the study. After each fish release, trout were left in the fishway for 6-7 days, allowing them to settle, before electrofishing (flat DC, LUGAB, L1000, Sweden) on 17 August, 26 August, 8 September and 21 September 2015*.*

The position of the fish was estimated using a portable PIT-tag antenna (LF HDX RFID backpack reader with pole antenna; Oregon RFID, Portland, USA) before the electrofishing on 8 September and 21 September 2015. For the position of fish detected by the portable antenna (N=87), water depth was immediately measured. Water velocity, substrate composition (see Gustafsson et al. 2012) and access to shelter (number of interstitial spaces > 10 cm deep, measured using a 13-mm tube, similar to the method described in Finstad et al. (2007)) was measured at each fish position after electrofishing had been completed to minimize disturbance to the fish. In addition, water velocity, water depth, substrate diversity and access to shelter was measured at ten randomly selected positions in each experimental stream section and each buffer within the biocanal.

Statistical analyses

Fish collected on all sampling dates were pooled, the same applies for fish positioning. To test whether the fish were randomly distributed between the experimental stream sections a Fisher's Exact test was used (Kirkman 1996). To find out whether the probability of a fish leaving the experimental stream section into which it was released was affected by habitat type, the amount of LWD in the experimental stream section, or release date, and the interaction between these factors, a Generalized Linear Model (GLM) assuming a binomial error distribution and a logit link function was performed. To test whether large fish were more inclined to stay in the experimental stream section into which it was released, an independent samples Mann-Whitney U-test was used to compare body length between staying and leaving fish individuals. To compare the number of fish caught in the experimental stream sections with the number of fish caught in the buffers an independent samples t-test was performed. Fish in proximity of the downstream fyke net were removed from testing as the placement of the fish trap may have influenced their habitat choice. IBM SPSS statistics version 22.0.0.1. was used for statistical testing. Trends in microhabitat preference of brown trout were examined using values for water velocity, depth, number of shelter and substrate composition from sites where trout had been positioned with the portable antennae. A Principal Components Analysis (PCA) was used to integrate information on trout microhabitat and the general habitat characteristics of the fishway into a minimum of dimensions using the CANOCO program for Windows, version 5.

Results

Of the 480 released brown trout, 257 were recaptured during the study (54% recapture). The majority were caught during electrofishing (N = 206; Fig. 2) and the remainder in the fyke-nets placed by the downstream (N = 50) and upstream (N = 1) ends of the fishway.
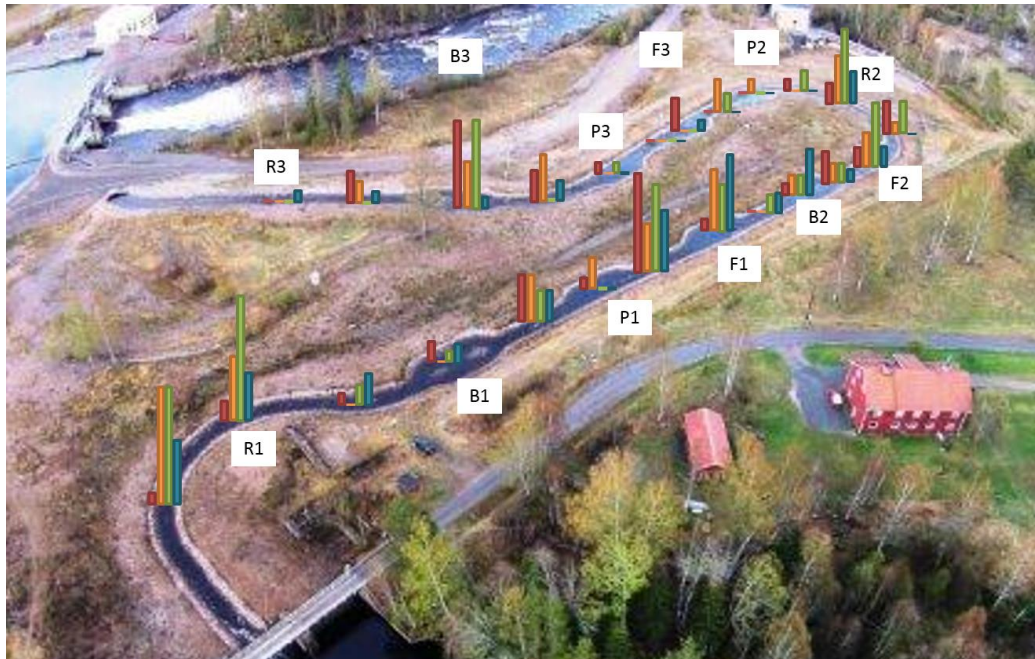
Figure 2. Number of fish caught during electrofishing 2015. Red bars August 17, orange bars August 26, green bars September 8 and blue bars September 21. Abbreviations; R = riffle, B = braided, P = pool, F = floodplain.

Fish caught in the experimental stream sections (N=110) were not randomly distributed between these (Fisher's Exact test, p < 0.001), but instead primarily selected experimental stream sections with high concentration of LWD (N = 58, 53%), followed by experimental stream sections without wood (N = 32, 29%) and experimental stream sections with low concentration of wood (N = 20, 18%; Fig. 3). Furthermore, tagged fish were more or less equally distributed between the habitat types riffle (35%), braided (30%) and floodplain (29%), whereas fewer fish were caught in the pool habitats (6%, Fig. 3).
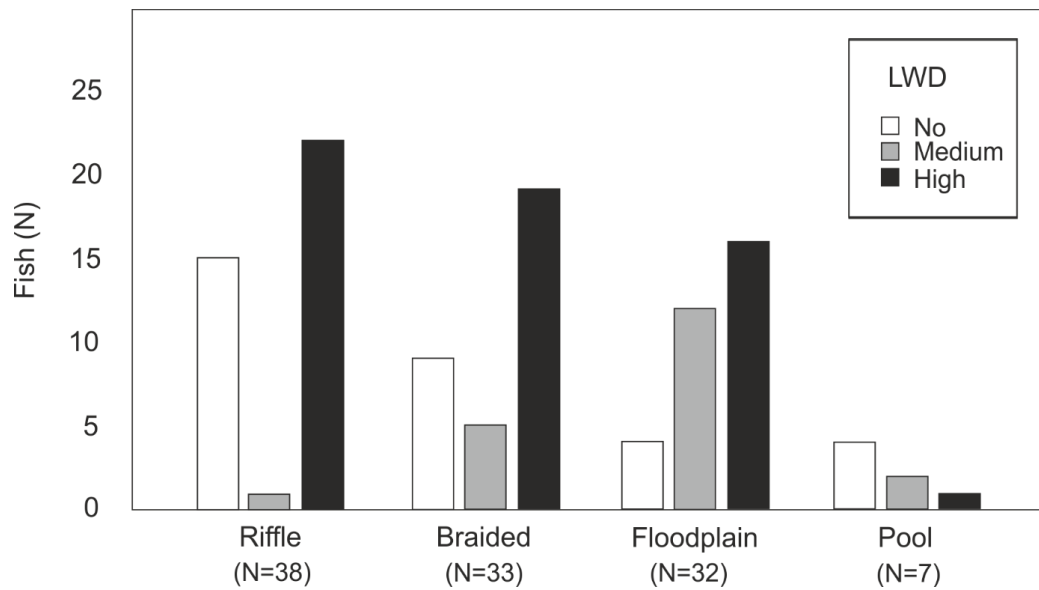
Figure 3. The number of fish caught in each habitat-LWD combination.

The majority of the fish (91%) left the experimental stream section they were released in, but the amount of wood still had a significant effect on the probability of a fish staying in the stream section it was released in (GLM: Wald X^2 = 12.421, df = 2, p = 0.002 (after removing the non-significant habitat type x LWD interaction term, Wald X^2 = 2.507, df = 2, p = 0.868, from the full model)). Release date (Wald X^2 = 2.684, df = 3, p = 0.443) and habitat type (Wald X^2 = 2.052, df = 3, p = 0.562) had no significant effect on probability of leaving. The 22 fish that did not leave the experimental stream section in which they were released were predominantly found in experimental stream sections with a high density of wood (68%), followed by experimental stream sections with a low density of wood (18%) and experimental stream sections without added wood (14%). The tendency to stay in the experimental stream section of release was not related to body length (U = 1722, p = 0.126). Fish that moved away from the experimental stream section of release mostly did so in a downstream direction (83%) and consequently the majority were recaptured downstream by electrofishing (N = 146) or in the downstream fyke-net (N = 50). The median distance from release site to recapture was 90 m, with the farthest distance travelled recorded for an individual released in the upstream riffle habitat (Fig. 2, R3) and recaptured in the fish trap approximately 430 m downstream.

The study fish were caught to the same extent in the experimental stream sections (N=110) compared to the buffers (N = 74; Fig. 2) (t(23) = 0.45, p = 0.660). In order not to lose valuable insights regarding the microhabitat preference of the trout, the buffers were included in the following statistical testing. As the buffers in the fishway were identical in design to the riffle habitats, these stream stretches are henceforth combined.

Table 1. General habitat characteristics of the habitat types in the biocanal. The riffle habitats and buffer habitats are pooled into the category riffle. Average values for depth, velocity, number of shelter and percentage substrate cover are given. ± indicates standard deviation.

Parameter	Braided (N=3)		Floodplain (N=3)		Pool (N=3)		Riffle (N=14)	
Depth (cm)	52.1	± 16.6	45.7	± 17.6	64.7	± 33.8	44.4	± 14.2
Velocity (m/s)	0.5	± 0.3	0.46	± 0.2	0.31	± 0.3	0.7	± 0.3
Shelter (N/m²)	5.6	± 5.4	7.8	± 6.6	9.7	± 7.8	7.9	± 7.1
Boulder (%)	46.9	± 25.1	40.6	± 29.6	30.6	± 23.2	43.2	± 25.7
Cobble (%)	42.7	± 23.9	40.0	± 23.2	51.7	± 30.9	47.5	± 25.1
Pebble (%)	10.0	± 15.3	11.5	± 19.4	16.7	± 26.5	8.5	± 12.8
Gravel (%)	0.4	± 1.6	3.8	± 7.4	0.2	± 1.1	0.6	± 3.0
Sand (%)	0.0	± 0.0	2.5	± 8.6	0.8	± 2.7	0.2	± 1.3
Organic (%)	0.0	± 0.0	1.7	± 9.1	0.0	± 0.0	0.0	± 0.0

On average, fish in the biocanal occupied areas with 11.2 ± 7.7 shelters/m², a mean velocity of 0.57 ± 0.25 m/s and a mean depth of 42.3 ± 15.6 cm. A PCA of the microhabitat used by brown trout and randomly placed samples representing average habitat characteristics of the biocanal, revealed that fish were found in areas with more shelters/m² and a higher proportion of boulder substrate than was found in general in the biocanal (Fig. 4).
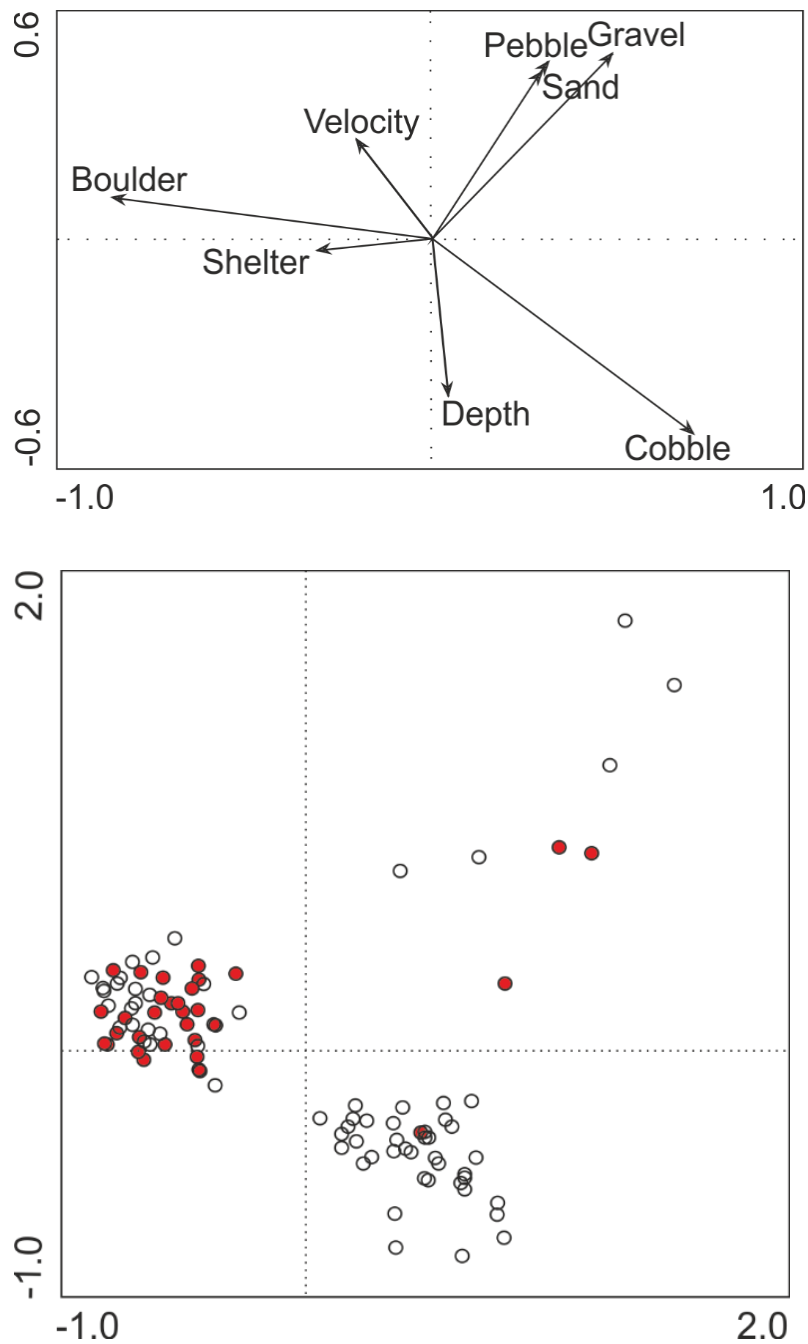
Figure 4. a) Principal Components Analysis (PCA) for seven physical traits of the microhabitat in the biocanal. Vectors point in the direction of increasing value, with length indicating the strength of the relationship. The first axis explains 23.5% of the variance and the second axis explains 16.0%. b) Plot of the factor scores for microhabitat observations. Each circle represents an individual sample. Filled circles represent fish positions whereas open circles represents random subsets.

Even though the biocanal was electrofished before the study to remove as many predators as possible, pike and burbot were still present. All burbots caught with a length exceeding 27 cm (N = 10) contained one tagged trout. In total 47 burbots and four pike were caught during the study.

Discussion

Our results indicate that high densities of LWD increase the probability of brown trout release site fidelity, while habitat composition in general has no such effect. The fish that were caught during electrofishing were distributed relatively evenly among the habitat types riffle, braided and floodplain, whereas the deep and slow-flowing pool habitat was less preferred. When constructing nature-like fishways as 1+ brown trout habitat our study indicates that it is sufficient to create riffle like-stretches with the addition of LWD. Brown trout habitat preferences during winter conditions along with age classes other than 1+ should, however, be considered, as should possibilities to create habitat for other species to promote biodiversity. Such added values from created fishways should not be neglected.

Large woody debris

In this study, the addition of high densities of LWD had a positive effect on the abundance of brown trout, and also affected the likeliness that a fish would remain in the experimental stream section into which it was released. LWD has previously been shown to promote increased salmonid densities (Degerman et al. 2004; Lehane et al. 2002; White et al. 2011; Zika and Peter 2002), and addition of LWD is a common practice in stream restorations (Larson et al. 2001; Miller et al. 2010). Nevertheless, there are studies where the addition of LWD has failed to show an effect on salmonid populations. It has been proposed that the spatial scale of the restoration, a lack of long-term monitoring, or the presence of large boulders already providing sufficient habitat complexity may explain the lack of effects (Sweka and Hartman 2006; Sweka et al. 2010). In our study,

the treatment with a low concentration of wood, representing streams in forests affected by modern Swedish forestry, did not have an effect on the brown trout habitat choice. More fish were even caught in experimental stream sections of riffle-, braided- and pool-type with no LWD than in the corresponding experimental stream sections with a low density of LWD.

Brown trout are not the only organism to benefit from high densities of LWD. Previous studies have shown that the presence of LWD has a positive influence on the density of macroinvertebrates (Miller et al. 2010) (but see: Palmer et al. 2010). LWD may create slow-flowing deposition areas with higher retention of organic matter as well as more fine-grained substrate, opening colonization opportunities for macroinvertebrates that normally are rare in channelized reaches (Wallace et al. 1995). It also provides food for xylophagous species as well as grazers feeding on periphytic algae (Hoffmann and Hering 2000). Moreover, it presents a surface to attach to or can act as a refuge (Hoffmann and Hering 2000). As decaying wood has a more complex surface than fresh wood, and thereby also more potential shelters for macroinvertebrates (Czarnecka et al. 2014; Smokorowski et al. 2006; Spanhoff et al. 2000), it is also likely that the potential benefits of added LWD will increase with time after addition.

Habitat

We found no major effect of the addition of more heterogeneous habitat types, floodplain and braided, on brown trout habitat choice in the fishway. Based on electrofishing the trout were relatively evenly distributed between the riffle, floodplain and braided habitats, but only seven brown trout (3.4%) were caught in the pool habitats. Earlier studies of brown trout habitat choice have shown a preference for pool habitats, albeit those studies refer to larger trout (Heggenes 1988; Heggenes et al. 1999; Heggenes et al. 1993). The lack of trout in the pool habitats may also be an effect of the presence of predators in the biocanal. The biocanal was electrofished before the study to remove as many predators as possible, but pike and burbot were still present during the study. Both burbot and pike have been shown to have a negative effect on presence and abundance of brown trout (Degerman and Sers 1993) and

trout have been shown to avoid pools when pike are present (Greenberg 1994). Even though the pool habitats were only used to a small extent in this study, the importance of having high habitat diversity should not be underestimated. Palm et al. (2007) found that the restoration of streambed heterogeneity was insufficient to promote increased trout densities as the trout were limited by a lack of spawning grounds. In the same way, creating high quality summer habitat may have little impact if there is little or no high quality overwintering habitat. The present study follows 1+ fish during late summer, but the fish might use different habitats as the temperature drops, and larger fish have been seen to aggregate in deeper and more slow-flowing areas (Heggenes et al. 1993). In addition, an increased habitat heterogeneity has been shown to have a positive effect on other riverine organisms, such as the benthic fauna. In fact, the pool habitats that were avoided by the trout in this study were previously shown to have the highest number of macroinvertebrate families in the channel (Gustafsson et al. 2013).

Implications for future projects

In our study, fish occupied areas with a mean velocity of 0.57 ± 0.25 m/s and a mean depth of 42.3 ± 15.6 cm, which is in accordance with previos studies (Degerman et al. 2001). Fish also preferred areas with larger substrate sizes than was found on average in the fishway, and consequently also with more available shelter. The results of this study therefore indicate that when creating artificial brown trout habitat, the addition of relatively homogeneous stream stretches, 30-60 cm deep with coarse substrate and access to shelter may be sufficient. In Canada, to achieve no net loss in habitat productivity, it has been suggested that the new habitat must be at least twice as large as the lost habitat it is created to compensate for (Minns and Moore 2003). A need for even larger compensation ratios has, however, been proposed due to the uncertainties in compensatory success (Quigley and Harper 2006). Due to their small size, the construction of nature-like fishways will probably never fully compensate for all lost stream habitat in impounded rivers. The use of fishways as compensation measures may however make a valuable contribution in streams with little or no free-flowing water.

Where space and budget allows, it would probably be beneficial to create as large fishways as possible to increase the available habitat area. Our study shows that the addition of high densities of LWD is a relatively easy and inexpensive way of improving habitat function for brown trout in nature-like fishways. To increase structural diversity and to enhance the habitat quality for brown trout as well as for macroinvertebrates, we recommend the addition of LWD to nature-like fishways.

Acknowledgements

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32. Lea D. Schneider. Conservation ecology of the thick-shelled river mussel *Unio crassus* – the importance of parasite-host interactions. Doctoral thesis, 24 February 2017.

33. Anna Mogren. Implementering av lärande för hållbar utveckling – En studie av rektors förståelse av kvalitet i skolans organisation. Licentiate thesis, 17 November 2017.

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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