The Macroinvertebrate Community in a Nature-like Fishway with Habitat Compensation Properties

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Biology

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Abstract

The construction of nature-like fishways has become an increasingly common action to restore longitudinal connectivity in streams exploited for hydropower. If constructed properly, these fishways also have the potential to act as compensation measures when important habitats have been degraded or lost. Most conventional nature-like fishways, however, often have a static flow regime, a steep slope, coarse uniform substrate and high water velocities, which do not constitute a template for a high biodiversity.

The aim of this thesis was to improve knowledge of the concept of nature-like fishway design, with special focus on their habitat compensation potential. This was done by comparing a nature-like fishway with habitat compensation properties, termed the biocanal, to six natural reference streams in its vicinity. The potential for the biocanal to contain a more diverse fauna of benthic macroinvertebrates, compared to a conventional nature-like fishway, was investigated by comparing different habitat structures in the biocanal. Furthermore, macroinvertebrate colonization of the biocanal was studied to find out if the community composition converged over time with what was found in natural reference streams. And lastly, the functional organization of the biocanal was studied using the functional feeding group approach.

Our studies showed that the family composition, diversity and functional organization of the benthic fauna in the biocanal were approaching that of the reference streams two years after the biocanals' construction. The different habitats in the biocanal contributed to an increased family diversity and the biodiversity in the biocanal was therefore higher than it would have been if it had been designed as a conventional nature-like fishway.

In the future a more developed riparian zone will increase the biocanal's suitability as macroinvertebrate habitat. Additional measures to facilitate the habitat potential of the biocanal could be the addition of a more variable substrate and woody debris to further increase habitat heterogeneity.

Publications

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

I. Gustafsson, S., Österling, M., Skurdal, J., Schneider, L., Calles, O. 2012.
Macroinvertebrate colonization of a nature-like fishway: the effects of habitat design. *Manuscript.*

II. Gustafsson, S., Calles, O., Skurdal, J., Vezza, P., Österling, M. 2012. The functional organization of the macroinvertebrate community in a nature-like fishway with habitat compensation properties. *Manuscript.*

Contents

Introduction

Nature-like fishways

The construction of hydropower facilities often degrade habitats and disrupt migration routes, something that has a negative impact on fish and other aquatic organisms. To re-establish connectivity in streams, a common action is to construct fishways, often with the main goal of facilitating upstream migration of adult salmonids (Katopodis, 2002). The loss of habitats, however, is often not compensated for; and when it is, the action taken is often to re-create habitats and spawning areas for fish (Enders et al., 2007, Jones et al., 2003, Scruton, 1996), whereas little consideration has traditionally been given to other taxa and to the overall ecological function and integrity of the stream. Nevertheless, during the last decades the construction of nature-like fishways, which have the potential to provide habitat for the fauna in the ecosystem (Pander et al., 2011) and thereby to act as rehabilitation measures, have become increasingly common. Their habitat potential, however, has so far not been fully realized.

Benthic fauna

The habitat potential of most nature-like fishways, with a few exceptions (Jansen et al., 2000), have only been evaluated for fish. Therefore the knowledge of the macroinvertebrate community composition in such structures is lacking. Macroinvertebrates constitute an important part of natural streams since they serve as key components in food webs and are a significant prey source for fish (Sanchez-Hernandez et al., 2011, Skoglund and Barlaup, 2006). Moreover, they also create an important link between the stream and the terrestrial environment since emergent adults are an important food source for many insectivores (Fukui et al., 2006, Jackson and Fisher, 1986, Sabo and Power, 2002).

Also, much is known concerning tolerances and preferences of different taxa, and macroinvertebrates can be used as bio-indicators of stream deprivation and contamination (Kerans and Karr, 1994, Weigel et al., 2002, Bennett et al., 2004). Macroinvertebrates have various functions in the ecosystem, depending on how they acquire their food (Cummins and Klug, 1979, Wallace and Webster, 1996). These different functional feeding groups (FFGs) can be used as substitutes for ecosystem attributes (Merritt et al., 1996, Stone and Wallace, 1998, Merritt et al., 2002, Cummins et al., 2005). This can give information concerning the origin of the main carbon source in the streams, if there is enough stable substrate to accommodate a shredder and filterer community, and if there is enough suspended FPOM to provide food for a community of filtering collectors.

In Västerdalälven, Sweden, a new powerhouse was constructed at the Eldforsen hydroelectric facility in the vicinity of the village Eldforsen in 2009. In addition to the new powerhouse construction the reservoir level was also raised 2.33 m, consequently inundating a large area of the river and not only disrupting the longitudinal connectivity, but also destroying and degrading habitats for many different species. To mitigate the negative effects of the new constructions a 500 m long nature-like fishway with habitat compensation properties, termed the biocanal, was created. According to the nature-like philosophy, the biocanal was constructed to mimic the properties of an equal sized natural stream with a variable substrate, a low gradient and a variable flow regime. Such man-made stream habitats as the biocanal are likely to become increasingly important as river restoration and connectivity issues are addressed. The integrity of these structures is therefore of major concern and the evaluation of these constructions is of great importance.

Objectives

Whereas the main objective of nature-like fishways is to provide passage for all organisms of all life stages in the system, they also possess a potential for habitat compensation, something that often has been neglected. The aim of this thesis was to improve the knowledge of the habitat potential in nature-like fishways. In paper I we investigated if the biocanal would host a more diverse fauna of benthic macroinvertebrates compared to a conventional nature-like fishway, through in-stream comparisons of the different habitat types in the biocanal. We also studied the colonization of the biocanal to find out if the community composition converged over time with what was found in natural reference streams nearby.

In paper II we studied the functional organization of invertebrates in the biocanal, using the functional feeding group approach, and compared it to what was found in the natural reference streams.

Material and methods

Study area

The study area is located in the province of Dalarna, in central Sweden (Fig. 1). The biocanal was constructed next to the Eldforsen hydroelectric facility in the Västerdalälven river system, diverting water around the power plant and into the old river bed.

To compensate for the habitats that had been lost following dam construction, four different habitat types were created within the biocanal:

1) Pools, with a low water velocity and gravel substrate to compensate for lost freshwater pearl mussel (*Margaritifera margaritifera)* habitat and spawning areas for brown trout *(Salmo trutta).*
2) Floodplains, with winding channels and shallow ponds and
3) Braided habitats, where the canal has been diverted into narrow channels with islands in-between. These two habitat types were created to accommodate young individuals of brown trout.
4) Riffles, with a straight watercourse and high water velocity, representing a conventional nature-like fishway and providing habitat for rheophilic taxa in general.

Each habitat type was replicated three times within the canal using a randomized block design. All habitat units were 18 meters long and separated by 18 m long riffle-like buffer zones, constructed according to the same design as a conventional nature-like fishway.

placed parallel to the water. In each frame the plant cover of existing plant species was noted, after which the vegetation was divided into three groups consisting of; grasses and sedges, mosses and lichens and vascular plants.

Summary of results

Paper I

In paper I we found that the four habitat types in the biocanal differed in regards of their physical appearance. The pool habitats were deeper than all other habitats in the biocanal and the braided and riffle habitats had the highest water velocity, whereas the floodplain habitats with their high substrate diversity were the habitats with the closest physical resemblance to the habitats in the reference streams (Fig. 2).

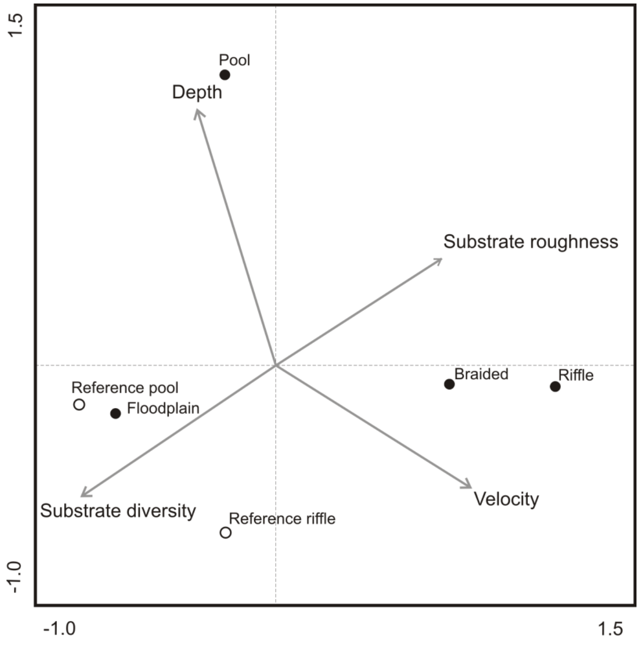

Figure 2. Principal Components Analysis (PCA) for four physical traits in the habitats in the biocanal and the reference streams. The first axis explains 51.3% of the variance and the second axis explains 34%. Black circles represent biocanal samples and empty circles represent reference streams. Vectors point in the direction of increasing value, with length indicating the strength of the relationship.

The different habitat types in the biocanal also differed in regards of their taxonomic composition. The lowest number of families of benthic fauna in the biocanal was found in the riffle habitats, designed to resemble the normally homogenous design of a conventional nature-like fishway, whereas the highest number of families was found in the most heterogeneous habitats in the biocanal; the pool and floodplains at all sampling dates, except for the first sampling date (Fig. 3).

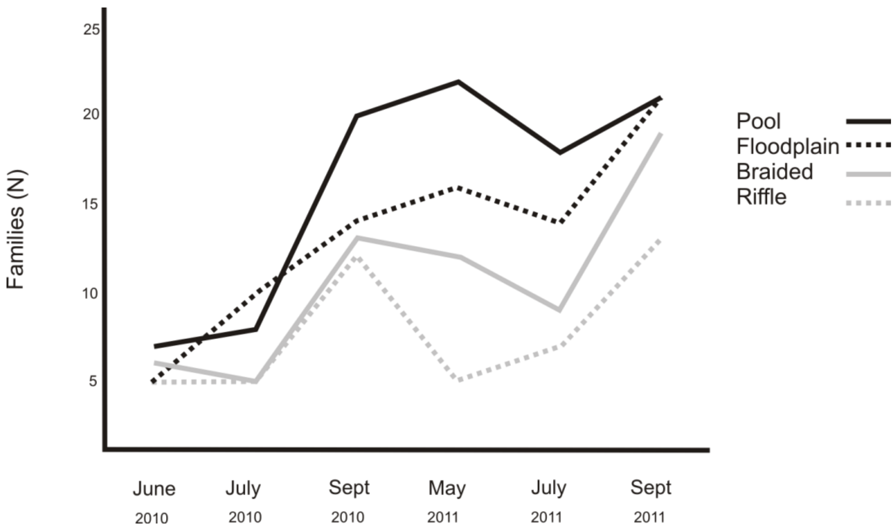

Figure 3. Number of macroinvertebrate families found in the different habitats in the biocanal during the different sampling dates.

The total number of families in the different habitat types added up to 32 in the floodplain habitats, 29 in the pool habitats, 28 in the braided habitats and 20 in the riffle habitats.

We also found that the macroinvertebrate community composition in the biocanal and the reference streams showed a partial convergence over time and that two thirds of the benthic fauna families found in the reference streams had colonized the biocanal two years after its construction.

Paper II

The most important findings in paper II was that all FFGs found in the reference streams also where found in the biocanal (Fig. 4).

Only one major FFG showed any significant difference in abundance between the systems. These were the shredders which were significantly more abundant in the biocanal than in the reference streams (p= 0.011). This group constituted 4.9% and 5.5% of the FFG abundance in the biocanal and the reference streams, respectively. The most common group in the biocanal was the scrapers which represented 32% of the FFG abundance. This group constituted 25% of the FFG abundance in the reference streams. The most common group in the reference streams was the gathering collectors constituting 28% of the FFG abundance. In the biocanal this group represented 27% of the FFG abundance. The filtering collectors constituted 15% and 13% of the FFG abundance in the biocanal and the references streams, respectively, and in both systems the percentage of passive filter feeders was higher than the percentage of active filter feeders. The predators represented 11% of the FFG abundance in the biocanal and 19% of the FFG abundance in the reference streams.

When comparing ratios acting as substitutes of ecosystem attributes (Table 1) in the biocanal and the reference streams we found that both the biocanal and the reference streams were heterotrophic systems with an adequate amount of stable substrates for filtering collectors and scrapers. The ratios also indicated that the biocanal was enriched in suspended FPOM.

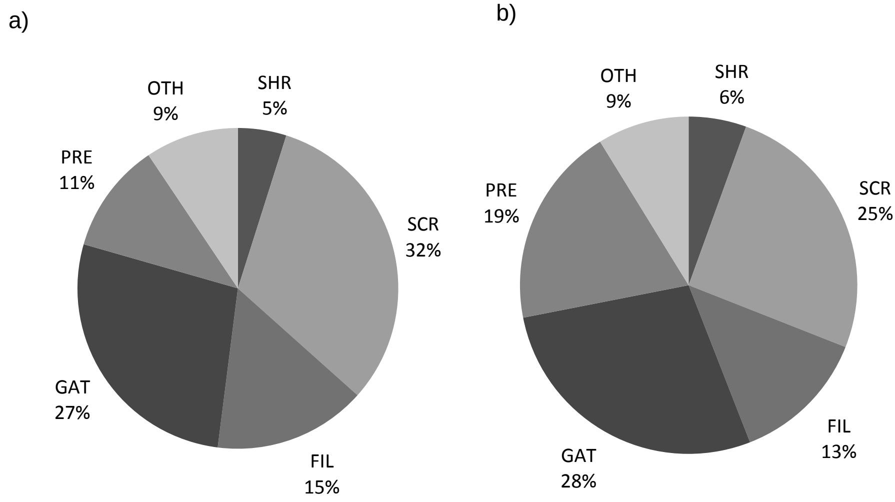

Figure 4. The proportions of the different FFGs in a) the biocanal and b) the reference streams. Abbreviations: SHR: shredders, SCR: scrapers, FIL: filtering collectors, GAT: gathering collectors, PRE: predators, OTH: comprise the groups other, miner, xylophagous, piercer and unknown.

Table 1. Ratios of FFGs and the stream ecosystem attributes for which they can serve as surrogates (Modified after Merritt et al. 1996).

Ecosystem Parameter	**FFG-ratios**	**Ratio thresholds**	**Bio**	**Ref**
Autotrophy to Heterotrophy	Ratio grazers to shredders and total collectors	Autotrophic > 0.75	0.66	0.55
FPOM in transport to FPOM in storage	Ratio filtering collectors to gathering collectors	FPOM transport greater than normal > 0.50	0.56	0.47
Substrate stability	Ratio grazers and filtering collectors to shredders and gathering collectors	Stable substrates plentiful > 0.50	1.5	1.2

Discussion

Biodiversity

One of the greatest threats to global freshwater biodiversity is habitat degradation (Dudgeon et al., 2006), which can be mitigated by the construction of nature-like fishways with habitat compensation properties.

The study of the different habitat types in the biocanal revealed differences in their physical properties as well as in their taxonomic composition, suggesting that the biocanal with its heterogeneous habitat structure has the potential to support a higher biodiversity than a conventional nature-like fishway. The fact that the lowest number of families was found in the most homogenous habitat, e.g. the riffle, designed to resemble a conventional nature-like fishway, whereas the highest number of families was found in the most heterogeneous habitats, i.e. the pool and floodplains, further supports the hypothesis that the biodiversity in the biocanal is higher than it probably would have been if it instead had been designed as a conventional nature-like fishway. However, there are several factors affecting the species composition of a newly constructed nature-like fishway besides the physical suitability of the habitat, for example; the habitats ability to provide food for the species as well as the species ability to colonize the area and the distance between species pools.

Functional organization

Although the benthic fauna community composition in the biocanal and the reference streams differed two years after the biocanals' construction, the ecological function of the biocanal may already be equivalent to that of the reference streams, since all FFGs were found in both systems. Only one major FFG, the shredders, differed in abundance between the biocanal and the reference streams. This group was the one we deemed most likely to occur in lower abundances in the biocanal due to the lower leaf litter input, but instead the shredders were more abundant in the biocanal than in the reference streams. One reason for the relatively high abundance of shredders in the biocanal may be that the benthic fauna community in the biocanal to a larger extent was comprised by taxa with a more omnivorous life style compared to the more specialized taxa found in the reference streams. Taxa with shedder-abilities in the biocanal therefore have the ability to exploit other energy sources in the absence of CPOM and might still exist in high densities despite a shortage of this energy source.

The results from the FFG ratios expressed as ecosystem attributes suggested that the biocanal contained an adequate amount of stable substrates to accommodate a community of scrapers and filtering collectors and that the amount of suspended organic material was enough to support a community of filter feeders. Since the biocanal was created to host a population of freshwater pearl mussels these results are especially important. Since these mussels are filter feeders the suitability of the biocanal as habitat for taxa belonging to this FFG is vital for their health and survival.

What can we expect in the future?

A more developed riparian zone would probably increase the suitability of the biocanal as macroinvertebrate habitat through its contribution of allochthonous CPOM and shading, thereby increasing the potential for an even more nature-like benthic fauna composition. With time the plant cover along the biocanal will become denser, but the species composition will most likely differ from what is found along the reference streams for many years to come. Many of the reference streams are surrounded with mixed forest stands, a successional stage that the riparian zone along the biocanal will take decades to reach. The tree assemblage along the biocanal is currently mainly composed by alders (S. Gustafsson, personal observation), whose leaves have been shown to be the preferred food source for many kinds of shredders (Wallace et al., 1970, Otto, 1974). However, a more diverse riparian zone with leaves with different rates of decomposition is needed to provide a continuum of CPOM during the whole year (Petersen and Cummins, 1974, Haapala et al., 2001).

Recommendations to improve the biocanal

The riffle areas in the biocanal, constructed in the same way as a conventional nature-like fishway, did not contain any families that did not occur in one or more of the other habitat types and did therefore not contribute to the family diversity in the biocanal. Such fast flowing areas could be made more attractive by creating a more nature-like and variable substrate by the addition of pebbles and cobbles and a few larger boulders to create a variable flow regime. Addition of supplementary woody debris to increase structural complexity and create additional habitats could be made in all habitat types. To assist the succession of the riparian vegetation and to facilitate detritus based energy pathways the riparian zone could be sown or planted with plant species from the area.

Conclusions

The first study of the biocanal showed that the family composition and the diversity of the benthic fauna in the biocanal were approaching that of the reference streams. The second study showed that all FFGs found in the reference streams also occurred in the biocanal and that only one major FFG showed any difference in abundance between systems. It appears, therefore, that the timeframe, over which the functional organization might be expected to approach natural levels might be as short as two years, whereas the biodiversity might take longer.

However, a high biodiversity may not always be the primary goal of aquatic rehabilitation measures; in some cases it may instead be more important to compensate for the damage human activity has had on a given species. The biocanal was created to host a population of freshwater pearl mussels and future studies of the biocanal should be focused on the functionality of the fishway as habitat for these bivalves. The presence of brown trout is also important for the reproduction of the freshwater pearl mussel (Arvidsson et al., 2012) and the potential of the biocanal to act as habitat for these fishes should also be investigated.

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Paper I

Macroinvertebrate colonization of a nature-like fishway: the effects of habitat design

Gustafsson, S., Österling, M., Skurdal, J., Schneider, L., Calles, O

Abstract

Nature-like fishways are designed to imitate the characteristics of natural streams, thereby providing passage and habitat for a variety of aquatic organisms. The potential for habitat rehabilitation in such structures has, nevertheless, so far not been fully realized. To develop the concept of how to create a nature-like fishway design, a 500 meter 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) habitats, each replicated three times. The biocanal resembled a natural stream in terms of hydraulics, gradient, flow regime, substrate etc. and provided a range of habitats to potentially harbor a high biodiversity. Thus the biocanal had a much 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 both among the four biocanal habitat types, and between the biocanal and six natural reference streams. After two years 66.7% 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.

Key words: Nature-like fishway, habitat compensation, macroinvertebrate, diversity

Introduction

Hydropower development degrades river ecosystems, disrupting longitudinal connectivity and causing habitat loss for different lotic organisms (Reyes-Gavilan et al., 1996, Rosenberg et al., 1997). This has a negative impact on many stream fishes and can even lead to the extinction of migratory fish populations (Northcote, 1998). To mitigate the effects of hydropower development, the construction of fishways is a common action to restore connectivity and to re-establish migration routes (Clay, 1994). However, most fishways are technical designs, i.e. they are made of wood and/or concrete, and they are mainly constructed to facilitate upstream migration of commercially important salmonids (Katopodis, 2002). During the last decades the importance of designing passages suitable for other fish species and aquatic organisms of different life stages has been recognized (Eberstaller et al., 1998). Nature-like fishways have the potential not only to facilitate passage but also to provide habitat for the organisms present in the system (Pander et al., 2011), thereby acting as rehabilitation measures in areas where longitudinal connectivity and important habitats have been degraded or lost. Based on nature-like design philosophy, nature-like fishways should resemble similar-sized natural streams in the vicinity (Katopodis, 2002). The habitat quality aspect of nature-like design, however, is often overlooked, and hence one of the major potential benefits of nature-like fishways is generally not realized. Instead, the constructed watercourses often have a static flow regime, a steep slope with coarse uniform substrate and high water velocities, which do not constitute a template for a high biodiversity (Allan and Castillo, 2007, Richter et al., 1997, Allan, 1975, Vinson and Hawkins, 1998, Gorman and Karr, 1978). The hypothesis that habitat heterogeneity is positively correlated to biodiversity is one of the key elements of ecology (Ricklefs and Schluter, 1993). This correlation has been shown for different taxa on different scales, from macroinvertebrates on submerged plants (Taniguchi et al., 2003) to butterflies in agricultural landscapes (Weibull et al., 2000). A nature-like fishway with a more varied habitat composition should thus accommodate more species with different habitat criteria and act as a rehabilitation measure with added value.

The function of most nature-like fishways has only been evaluated for fish (Aarestrup et al., 2003, Calles and Greenberg, 2005, Eberstaller et al., 1998, Jansen et al., 1999, Jungwirth, 1996, Mader, 1998, Santos et al., 2005, Calles and Greenberg, 2009); however exceptions can be found (Jansen et al., 2000). Yet, for a nature-like fishway to mimic a natural watercourse, thereby being an integrated part of the landscape, the presence of other aquatic organisms is important. Macroinvertebrates are an especially key component, 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, Sabo and Power, 2002, Jackson and Fisher, 1986).

The study of a benthic fauna assemblage in a nature-like fishway could give knowledge about the potential for habitat compensation in such constructions, which could offer insights needed to provide guidelines in future developments of nature-like fishways with enhanced rehabilitation potential. 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, henceforth 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.

Since the different habitat types in the biocanal were created to exhibit different physical traits, we predicted that the family composition of benthic fauna consequently also would differ between 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 rehabilitation, 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 and present an estimation of the potential community composition in a fully developed biocanal. We anticipated initial differences in benthic fauna composition between the biocanal and 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: 1) studied the degree to which the biocanal resembled a natural stream through comparisons of physiochemical parameters and comparisons of benthic fauna assemblages between the biocanal and six natural streams is the area during the first two years after the construction of the biocanal, 2) examined if the combined habitat heterogeneity was increased in the biocanal in comparison to 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) investigated if the potentially increased habitat heterogeneity had any effect on the biodiversity by means of studying the benthic fauna composition in the different habitat types in the biocanal.

Material and Methods

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℃ (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 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. The biocanal has a head of 5 m and a length of 500 m, resulting in a gradient of 1%. To make the flow as nature-like as possible, the intake of the biocanal is constructed to allow a variable flow regime.

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 were selected to resemble the biocanal in size and they were regarded as potential sources of colonization of benthic fauna. In each reference stream, one pool area and one riffle area were chosen, each 18 meters in length, in which sampling took place. The riparian vegetation along the reference streams mainly consisted of *Vaccinium myrtillus*, grasses, mosses *(Sphagnum sp., Pleurozium schreberi*) and C*arex* species, whereas the in-stream macrophyte vegetation was mostly represented by *Fontinalis sp., Sparganium sp*., *Utricularia sp*. and *Myriophyllum sp*.

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 within a metal frame (0.64 m^2) at six points in each habitat unit in July 2011. The substrate was classified according to the Wentworth scale, modified by Cummins (Cummins and Lauff, 1969) e.g. sand and silt (<2 mm), gravel (2-16 mm), pebble (17-64 mm), cobble (65-256 mm), and boulder (>256mm). In addition a category for coarse particulate organic matter (CPOM) was added. To ensure consistency in the visual estimates of substrate composition, all estimates were performed by the same person.

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 on a frame, similar to that described in Lepori et al. (2005). At each point the contour tracing device was placed orthogonal to the flow and pressed against the stream bottom. The length of the sticks 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 stick length below water level.

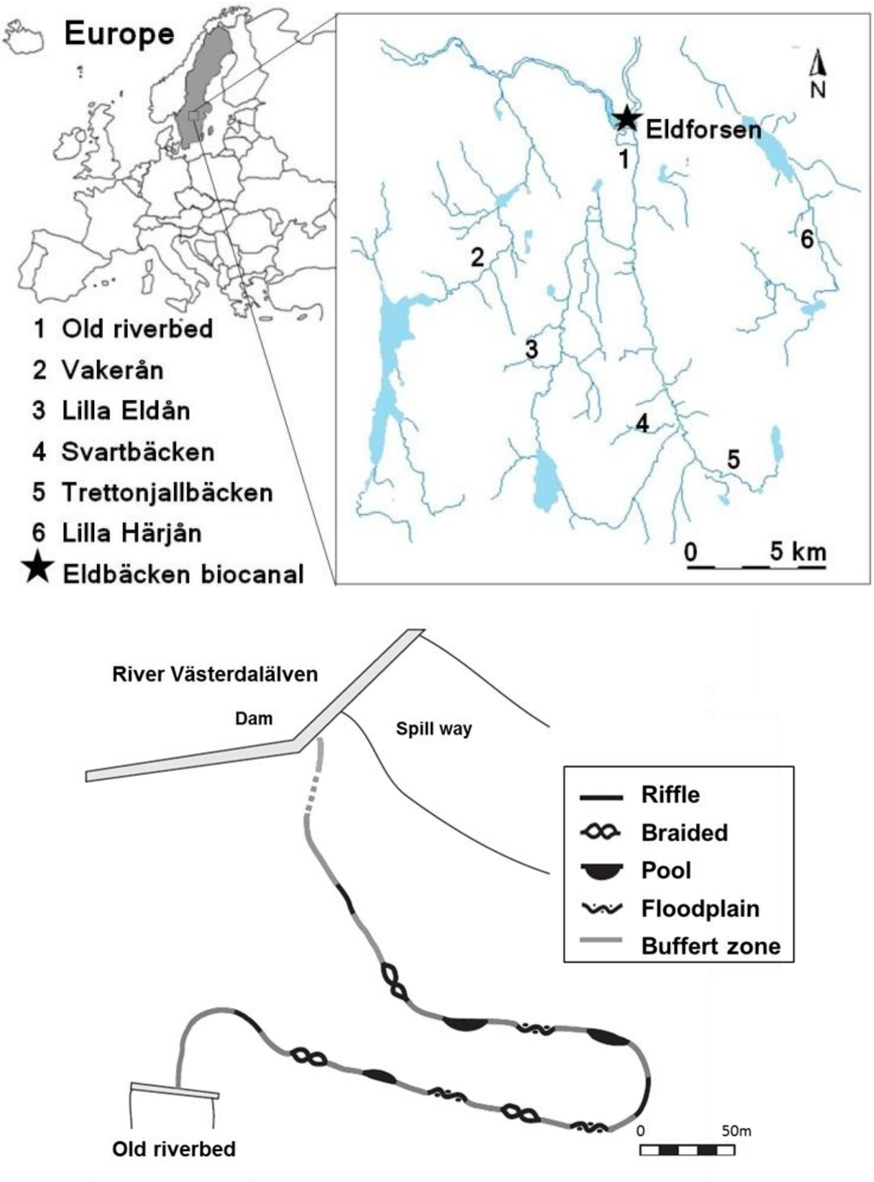

Figure1. The geographic location of the reference stream and the biocanal with its habitat types.

Benthic fauna

Benthic fauna samplings were performed at six occasions in the biocanal (spring, summer and autumn, in 2010 and 2011) and at four occasions in the reference streams (spring and autumn 2010 and 2011). The benthic samples were collected from six randomly selected points within each habitat unit in the biocanal (N= 72, for each sampling date) and from each of the pool and riffle areas in the reference streams (N = 72, for each sampling date). Samples were collected using a 0.04 m^2 Surber sampler fitted with 500 μm net, following standard procedure (eg. placing the Surber sampler on the stream bed and disturbing the substrate). All samples were immediately preserved in 70% ethanol. In the laboratory, invertebrates were sorted from organic matter in four samples randomly selected from the six collected for each habitat unit after which all individuals were identified to family, with the exception of Nematoda, which were identified to order. Identifications were based on taxonomic keys (Nilsson, 1996, Nilsson, 1997, Waringer and Graf, 1997, Lechthaler, 2007).

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).

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.

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 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. The ASPT is an index for unpolluted water, and the index is based on tolerance differences among different families of benthic fauna. The different families have been assigned indicator values for tolerance and sensitivity. The index is calculated as the average of the tolerance values of the different families found and ranges from 0 to 10, where high index values indicate the presence of mainly sensitive groups and high ecological status, whereas low values indicate tolerant groups and a degraded ecological status. Calculations of the ASPT index were based on information from the Swedish Environmental Protection Agency (1999).

Results

Habitat characteristics

The physiochemical measurements in the biocanal and in the reference streams showed that the biocanal was quite similar to the reference streams. Because they belong to the same watershed, the chemical measurements showed few significant differences. 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 noticeable differences in their physical structure. 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).

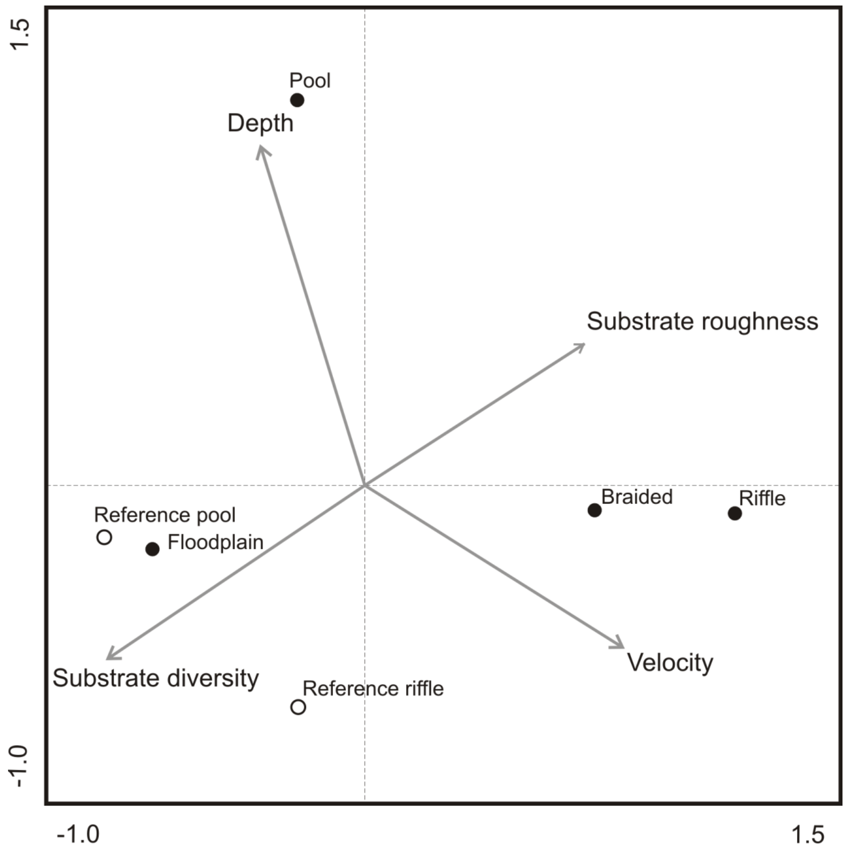

Figure 2. Principal Components Analysis (PCA) for four physical traits in the habitats in the biocanal and the reference streams. The first axis explains 51.3 % of the variance and the second axis explains 34 %. Black circles represent samples from the biocanal and empty circles represent samples from the reference streams. Vectors point in the direction of increasing value, with length indicating the strength of the relationship.

The 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 ($p < 0.001$).

Benthic fauna

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). In the biocanal, a gradual increase in the number of families was observed over time, 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.

Table 1. List of taxa found during the study.
Abbreviations: p = reference pool, r = reference riffle, R = riffle, B = braided, P = pool, F = floodplain.

Family	Ref	Biocanal	Family	Ref	Biocanal
Aeshnidae	p		Limoniidae	p r	R B P F
Athericidae	p r		Lumbriculidae	p r	B F
Baetidae	p r	R B P F	Lymnaeidae	p	
Caenidae	r	R P F	Muscidae	p	F
Calopterygidae	p		Molannidae	p	
Ceratopogonidae	p r	R B P F	Naididae	p r	R B P F
Chironomidae	p r	R B P F	Nematoda	p r	R B P F
Cordulegastridae	p r	F	Nemouridae	p r	R B P F
Corduliidae	p		Pediciidae	p r	P
Dryopidae	p r		Perlodidae	p r	B P F
Dytiscidae	r	R B P F	Pilopotnamidae	r	
Elmidae	p r	B P	Planorbidae	p r	
Empididae	p r	B P F	Platycnemididae	p	
Ephemerellidae	p r	R B P F	Polycentropodidae	p r	R B P F
Ephemeridae	p r	P	Psychomyiidae	p r	R B P F
Glossosomatidae	p r	F	Pulmonata	p	
Goeridae	p r		Rhyacophilidae	p r	R B P F
Gomphidae	p r		Sericostomatidae	p r	
Gyrinidae	p r	B	Sialidae	p	
Heptageniidae	p r	R B P F	Simuliidae	p r	R B P F
Hydrophilidae	r		Siphlonuridae	p r	P
Hydropsychidae	p r	R B P F	Sphaeriidae	p r	
Hydroptilidae	p r	R B P F	Tabanidae	p r	B P F
Lepidostomatidae	p r	B P F	Taeniopterygidae	p r	R B F
Leptoceridae	p r	R B P F	Tipulidae		P F
Leptophlebiidae	p r	B P F	Tubificidae	p r	B P F
Leuctridae	p r	F	Valvatidae	p	
Limnephilidae	p r	F	**Tot**	**54**	**37**

The similarities in family composition between the biocanal and the reference streams, expressed as the Sorensen index, showed an increasing similarity with time (Fig. 3). 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.

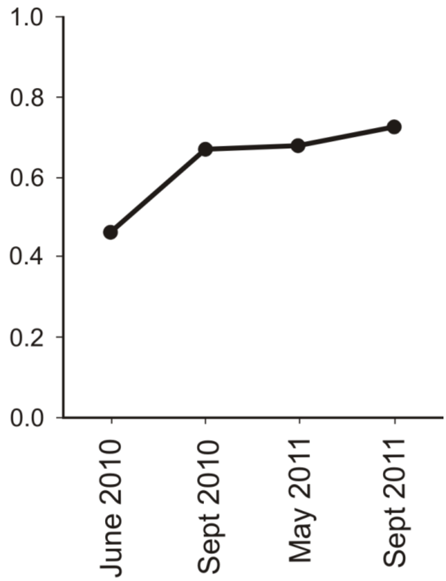

Figure 3. Sorensens similarity index for the family-level between the biocanal and the reference streams.

The converging similarities between the biocanal and the reference streams were also shown by the Shannon Weaver diversity (Table 2) and the EPT densities (Table 3), of which both were significantly higher in the reference streams than in the biocanal at all dates, except for the last sampling date in September 2011.

Table 2. Differences in Shannon Weaver diversity between the biocanal and the reference streams. All p values are bonferroni corrected to avoid bias caused by multiple testing.

2010		2011	
June	Sept	May	Sept
Ref>Bio <0.001	Ref>Bio <0.001	Ref>Bio <0.001	No sig. diff.

Table 3. Differences in EPT density between the biocanal and the reference streams. All p values are bonferroni corrected to avoid bias caused by multiple testing.

2010		2011	
June	Sept	May	Sept
Ref>Bio <0.001	Ref>Bio <0.001	Ref>Bio <0.001	No sig. diff.

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. 4). 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 seemed to have rather similar benthic fauna composition, the pool and braided habitats having the highest similarities (Table 4).

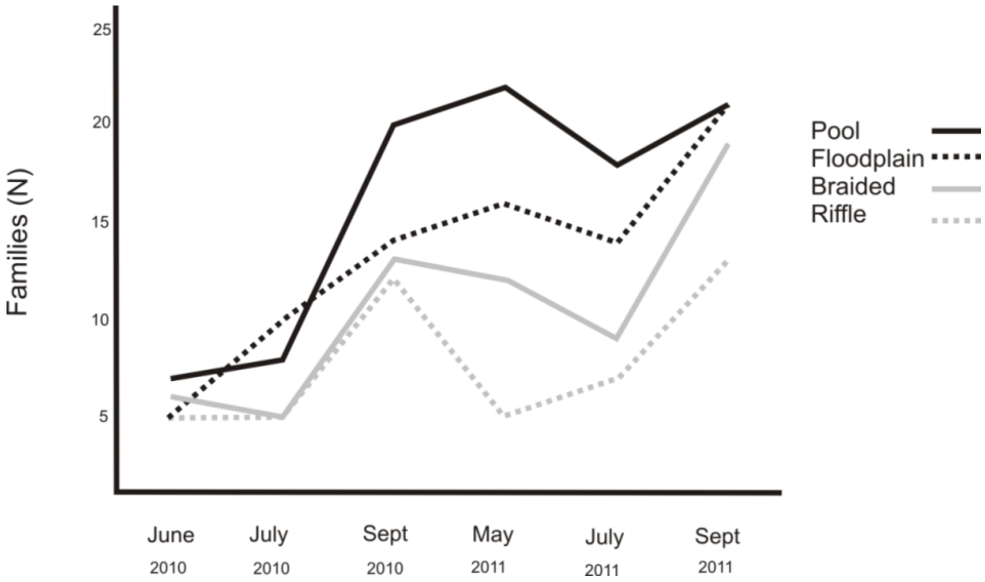

Figure 4. The number of macroinvertebrate families found in the different habitats in the biocanal during the different sampling dates.

Table 4. Sorensens similarity index for the different habitats in the biocanal, all sampling dates combined. Abbreviations: R = riffle, P = pool, F = floodplain, B = braided.

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

The density of the different families in the biocanal differed between habitat types and sampling date. A peak in Chironomidae density could be seen in the pool and floodplain habitats in July 2010. This sampling date was also the occasion when the overall highest number of individuals of benthic organisms was found. The high number was mainly represented by Naididae, which occurred in high abundances in all habitat types, but predominately so in the pool habitats. However, only one family, Simuliidae, showed any significant preferences for a specific habitat. This family occurred in higher densities in the riffle and braided habitats compared to the pool habitats in May 2011 ($p < 0.05$). The pool habitat types had the highest mean EPT densities at all sampling dates. High EPT densities was also found in the floodplain habitat types during the last sampling date, whereas EPT densities generally were low in the riffle habitats (Table 5).

Table 5. Differences in 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 Braided>Riffle	<0.01 <0.05
July	-	No sig. diff	Pool>Braided	<0.05
Sept	Pool>Riffle Pool>Braided Braided>Riffle	<0.05 <0.05 <0.05	Floodplain>Riffle Floodplain>Braided	<0.01 <0.05

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 6), a pattern which mirrors the EPT densities. Comparisons of samples taken in 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 No 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.

Table 6. Differences in 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 Pool>Floodplain Pool>Braided	<0.001 <0.01 <0.01
Sept	-	No sig. diff	Floodplain>Riffle Floodplain>Braided	<0.01 <0.05

Discussion

The two-year investigation of the benthic fauna assemblage in the biocanal showed that the different habitat types differed in regards of taxonomic composition. 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 nature-like fishway, whereas the highest number of families was found in the most heterogeneous habitats, i.e. the pool and floodplains. The conclusion is that the biodiversity in the biocanal probably is 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. The biodiversity in the biocanal remained lower than the biodiversity in the reference streams throughout the study, however, the colonization of the biocanal appears to be ongoing and the community composition will continue to develop in the future.

A prerequisite for colonization success is an intact longitudinal connectivity and the suitability of the area as habitat. Since the biocanal belongs to the same watershed as the reference streams, 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, 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 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 for explaining the biodiversity patters in the biocanal. In a study of streams restored after timber floating Lepori (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. It is suggested that such gaps might be filled with fine sediments with time, thereby providing a more nature-like substrate roughness (Lepori et al., 2005), something that might increase the habitat suitability for benthic fauna in the future.

Another way of quantifying structural heterogeneity is by means of substrate diversity, 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 they match their optimum velocity (Gore et al., 2001). Lastly, the pools and, to some degree the ponds on the floodplains, contained areas with backwaters. This may also have contributed to the higher benthic fauna diversity, since such areas have been shown to act as flow refugia for macroinvertebrates during high flow (Negishi et al., 2002).

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 (Yount and Niemi, 1990, Wallace, 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. Families that were found in the reference streams but not in the biocanal, i.e. potentially representing the slowest colonizers, belonged to a large extent to classes with poor dispersal capabilities like the Gastropoda or Bivalvia (Kappes and Haase, 2012), or to families with life stages associated to the riparian vegetation, like the Sialidae (Evans and Neunzig, 1996). Still, new families of Trichoptera and Coleoptera were found during the last sampling in September 2011, indicating that the colonization is still in progress. However, it might take time for the benthic fauna composition in the biocanal to reach the successional stage of the reference streams and it has been proposed that such colonization processes 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). In our study the benthic fauna composition in the biocanal approached the one in the reference streams after two seasons.

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 well-studied 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 1.6-1.9 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). In the old riverbed three families of mollusks were found, 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 three kilometers away within in a time span of 3-10 years (Kappes and Haase, 2012).

The colonization of macroinvertebrates also depend on food availability in the new habitats. Alloctonous 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 colonization of the riparian zone may therefore facilitate the colonization of new families of benthic fauna in the future.

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 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 biocanal as macroinvertebrate habitat through its contribution of allochthonous CPOM, and thereby increasing 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.

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Paper II

The functional organization of the macroinvertebrate community in a nature-like fishway with habitat compensation properties

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Abstract

Stream habitat compensation can be integrated in the construction of nature-like fishways, creating structures that both facilitate passage and provide habitat. Few existing nature-like fishways, however, have been designed to maximize the habitat function. In 2009 a nature-like fishway with habitat compensation properties, termed the biocanal, was constructed in Eldforsen, Sweden. The functional feeding group approach was used to investigate the functional organization of the benthic community in the biocanal two years after its construction. Samples were also collected from six natural streams in the area to be used as references. Comparisons of functional feeding group ratios, acting as substitutes of ecosystem attributes, implied that both the biocanal and the reference streams were heterotrophic systems with an adequate amount of stable substrates for filtering collectors and scrapers. The ratios also indicated that the biocanal was enriched in suspended FPOM. Even though the benthic fauna community composition differs between the biocanal and the reference streams, all functional feeding groups found in the reference streams were also present in the biocanal. It hence seems like the ecological function of the biocanal is approaching that of the natural reference streams in the area.

Key words: nature-like fishway, habitat compensation, macroinvertebrate, functional feeding groups, biocanal

Introduction

Stream restoration efforts are increasing world-wide and in areas where important habitats have been degraded or destroyed by human activities, new habitats can be created to compensate for these losses. In streams such compensatory measures are often constructed to improve spawning areas or habitat for fish (Enders et al., 2007, Jones et al., 2003, Scruton, 1996). Another way to provide habitat for the fauna in the system but also to maintain connectivity in streams exploited for hydropower is to construct nature-like fishways (Pander et al., 2011). This form of habitat compensation, however, has so far not been fully realized and little attention is often given to other taxa and the function of the aquatic ecosystem. Only a few studies have focused on the benthic fauna composition in compensatory measures (Jansen et al., 2000, Gabriel et al., 2010) and knowledge of the macroinvertebrate communities in such structures is therefore to a large extent lacking.

Macroinvertebrates are an important component in the nutrient cycling of the stream (Cummins and Klug, 1979) and thereby also a fundamental part of a functional aquatic ecosystem. Macroinvertebrates can be divided into functional feeding groups (FFGs), depending on the manner in which they acquire their food, and the different groups have different functions in the ecosystem (Cummins and Klug, 1979, Wallace and Webster, 1996). As the abundance of FFGs are expected to differ between impaired and pristine streams, the relative abundance (Rawer-Jost et al., 2000, Bennett et al., 2004) as well as the ratios (Merritt et al., 1996, Merritt et al., 2002, Cummins et al., 2005, Stone and Wallace, 1998) of FFGs have been used in bioassessments and community descriptions. Such results can provide indirect information on stream ecosystem attributes, indicating if the system is autotrophic or heterotrophic, i.e. if the origin of the main basal energy source derives from allochthonous or autochthonous carbon. Additional information deduced from FFG ratios can be on the availability of suspended food for filtering collectors and the availability of stable substrates required for scrapers and filtering collectors (Merritt et al., 1996).

In Eldforsen, Sweden a nature-like fishway with habitat compensation properties, termed the biocanal, was created in 2009. The family composition and diversity of macroinvertebrates in the biocanal has been the focus of a previous study (Gustafsson et al., 2012), which showed that 66.7% of the families of benthic fauna found in six natural streams in the vicinity, acting as references, had colonized the biocanal two years after its construction. Family number and density, however, are not necessarily good indicators of the function of a system. Since the functional organization in the biocanal is unknown, the aim of this study was to use the FFG approach to find out if the biocanal had achieved a functional organization similar to natural streams in the same area two years after its construction. To do this we 1) compared the abundance and the proportions of the FFGs in the biocanal with six reference streams in the surrounding area and 2) assessed a number of stream ecosystem attributes through studies of ratios of FFGs. To evaluate the differences in FFG distributions we 3) tested how environmental factors affected the presence and abundance of FFGs.

Material and Methods

Study area

A new powerhouse was constructed at the Eldforsen hydroelectric facility in 2009 in Västerdalälven, Sweden (Fig 1). The new powerhouse was built to increase intake capacity and replaced an old powerhouse at approximately the same site. In addition to constructing a new powerhouse, the reservoir level was elevated 2.33 m, thereby inundating the last free-flowing stretch between Eldforsen and the next hydroelectric facility upstream. The intake channel to the old powerhouse was abandoned and both the intake channel and about 100 m of the old riverbed were filled with material from the excavation of the new intake channel. To maintain connectivity and facilitate passage a 500 m long nature-like fishway, the biocanal, with a maximum discharge of approximately 800 L s^{-1} was constructed, connecting the dam to the old riverbed. According to the philosophy of nature-like design (physiomimesi), the biocanal was constructed to mimic the properties of an equal-sized natural stream with a variable substrate, a low gradient (1%) and a variable flow regime. To compensate for lost habitat, the biocanal was equipped with four different habitat types, replicated three times, to create a habitat mosaic. For further information see (Gustafsson et al., 2012). Six reference streams located in the same riverine system as the biocanal were chosen due to their resemblance to the biocanal in terms of size. The sampling took place at six points in each habitat unit in the biocanal and in one pool area and one riffle area within each reference stream.

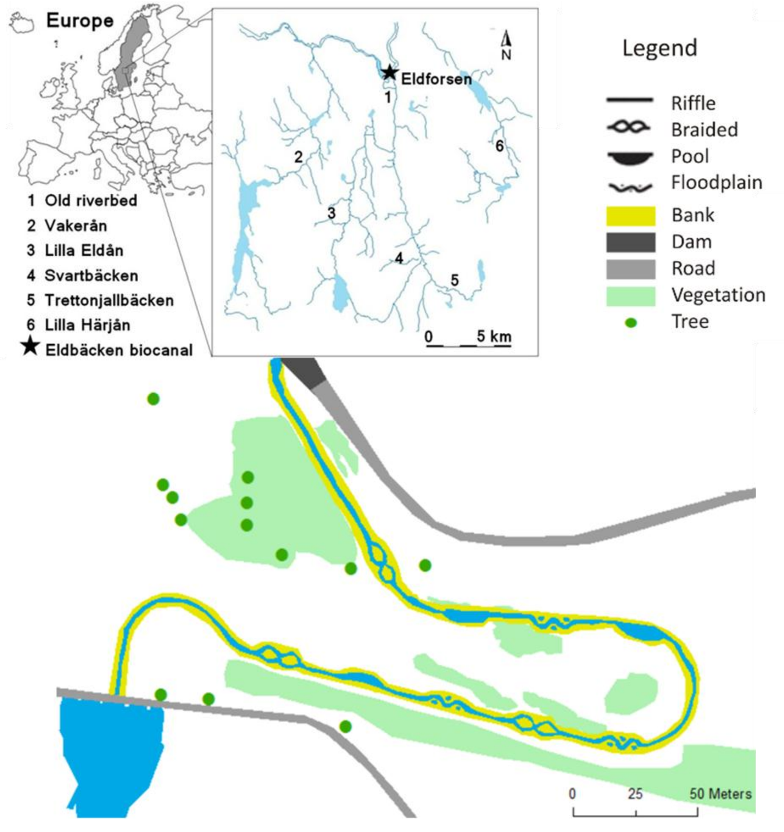

Figure 1. Locations of the biocanal and six natural streams in the Dalarna region, in Sweden. The map of the biocanal illustrates minimum flow (200 L s^{-1}).

Sampling

Benthic fauna

The benthic samples were collected in September 2011, using a 0.04 m^2 Surber sampler fitted with 500 µm net. Sampling was performed by placing the Surber sampler on the stream bed and scrubbing the substrate with a brush. Samples were gathered from six randomly selected points within each habitat unit in the biocanal and from each pool and riffle area in the reference streams. All six samples were preserved in 70% ethanol in the field, and of these, four samples were randomly selected for further analysis (N= 96).

Individuals from the selected samples were identified to the taxonomic level needed to assign FFG properties to the given individual (order, family, subfamily or genus). Identifications were based on taxonomic keys (Nilsson, 1996, Nilsson, 1997, Waringer and Graf, 1997, Lechthaler, 2007). A common way of separating taxa in FFGs is to assign each taxon to one preferred FFG. This method does not take the taxa's potential to utilize different food sources into account and information is lost. Since many taxa are generalists (Mihuc, 1997) a weighted list was used, where each individual was assigned 10 points distributed among the preferred feeding modes. The classifications were mainly based on (Moog, 2002). However, classification of invertebrates of the subfamilies Chironominae, Orthocladiinae, Tanypodinae and Podonominae (family Chironomidae) was based on information in Berg (1995), Merritt and Cummins (1996), Moog (2002) and Syrovatka and Brabec (2010).

Physiochemical parameters

Water velocity was measured using a Model 801 electromagnetic flow meter (Valeport Ltd, England) at six points in each habitat unit and at the same time the water depth was noted. The substrate of the biocanal and the reference streams were quantified by visual estimation of the substrate composition and by measurements of the structural heterogeneity of the stream bed using a contour tracing device similar to that described in Lepori et al. (2005). Conductivity, pH and oxygen were measured in each habitat unit in free flowing water using an HQ40d multimeter (HACH LANGE, Sweden).

Vegetation sampling

The riparian zone along the reference streams and the biocanal was sampled in July 2010 and July 2011, respectively. Along each habitat unit in the biocanal and each pool and riffle area in the reference streams six 1 m² frames were placed parallel to the water. In each frame the plant coverage of existing plant species was noted, after which the vegetation was divided into three groups consisting of; grasses and sedges, mosses and lichens and vascular plants.

Data Analysis

Benthic fauna

To get an estimated measure of the condition of the ecosystem in the biocanal, the relationships among FFGs were studied and compared to measurements from the reference streams. Macroinvertebrate abundance was standardized by conversion to macroinvertebrate densities (individuals m^{-2}), after which the macroinvertebrates were assigned to their feeding type; each individual being assigned 10 points. The FFG 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, non-parametric Kruskal Wallis (alpha <0.05) was used when comparing the number of individuals m^{-2} of a specific FFG between the biocanal and the reference streams. All calculations were done in the open-source statistical software R version 2.14.1 (R Development Core Team, 2011). The proportions of different FFGs were also calculated and compared between the biocanal and reference streams. In addition, we used FFG ratios proposed by Merritt et al. (1996) and Merritt and Cummins (2006) to get an estimate of a number of ecosystem attributes. The ratio of grazers to shredders and total collectors was used as an indicator for autotrophy or heterotrophy. Values below 0.75 indicate a heterotrophic system dependent on allochthonous organic matter from the riparian zone. The ratio between filtering and gathering collectors was used to estimate the relationship between FPOM in transport and FPOM in storage in the systems. Values above 0.50 indicate a system with a high FPOM particulate loading that can provide sufficient food for filtering collectors. The ratio of scrapers and filtering collectors to shredders and gathering collectors is a measure of channel stability, where values exceeding 0.5 indicate an abundance of stable substrates for filter feeders and scrapers in the system.

Environmental factors

To analyze how the presence and abundance of different FFGs were related to a number of environmental factors (Table 1), a Random Forest analysis was performed using R version 2.14.1 (R Development Core Team, 2011) and the statistical package randomForest (Liaw and Wiener, 2002). Two different binary models (absence–presence and presence–abundance models) were developed to select the most important environmental variables influencing the FFG distribution. The cutoff value between FFG presence and abundance was determined as the inflection point of the FFG density values (Vezza et al., 2012). A model based on of the presence and abundance of gathering collectors, scrapers, filtering collectors and predators was made using data from the reference streams. However, due to the small number of observations an absence-presence model was carried out for shredders.

Table 1. Environmental variables used in the random forest model.

Name	Unit	Name	Unit
Depth	cm	pH	
Velocity	m s^{-1}	Conductivity	µS cm^{-1}
Boulder	% cover	O2	mg/l
Cobble	% cover	Temperature	℃
Pebble	% cover	Mosses and lichens	% cover
Gravel	% cover	Vascular plants	% cover
Sand and silt	% cover	Grass and sedges	% cover
Organic	% cover	Total plant cover	% cover

Results

A total of 2374 individuals from 41 families were found during the study (Table 2) representing eight FFGs. The most abundant taxon in the study was the Naididae, a family that also represented the most abundant taxon in the biocanal. The most common FFGs in the study were the scrapers followed by the gathering collectors.

Functional Feeding Groups

Shredders were significantly more abundant in the biocanal than in the reference streams ($p < 0.05$). The shredders in the biocanal were predominantly the trichopteans *Lepidostomatidae lepidostoma* and *Leptoceridae athripsodes*, whereas the shredder group in the reference streams was mainly composed of plecopterans. The shredders in the biocanal and the reference streams constituted 4.9% and 5.5% of the communities, respectively.

Scrapers were the most common group in the biocanal (32%) and the second most common group in the reference streams (25%). There was no significant difference in total scraper abundance between the systems ($p > 0.05$), however the most common taxa with scraper abilities in the biocanal, *Naididae nais*, occurred in significantly higher densities in the biocanal than in the reference streams ($p < 0.05$). In the reference streams the most common scraper was the ephemeropteran, *Centroptilum luteolum*, which was encountered 46.5 times more often in the reference streams than in the biocanal.

Gathering collectors constituted 27% and 28% of the community in the biocanal and the reference streams, respectively, and did not differ significantly in total abundance between the systems ($p > 0.05$). As with the scraper abundance in the biocanal, it was mainly represented by *Naididae nais*, whereas the most common gathering collector in the reference streams was the ephemeropteran, *Leptophlebiidae lepthophlebiia*.

Table 2. Taxa found during the study, and their corresponding functional feeding groups. Abbreviations: SHR; shredder, SCR; scraper, A.FIL; active filter feeder, P.FIL; passive filter feeder, GAT; gathering collector, MIN; miner, XYL; xylophagous, PIE; piercer, PRE; predator, OTH; other, UNK; unknown. Bio; Biocanal, Ref; Reference streams, Dif; p-value for differences in density, calculated using non-parametric Kruskal Wallis test.

Order	Family	Genus (Species)	SHR	SCR	A.FIL	P.FIL	GAT	MIN	XYL	PIE	PRE	OTH	UNK	Bio (N)	Ref (N)	Dif. (p)
Diptera	Athericidae										10				1	
	Ceratopogonidae										10			8	3	
	Chironomidae	*Chironominae*		1			5	2	1		1			69	20	
		Orthocladiinae		4	1		4				1			46	6	
		Podonominae		3			7								3	
		Tanypodinae					1				9			24	115	
	Limoniidae	*Antocha*					10							6	1	
		Eloeophila											10		1	
	Pediciidae	*Dicranota*									10		10		1	
	Simuliidae	*Simulium*				10								112	43	
	Tabanidae	*Chrysops*					10								1	
	Tipulidae		7				3							1		
	Empididae										10			3		
Ephemeroptera	Baetidae	*Baetis*		5			5							71	5	
		Nigrobaetis (niger)		5			5							13	2	
		Centroptilum (luteolum)		7			3							2	93	
	Caenidae						10							4	1	
	Ephemerellidae			5			5							5	2	0.025
	Heptageniidae	*Heptagenia*		5			5							8	8	
	Heptageniidae	*Kageronia (fuscogrisea)*		5			5							9	3	
	Leptophlebiidae	*Leptophlebia*					10							10	104	
Odonata	Aeshnidae										10				1	
	Cordulegastridae										10				1	
	Gomphidae										10				1	
Plecoptera	Nemouridae	*Amphinemura*	2	5			3							2	25	0.049
		Nemoura	7				3								13	
		Nemurella	2	3			5								2	
		Protonemura	5	3			2								4	

Table 2.
Continued

Order	Family	Genus (Species)	SHR	SCR	A.FIL	P.FIL	GAT	MIN	XYL	PIE	PRE	OTH	UNK	Bio (N)	Ref (N)	Dif. (p)
Plecoptera	Perlodidae	*Isoperla*	1	1			1				7			6	23	
		Diura									10				1	
	Leuctridae	*Leuctra*	3	3			4								40	
	Taeniopterygidae	*Taeniopteryx (nebulosa)*	2	3			5							5	14	
Coleoptera	Dytiscidae										10				1	
	Elmidae			10										4	64	
	Gyrinidae										10			1	2	
Trichoptera	Glossosomatidae	*Agapetus (ochripes)*		8			2							1	3	
	Hydropsychidae			2		5					3			22	59	0.002
	Hydroptilidae	*Hydroptila*								10				34	10	
		Oxyethira								10				7	13	0.043
		Ithytrichia								10				8	2	
	Lepidostomatidae	*Lepidostoma*	2	5					3					224	13	
	Leptoceridae	*Athripsodes (cinererus)*	3				3				4			50	8	
		Mystacides	2	2			5				1				14	
	Limnephilidae		5	2			1				2				1	
	Polycentropodidae					1					9			47	44	
	Psychomyiidae	*Psychomyia*		7		1	1				1			6		
		Tinodes		8		1	1								3	
	Rhyacophilidae	*Rhyacophila*									10			24	4	
Megaloptera	Sialidae														2	
Non-Insects	Lymnaeidae	*Lymnaea*	2	6								2			13	
	Planorbidae	*Gyraulus*			10										37	
	Spaeriidae	*Pisidium*		5			5								52	
	Naididae	*Nais*					10							372	32	0.032
		Stylaria					10									
	Tubificidae												10		24	
	Nematoda													3	1	

Filtering collectors constituted 15% and 13% of the taxa collected in the biocanal and the references streams, respectively, and no significant difference could be found in total abundance between the systems ($p > 0.05$). In both the biocanal and the reference streams, the percentage of passive filter feeders was higher than the percentage of active filter feeders. In the biocanal the percentage of passive filter feeders was 14.6% and in the reference streams it was 7.1% and in both stream types Simuliidae was the most abundant passive filter feeder. The percentage of active filter feeders in the biocanal was 1.4% and in the reference streams it was 5.3%. *Sphaeriidae pisidium* was the most common active filter feeder in the reference streams and these small bivalves were not encountered in the biocanal.

Predators constituted 11% and 19% of the communities in the biocanal and the reference streams and did not differ significantly in total abundance between the systems ($p > 0.05$). A large proportion of the predators in the reference streams was represented by *Tanypodinae,* a taxa that was > 4 times more common in the reference streams than in the biocanal. Large predators belonging to the orders Odonata and Megaloptera were completely absent from the biocanal.

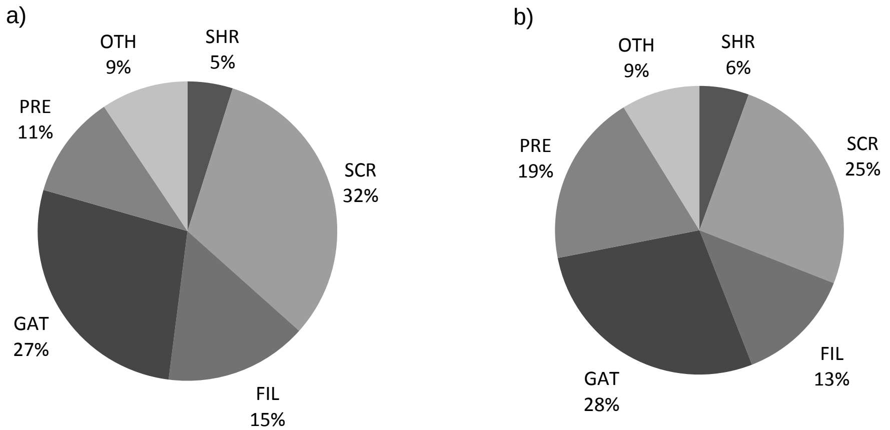

Figure 4. The proportions of the different FFGs in a) the biocanal and b) the reference streams. Abbreviations: SHR: shredders, SCR: scrapers, FIL: filtering collectors, GAT: gathering collectors, PRE: predators, OTH: comprise the groups other, miner, xylophagous, piercer and unknown.

Ecosystem attributes

The ratio between filtering and gathering collectors was 0.56 in the biocanal and this indicates that the system has a high FPOM particulate loading and provides sufficient food for filtering collectors. The ratio between filtering and gathering collectors in the reference streams was just below the threshold value at 0.47 (Table 3).

In the biocanal and the reference streams the ratios between grazers to shredders and total collectors were 0.66 and 0.55, respectively. These results suggest that both the biocanal and the reference streams are heterotrophic systems.

The ratio of scrapers and filtering collectors to shredders and gathering collectors was 1.5 in the biocanal and 1.2 in the reference streams, indicating an abundance of stable substrates for filtering collectors and scrapers in the systems.

Table 3. Ratios of functional feeding groups and the stream ecosystem attributes for which they can serve as surrogates (Modified after Merritt et al. 1996).
Abbreviations: Bio; Biocanal, Ref; Reference streams

Ecosystem Parameter	**FFG-ratios**	**Ratio thresholds**	**Bio**	**Ref**
FPOM in transport to FPOM in storage	Ratio filtering collectors to gathering collectors	FPOM transport greater than normal > 0.50	0.56	0.47
Autotrophy to Heterotrophy	Ratio grazers to shredders and total collectors	Autotrophic > 0.75	0.66	0.55
Substrate stability	Ratio grazers and filtering collectors to shredders and gathering collectors	Stable substrates plentiful > 0.50	1.5	1.2

Environmental factors

The random forest analysis indicated that high oxygen levels had a negative influence on the presence of shredders and the abundance of gathering collectors and filtering collectors (Fig 5 and Fig 6). A high water velocity also seemed to be negative for many FFGs. Both the presence of shredders and the abundance of scrapers and predators were negatively influenced by high water velocities. A higher pH, however, appeared to have a positive effect on some FFGs and scrapers and gathering collectors were more likely to occur at high abundances in areas with high pH. The models also indicated that a high water temperature had a positive effect on some FFGs, and seemed to influence the presence of shredders and the abundance of scrapers positively. A habitat deeper than 40 cm appeared to have a positive effect on the abundance of gathering collectors. The models indicated that scrapers and filtering collectors were more likely to occur at high abundances in areas with stable substrates. The scrapers seemed to be positively affected by a high percentage of boulder substrate, whereas the filtering collectors seemed to be more likely to occur at high abundances in areas with a high percentage of cobble substrate. The random forest analysis also indicated that the plant cover of the riparian zone had an effect on the abundances of FFGs. Filtering collectors appeared to be less likely to occur in areas with a riparian zone with a dense plant cover of grass and sedges, whereas a dense plant cover of this type had a positive influence on the abundance of gathering collectors. The predators seemed to be less likely to occur in high abundances in areas with a riparian zone with a dense plant cover of vascular plants. The accuracy of the models varied between 60.42 and 85.42 (Table 4).

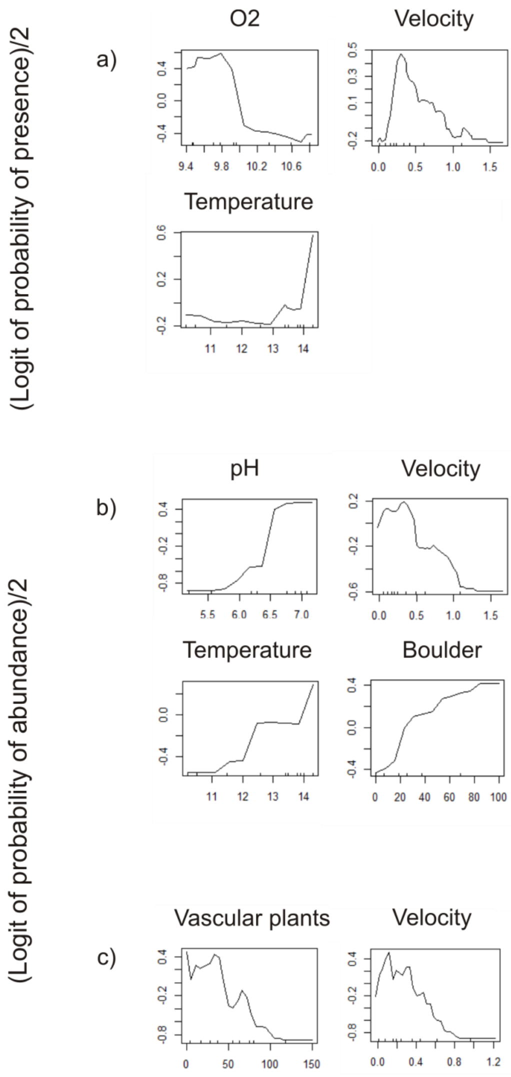

Figure 5. Partial dependence plots for the most important environmental vectors for random forest predictions of the presence/absence of a) shredders and the presence /abundance of b) scrapers and c) predators. Partial dependence is the dependence of the probability of presence on one environmental variable after averaging out the effects of the other environmental variables in the model.

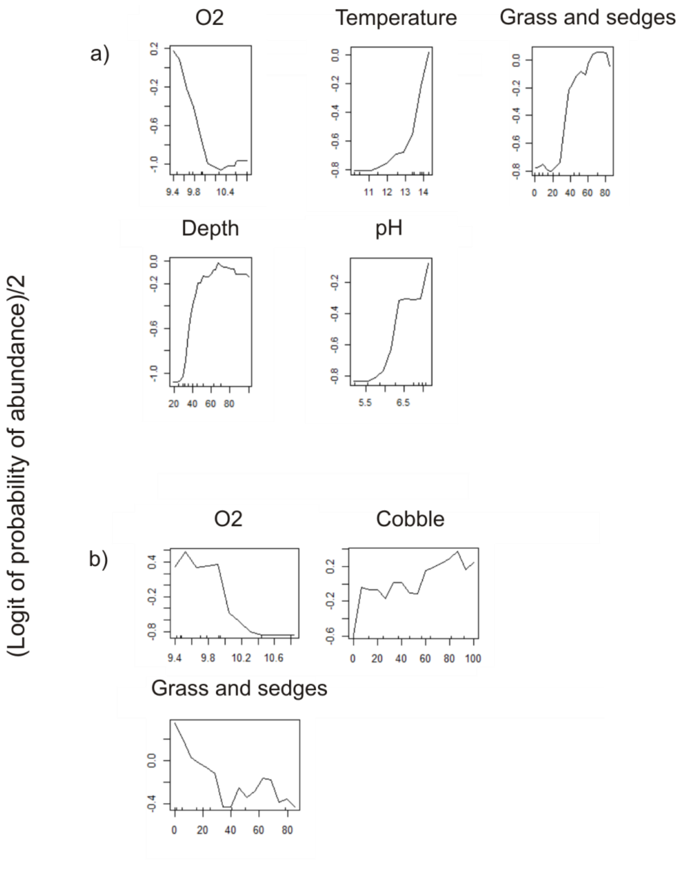

Figure 6. Partial dependence plots for the most important environmental vectors for random forest predictions of the presence /abundance of a) gathering collectors and b) filtering collectors in the reference streams. Partial dependence is the dependence of the probability of presence on one environmental variable after averaging out the effects of the other environmental variables in the model.

Table 4. Accuracy of the random forest models for the different FFGs.
Accuracy equals the proportion of correctly classified instances. Abbreviation: FFG: SHR; shredder, SCR; scraper, GAT; gathering collector, FIL; filtering collector, PRE; predator

Model	FFG	Abundance threshold	Total Error	1 Class Error	0 Class Error	Accuracy %
absence/presence	SHR	-	40	0.41	0.37	60
presence/abundance	SCR	1800	27	0.25	0.28	73
presence/abundance	GAT	500	20	0.33	0.15	80
presence/abundance	FIL	500	35	0.35	0.32	65
presence/abundance	PRE	1700	43	0.44	0.42	57

Discussion

Benthic macroinvertebrates are important components of lotic ecosystems; nevertheless the abundances and functional organization of these taxa are often overlooked when studying the effect of habitat compensation measures in streams. In this study the biocanal contained all FFGs found in the reference streams two years after the biocanal was constructed and only one of the major FFGs showed any differences in density between the biocanal and the reference streams. This indicates that even though the family richness in the biocanal has not reached the same levels as in the reference streams (Gustafsson et al. 2012), the biocanal may still have a similar functional organization as the natural streams in the area.

Functional Feeding Groups

Shredders were more abundant in the biocanal than in the reference streams, even though the low levels of allochthonous coarse particulate organic matter (CPOM) in the biocanal should limit their abundance. The riparian vegetation along the biocanal was scarce and the leaf litter input must be limited, whereas the other potential food source for shredders, macrophytes, was missing entirely in the biocanal. As none of the taxa found in the study are obligate shredders, however, they must be exploiting other energy sources in the absence of CPOM. The macrobenthos classified as shredders in the reference streams contained more specialized taxa than the shredder taxa in the biocanal. Many organisms with shredder-abilities in the reference streams belonged to the taxa Nemoura, Protonemura, and Limnephilidae, all of which are predominantly shredders (see FFG values in Table 2), whereas the most common taxa with shredder-abilities in the biocanal were mainly scrapers and predators (*L. lepidostoma* and *L. athripsodes*). This supports the speculation that most taxa with shredder-abilities in the biocanal are utilizing other food sources.

There was no significant difference in the total filtering collector abundance between the biocanal and the reference streams, but there was a trend for a larger proportion of passive filter feeders in the biocanal and a larger proportion of active filter feeders in the reference streams. The low number of active filter feeders in the biocanal was mainly explained by the absence of bivalves, represented by *S. pisidium* in the reference streams. The absence of mollusks in the biocanal is probably an effect of their slow colonization abilities (Kappes and Haase, 2012). Despite the lack of bivalves, the biocanal contained a high proportion of filtering collectors. This may be a result of a high influx of nutrient-rich water due to its connection to the main river. Previous studies on the effects of surface releases from reservoirs on benthic fauna have shown that the high production and zooplankton abundance in the dam will have a positive effect on the nutrient content in the downstream area, increasing the abundance of mainly filter feeding taxa (Richardson and Mackay, 1991, Macfarlane and Waters, 1982, Parker and Voshell, 1983). This is referred to as the "lake outlet effect", which was further illustrated by the fact that Hydropsychidae, Polycentropodidae and Psychomyia had their highest densities in the first pool habitat downstream the hydropower dam (i.e. the first depositional area in the biocanal). The densities of filter feeding Simuliidae, however, decreased with distance from the dam, something that is not in accordance with the lake outlet effect. However, in July the same year, the densities of Simuliidae were indeed highest in the two uppermost habitats in the biocanal. Since the areas closest to the dam should be most beneficial for the Simuliidae most larvae might have been fully developed and left the biocanal by the time of the sampling in September. This is supported by the fact that >4 times more pupae were found in the two uppermost habitats compared to all other habitats combined in July.

The proportions of predators were higher in the reference streams than in the biocanal. Gore (1982) suggested that predators normally are the last FFG to colonize streams. This may explain why both small predators such as Tanypodinae and large predators such as *Perlodidae isoperla* occurred in lower densities in the biocanal than in the reference streams. The predator community in the biocanal was predominantly represented by trichopterans belonging to the families Leptoceridae, Polycentropodidae and Rhyacophilidae, whereas predators from other groups such as the Sialidae, Dytiscidae, Aeshnidae, Cordulegastridae and Gomphidae were absent from the biocanal. The lower proportion of these large predators in the biocanal may therefore be an effect of ongoing colonization.

Ecosystem Attributes

The ratio between filtering and gathering collectors in the biocanal suggested that FPOM in transport was greater than normal and that the amount of food for filtering collectors thereby was sufficient to support a vital filter feeding community, something that is supported by the high densities of Simuliidae in the biocanal. A comparison between the ratios in the biocanal and the reference streams indicated that FPOM in transport was higher in the biocanal than in the reference streams. The reason is probably that the biocanal receives much of its organic material from River Västerdalälven. The organic input in such high order streams often originates from FPOM from upstream areas, whereas much of the organic input in small forest streams, like the reference streams, instead derives from CPOM (Cummins, 1975).

The ratio of grazers to shredders and total collectors, however, indicated that both the biocanal and the reference streams are heterotrophic and thereby dependent on input of allochthonous organic material. There is plenty of riparian vegetation along the natural reference streams and the theory that these streams are heterotrophic is in consistence with the result from the ratio that represented FPOM in transport. Since there is a lack of riparian vegetation along the biocanal and since most of the input of allochthonous carbon in the biocanal most likely originates from the main river, the notion that the biocanal is heterotrophic might be questioned. The large proportion of scrapers in the biocanal also indicates that a proportion of the carbon in the biocanal is derived from autochthonous sources. But even though the scrapers were abundant in the biocanal, they were not common enough for the biocanal to be classified as an autotrophic system.

The ratio of scrapers and filtering collectors to shredders and gathering collectors indicated that both the biocanal and the references contained stable substrates for filter feeders and scrapers. The importance of stable substrates is also illustrated by the positive influence of a high percentage of gravel and cobble substrate on the abundance of filtering collectors and scrapers according to the random forest model (see below).

Environmental factors

The distribution of benthic macroinvertebrates is to a large extent influenced by abiotic factors (Rosemond et al., 1992, Statzner et al., 1988, Cummins and Lauff, 1969). In this study the random forest models indicated that the abundance of scrapers was positively influenced by a substrate dominated by boulders, while the abundance of filtering collectors was positively influenced by a high percentage of cobbles. This is not surprising, since diversity and abundance of macroinvertebrates usually increase with increased substrate stability (Giller and Malmqvist, 1998) and scrapers and filtering collectors are especially favored by stable substrates (Merritt and Cummins, 2006). The scrapers are connected to stable substrates since they cling on the substrate surface to graze on periphytic algae (Cummins and Klug, 1979), whereas the filtering collectors depend on stable substrates to either attach themselves to (e.g. Simuliidae) (Eymann and Friend, 1988) or attach their nets to (various Trichoptera larvae) (Fairchild and Holomuzki, 2002, Morse, 2003).

Scrapers, predators and shredders seemed to be negatively influenced by high water velocity and the highest abundances were found in samples with a velocity of 0.5 m s^{-1} or less. Earlier studies have found the optimum velocity to be 0.6 m s^{-1} for macroinvertebrates in general (Orth and Maughan, 1983) and 0.1 - 0.4 m s^{-1} for Ephemeroptera, Plectoptera and Trichoptera (Gore et al., 2001). The findings in this study, however, could also be related to the sampling technique since high water velocity might cause backwash in netted samplers, causing a loss of macroinvertebrates (Peckarsky, 1984).

Earlier studies have shown a decrease in taxa richness with decreasing pH in streams with poor buffering capabilities affected by acid downfall (Townsend et al., 1983, Kimmel et al., 1985, Rosemond et al., 1992, Raddum and Fjellheim, 2002). The region where the biocanal is situated is naturally acid and has a low buffering capacity, making the watersheds sensitive to acid rainfall (Petersen et al., 1995). This may explain why both scrapers and gathering collectors were more likely to occur in high abundances in streams with high pH levels.

Temperature has been shown to influence the benthic fauna composition, mainly through temperature variations within the habitat and the accumulation of degree days (Haidekker and Hering, 2008, Ward and Stanford, 1982). However, for this model only values from one measurement in September were used so the positive influence on the presence of shredders and the abundance of scrapers shown by temperature may be overestimated. The effect of temperature is also often related to altitude (Jacobsen et al., 1997) and land use (Sponseller et al., 2001) and the effects can be hard to distinguish.

The properties of the riparian zone are often tightly linked to the aquatic environment and may influence the FFGs through input of CPOM or through shading. In this study, however, it is possible that the perceived influence of the plant cover on gathering collectors, filtering collectors and predators derives from characteristics of the different reference streams. The negative connection between a dense cover of vascular plants and the abundance of predators is for example probably an effect of the scarce plant cover along the old riverbed, which was the reference stream with the highest family diversity and the highest density of predators.

What can we expect in the future?

A fundamental difference between the biocanal and the reference streams is the lack of riparian vegetation and in-stream macrophytes in the biocanal. The riparian vegetation is becoming denser along the biocanal, but even so the species composition will probably differ from what is found along natural streams in the area for many years to come. Many of the reference streams are surrounded by mixed forest stands, a successional stage that the riparian zone along the biocanal will take decades to reach. Alder, which is a pioneer species, is currently rapidly colonizing the area along the biocanal (S. Gustafsson, personal obs). This early stage of succession of the riparian zone might have a positive influence on the benthic fauna in the biocanal since alder leaves have been shown to be the preferred food source for many shredders (Wallace et al., 1970, Otto, 1974, Haapala et al., 2001). Furthermore, previous studies have shown that the leaf input from riparian plants in early successional stages is more easily decomposed (Webster and Benfield, 1986) compared to leaf input from mature forest stands, which could have a positive effect on the macroinvertebrate density. Nevertheless, a more diverse riparian zone with leaves with different rates of decomposition is needed to provide a continuum of CPOM during the whole year (Petersen and Cummins, 1974, Haapala et al., 2001). It is therefore possible that the shredder community in the biocanal will continue to constitute of more unspecialized taxa than the reference streams, at least during the first years of streamside succession.

Conclusions

One of the greatest threats to global freshwater biodiversity is habitat degradation (Dudgeon et al., 2006) which can be mitigated by the construction of nature-like fishways with habitat compensation properties. Since such artificial stream habitats are likely to become increasingly important as river restoration and connectivity issues are addressed, the integrity of these man-made structures is of major concern. The biocanal, with its mosaic of habitat types supported a family composition and diversity of benthic fauna that was approaching that of the reference streams in the area two years after its construction and the functional organization of the biocanal was also similar to that of the reference streams. Nature-like fishways may thus facilitate both passage for fish species and provide valuable habitat.

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The Macroinvertebrate Community in a Nature-like Fishway with Habitat Compensation Properties

Nature-like fishways are often constructed to restore connectivity in streams exploited for hydropower. They also, however, have the potential to compensate for important habitats that have been degraded or lost.

The aim of this thesis was to improve knowledge of the concept of nature-like fishway design, with special focus on their habitat compensation potential. This was done by comparing a nature-like fishway with four different habitat types, termed the biocanal, to six nearby natural reference streams. In paper I the macroinvertebrate colonization of the biocanal was studied and the community composition was compared to that of the natural reference streams. Furthermore, the potential for the biocanal to contain a diverse macroinvertebrate fauna was investigated. The results showed that the family composition of benthic fauna in the biocanal was approaching that of the reference streams and that the different habitat types in the biocanal contributed to the increased family diversity. In paper II the functional organization of the biocanal was studied using the functional feeding group approach. The results showed that the functional organization in the biocanal resembles that of the natural reference streams two years after the biocanal's construction.

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