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Effects of beaver dams on benthic macroinvertebrates

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ABSTRACT

In the 1870's the beaver (*Castor fiber*), population in Sweden had been exterminated. The beaver was reintroduced to Sweden from the Norwegian population between 1922 and 1939. Today the population has recovered and it is estimated that the population of *C. fiber* in all of Europe today ranges around 639,000 individuals. The main aim with this study was to investigate if there was any difference in species diversity between sites located upstream and downstream of beaver ponds. I found no significant difference in species diversity between these sites and the geographical location of the streams did not affect the species diversity. This means that in future studies it is possible to consider all streams to be replicates despite of geographical location. The pond age and size did on the other hand affect the species diversity. Young ponds had a significantly higher diversity compared to medium-aged ponds. Small ponds had a significantly higher diversity compared to medium-sized and large ponds. The upstream and downstream reaches did not differ in terms of CPOM amount but some water chemistry variables did differ between them. For the functional feeding groups I only found a difference between the sites for predators, which were more abundant downstream of the ponds.

SAMMANFATTNING

Under 1870-talet utrotades den svenska populationen av bäver (*Castor fiber*). Bävern återintroducerades till Sverige från den norska populationen mellan åren 1922 och 1939. Idag har populationen återhämtat sig och man beräknar att populationen av bäver i Europa idag består av 639000 individer. Huvudsyftet med den här studien var att undersöka om det är någon skillnad i artdiversitet mellan områden som ligger uppströms resp. nedströms bäverdammar. Jag hittade ingen signifikant skillnad i artdiversitet mellan prover tagna uppströms och nedströms och strömmens geografiska läge påverkade inte artdiversiteten. Detta innebär att man i framtida studier kan behandla alla strömmar som replikat oavsett deras geografiska läge. Dammens ålder och storlek å andra sidan påverkade artdiversiteten. Unga dammar hade en signifikant högre artdiversitet jämför med medel-gamla dammar medan små dammar hade en signifikant högre diversitet jämfört med medel-stora och stora dammar. CPOM-mängden skiljde sig inte åt mellan platserna uppströms och nedströms bäverdammarna men vissa vattenkemivariabler skiljde sig mellan platserna. Abundansen av funktionella födogrupper skiljde sig endast för gruppen predatorer som var signifikant högre nedströms bäverdammarna.

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1 INTRODUCTION

Once beavers (*Castor fiber* and *C. canadensis*) could be found throughout all of the northern forest belt from North America to Asia and Europe. Their distribution ranged from subarctic to subtropical regions (Rosell *et al.* 2005). Both the North American *C. canadensis* and the Eurasian *C. fiber* were heavily overexploited (Rosell *et al.* 2005) and around the 1870's the overexploitation due to the high prices of fur and castoreum led to extinction of the Swedish population of Eurasian beaver. By the time the authorities realized the condition of the beaver population, and banned hunting in 1873, nothing could be done to save the population (Hartman 1994). At the beginning of the 1900's only a small fraction of the Scandinavian beaver population remained in the southern part of Norway (Hartman 1994), and it has been estimated that only 1,200 individuals of *C. fiber* remained across Europe (Nolet and Rosell 1998). The beaver was reintroduced to Sweden from the Norwegian population between 1922 and 1939. Eighty beavers were introduced to a total of 19 sites and reproduction was observed at 11 of these sites (Fig. 1). In some of the localities where the beaver was reintroduced the population did not start to increase substantially in size until some 30 years after the introduction. This may partly be due to long dispersal distances when looking for a suitable habitat, which causes a decrease in beaver density and mate-finding becomes more difficult (Hartman 1994). The same overexploitation of beavers took place in North America as well, but as with the European population of *C. fiber*, the North American population of *C. canadensis* is increasing once again (Rosell *et al.* 2005). It is estimated that the population of *C. fiber* today ranges around 639,000 individuals in Europe (Rosell *et al.* 2005) of which probably more than 100,000 can be found in Sweden (Hartman 1995).

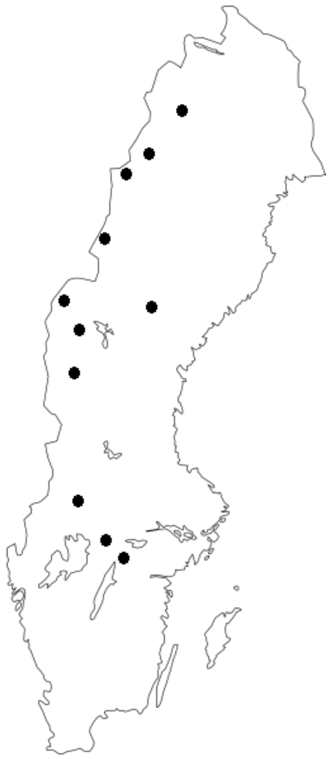

Fig. 1. The 11 sites in Sweden where reproduction of reintroduced beaver was observed after reintroduction between 1922 and 1939 (Based on a map from Hartman 1994).

Beavers are herbivours and their diet consists of leaves, twigs and bark of most species of woody plants growing near the water, as well as many herbaceous plants, such as aquatic macrophytes (Naiman *et al.* 1986). By their foraging activities beavers increase the amount of organic material available and thus create habitats for other species. Since the beaver is the only member, i.e. biomass-dominant species of its functional group it can be said to be a keystone species (Rosell *et al.* 2005).

1.1 Beavers - Environmental engineers

Beavers can alter the local environment by changing, maintaining or creating habitats in a way that few animals can and are considered to be ecosystem engineers (Naiman *et al.* 1986, Jones *et al.* 1994) and are known to increase the species diversity at a local scale (Rosell *et al.* 2005). One of the major effects caused by the construction of beaver dams is the increased proportion of water and wetlands in the landscape which creates habitats for other freshwater species (Johnston and Naiman 1990). Wetlands are also a sink of mercury (Hg) and are said to play an important role when it comes to concentrations and mobility of Hg. In addition, the wetlands are often a source of methylmercury (MeHG) (Driscoll *et al.* 1998, Galloway and Branfireun 2004). Except for increasing the local species diversity the activity of beavers favor regeneration of degraded habitats (Rosell *et al.* 2005). Beavers can noticeably alter the channels of streams by the construction of dams and may influence as much as 30-50 % of the total length of 2nd to 4th order streams (Naiman and Melillo 1984, Naiman *et al.* 1986). For streams of the 5th order and smaller, beavers drive key geomorphic processes, e.g. by dam construction which leads to sedimentation within the pond and in the formation of alluvial river valleys (Westbrook *et al.* 2011). Beavers rarely construct dams in 1st order streams and in streams above the 5th order the dams located in the main channel are often destroyed during the spring flood (Naiman *et al.* 1986).

The dams affect the surrounding environment in several ways by:

1) altering the geomorphology of the streams and impounding water and sediment in the dam itself (Naiman *et al.* 1986)

2) altering the patterns of organic matter, and nutrient deposition and retention (Naiman and Melillo 1984)

3) increasing the irradiation and the primary production of the pond by reducing the canopy cover surrounding the pond (Naiman *et al.* 1986)

4) affecting the vegetation succession (Terwilliger and Pastor 1999)

5) contributing to 25 % or more of the total herbaceous plant species richness in the riparian zone (Wright *et al.* 2002).

Beaver dams may cause discharge variations in the stream (Fairchild and Holomuzki 2002). The construction of a beaver dam may also cause a lowering of the discharge peaks downstream. During periods of low flows the discharge is increased while during periods with high flow the discharge is reduced. At the local scale the water level is increased and at the same time the dam reduces the overall flood risk (Nyssen *et al* 2011).

1.2 Beaver dam effects on species

1.2.1 Macroinvertebrates

Beaver-induced alterations may affect the taxa composition of macroinvertebrates downstream of beaver ponds, but results have been ambiguous. Margolis *et al*. (2001b). reported that the taxa composition upstream and downstream of beaver ponds do not differ from one another. In contrast, Pliūraitė and Kesminas (2012) found that the number of taxa of Ephemeroptera, Plecoptera and Trichoptera was higher in the upstream than in the downstream reaches. The upstream sites represent an area that has not been disturbed by beaver activity (Pliūraitė and Kesminas 2012). Some taxa are unique to above or below-impoundment sites and the dominant taxa differ between upstream and downstream sites (Margolis *et al*. 2001b). Species of the order Plecoptera are highly sensitive to environmental degradation (Maxted *et al.* 2000) and they are more abundant upstream (an area unaffected by beavers) of the beaver pond than downstream (Pliūraitė and Kesminas 2012). There are also differences in taxa composition between the stream and pond habitats. Streams are dominated by blackflies (Simuliidae), Tanytarsini (Chironomidae), scraping mayflies (Ephemeroptera) and net-spinning caddisflies (Trichoptera) while ponds are dominated by Tanypodinae and Chironomini (Chironomidae), predacious odonates, Tubificidae and filtering pelycopods (Mollusca) (McDowell and Naiman 1986). Differences between the stream and pond biota can also be seen in the number of taxa of Ephemeroptera, Plecoptera and Trichoptera found at the respective sites. The number of taxa from these three orders is significantly lower in the pond compared to the stream sections (Arndt and Domdei 2011). Even though the pond has a lower taxonomic richness it has a higher number of dragonflies (Anisoptera), damselflies (Zygoptera), Trichoptera and also some species of snails and mussels, than the stream (Rosell *et al.* 2005). In the pond it is also possible to find lentic (standing water) species of e.g. Odonata and Ephemeroptera that otherwise do not occur in streams (Arndt and Domdei 2011). For smaller streams the beaver ponds are created at the expense of riffle and glide habitats and these ponds favor lentic species instead of the original lotic (flowing water) species (Rosell *et al.* 2005). When a dam is constructed the typical running water communities that consists of Simuliidae, chironomid Tanytartarsini, scraping mayflies and net-spinning caddisflies are replaced by other groups of invertebrates. When the stream is transformed from a lotic to a lentic habitat it is instead inhabited by chironomid Tanypodinae and Chironomi, predatory dragonflies (Odonata), sludge worms (Tubificidae) and filtering mussels (Pelecypodae) (Rosell *et al.* 2005). During the spring and summer the densities of invertebrates in the pond is 2-5 times greater than the densities in the stream, while during autumn there is no significant difference in invertebrate density between the two systems (McDowell and Naiman 1986).

Beaver ponds differ from the stream sites in that they have a lower macroinvertebrate taxonomic richness (McDowell and Naiman 1986, Clifford et al 1993, Anderson and Rosemond 2007, Arndt and Domdei 2011, Pliūraitė and Kesminas 2012). Non-biting midges (Chironomidae) can make up roughly 35-70 % of the number of macroinvertebrate taxas of the ponds (Pliūraitė and Kesminas 2012) and many taxa can dominate either the ponds or the streams every year (Clifford *et al.* 1993). Fuller and Peckarsky (2011a, 2011b) concluded that beaver ponds have very few systematic effects on downstream ecosystems. They found that the effects of the pond on nutrients, basal resources and invertebrate consumers varied and depended on the pond morphology as well as on the annual hydrological variation. The expected effects of beaver ponds on the downstream insect development may also vary depending on the morphology of the pond (Fuller and Peckarsky 2011b). The water table of the pond contains about 10 times more carbon compared to the stream and receives three times more carbon per unit length (Naiman *et al.* 1986).

Depending on the morphology of the ponds also invertebrate life histories can be affected (Fuller and Peckarsky 2011b). The beaver-induced felling of trees surrounding the pond reduces the canopy cover and thus increases the irradiation (Naiman *et al.* 1986). Ponds with a high-head dam (i.e. a deep pond) and a small surface area cool the water, because of the relatively small irradiation/volume ratio, resulting in a cooler water temperature downstream of the dam compared to the upstream reaches. One effect of the cooler water temperature can be seen in the life history for the females of the mayfly species *Baetis bicaudatus* where the females downstream of the beaver ponds are significantly larger than their upstream counterparts (Table 1). In cases where the pond has a low-head morphology (shallow pond) and a large surface area the water is instead warmed and the females downstream of the pond emerge at smaller sizes (Fuller and Peckarsky 2011b). Since the egg size of *B. bicaudatus* do not vary this means that larger size females will also be able to produce more eggs (McPeek and Peckarsky 1998) which may affect the population size of future generations (Fuller and Peckarsky 2011b).

Aquatic organisms – like macroinvertebrates – have specific environmental requirements related to e.g. temperature, pH, nutrient availability and habitat stability and complexity in order to survive, reproduce and grow. This makes them suitable as indicators of changes in the aquatic environment (Brönmark and Hansson 2005, Naturvårdsverket 2007).

Table 1. Effects on the females of the mayfly species *Baetis bicaudatus* caused by the morphology of beaver dams (Fuller and Peckarsky 2011b).

Characteristics	**Dam type**	
	High-head dam	**Low-head dam**
Pond		
Surface area	Small	Large
Water depth	Deep	Shallow
Effects on water temperature downstream	Cool	Warm
Baetis bicaudatus		
B. bicaudatus female size downstream	Large	Small
B. bicaudatus female relative egg number per female	High	Low

One example of both the direct and indirect negative effects that can be caused by a beaver dam is the effects on the Louisiana pearlshell mussel (*Margaritifera hembeli*). It has become endangered due to the increased water level caused by beaver dams (U.S. Fish and Wildlife Service 1993, Rosell *et al.* 2005). Since the mussels must live in flowing waters the inundation caused by the dam as well as the increased accumulation of silt in the pond affects it directly and can kill the mussels. In addition to affecting species life histories the beaver dams may also prevent the migration of organisms (Schlosser 1995). The Louisiana pearlshell mussel requires a host fish to complete its lifecycle and it has been suggested that the beaver dam prevents the migration of this host fish and thus affecting the Louisiana pearlshell mussel indirectly (Johnson and Brown 1998).

1.2.2 Effects on other taxa

Beaver ponds also affect the fish community of the stream. The dam construction causes a division of the fish population of the stream with lentic species dominating in the pond while lotic species dominate in the stream (Hägglund and Sjöberg 1998). The beaver-induced changes caused by the construction of beaver dams also causes an increase in habitat diversity and have been proposed to stabilize relationships between e.g. dominant fish species in small forest streams (Hägglund and Sjöberg 1998).

In addition, construction of beaver dams increases the nightly activity of some bat species in areas with river valleys that have been transformed by beavers (Ciechanowski *et al.* 2010). Beaver ponds can provide refuge against the bottom ice for trout during the winter (Hägglund and Sjöberg 1998). Additionally, the beaver-induced alterations contribute to increase the herbaceous plant species richness in the riparian zone (Wright *et al.* 2002).

1.3 Functional feeding groups

Macroinvertebrates can be classified into different functional feeding groups (FFG) based on their choice of food and the way they acquire their food. The categories used for the macroinvertebrates of this study were predators, piercing predators, suctorial predators, scrapers, shredders, omnivores, filtering collectors and gathering collectors (for further information about the FFG's see Appendix 1). Several studies have shown that gatherers are the dominant FFG, both in terms of relative abundance as well as biomass, for sites both upstream and downstream of beaver ponds as well as in the ponds themselves (Anderson and Rosemond 2007, Arndt and Domdei 2011, Pliūraitė and Kesminas 2012).

Shredders, predators and collectors have been found to dominate both the lentic and the lotic habitats of the streams. The proportion of shredders in ponds is significantly lower than in the stream and there is a lower proportion of passive filter feeders in the ponds, and a higher proportion of predators in the ponds compared to the downstream section (McDowell and Naiman 1986, Arndt and Domdei 2011). The dominance of collectors and predators in the pond reflects the increases in FPOM (fine particulate organic matter), VPOM (very fine particulate organic matter) and prey types in the pond (McDowell and Naiman 1986).

Fuller and Peckarsky (2011a) found no difference in abundance between upstream and downstream sites for FFGs. In addition they did not find any connection between pond morphology and upstream and downstream ratios of grazers, predators or detritus feeders. They did however find a positive relationship between pond morphology and the upstream/downstream ratio of suspension feeders. In cases when the ponds were high-head and had a small surface area the abundance of suspension feeders increased. In contrast the abundance decreased in cases when the pond had a low-head and a large surface area (Fuller and Peckarsky 2011a).

1.4 Effects on water chemistry and water temperature

The beaver dam can affect both the downstream water chemistry and water temperature. The retention of heat in the pond causes the water at the outflow of the pond to be warmer than the water at the inflow of the pond. The heating effect on the outflow water can however be seen as a minor effect since there is only a slight temperature increase compared to the upstream reaches (Rosell *et al.* 2005, Margolis *et al.* 2001b). For the water chemistry both DOC (dissolved organic carbon) and TOC (total organic carbon) concentrations are higher at the pond outflow (Naiman *et al.* 1986, Smith *et al.* 1991, Margolis *et al.* 2001a). The increased concentration of MeHg in the waters downstream of the beaver ponds indicates that the ponds also are sources of MeHg (Driscoll *et al.* 1998, Galloway and Branfireun 2004).

1.5 The aim of the study

The goal of this study was to investigate if there is an effect of beaver dams on macroinvertebrate assemblages. Most studies that have compared the macroinvertebrate assemblage in streams with beaver ponds have looked at differences between the pond and the stream habitats (McDowell and Naiman 1986, Naiman *et al.* 1986, Clifford *et al.* 1993, Arndt and Domdei 2011, Anderson and Rosemond 2007). Margolis *et al*. (2001b) compared the upstream and downstream reaches but did not find any difference in diversity between the sites. They did however find species that were unique to either the upstream or downstream area and the dominant taxa also differed between the upstream and downstream sites. Filter feeders such as Hydropsychidae have been found to be more abundant downstream of dams (Mackay and Waters 1986). The results gained so far are however ambiguous and do not allow any general conclusions concerning the effect of beavers on macroinvertebrates (see also 1.2.1). To shed light on the role of beaver dams, I aimed at evaluating if the age and size of beaver ponds are important explanatory variables for potential upstream-downstream differences in macroinvertebrate assemblage. My main hypothesis was that there is higher species diversity downstream of beaver dams than upstream.

In addition to my main hypothesis I also evaluated:

1) If there is a difference in species diversity between different geographical regions.
2) If there is a difference in abundance of FFG's between upstream and downstream reaches.

2 MATERIALS AND METHODS

2.1 Study sites

The streams studied were located at five different localities with a total of 12 streams (Fig. 2). The sites were, from north to south, Luleå (n=3), Sundsvall (n=3), Skinnskatteberg (n=2), Surahammar (n=2), and Örebro (n=2). The sites chosen for the study were categorized into three different geographical regions, i.e. Luleå, Sundsvall and South (including the three sites Surahammar, Örebro, and Skinnskatteberg) – which represented a north-south gradient.

The streams were also categorized into four 'age groups' and four 'size groups' (by visual observation). The age classes used were young, medium, old and special. The group 'special' included ponds that were old and big but with an additional small pond before the downstream site causing the downstream site to act more like a site with a young and small pond. For the size classes I used the groups small, medium, large and special with 'special' meaning the same as for the 'age group' (for summary of categories see Table 2).

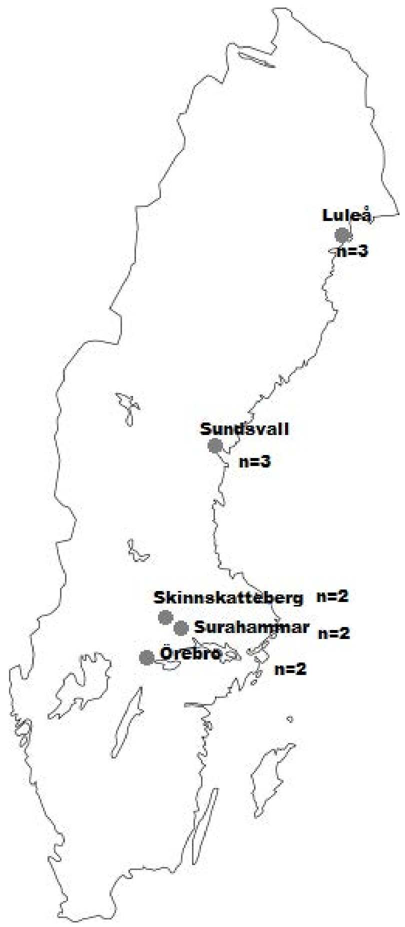

Fig. 2. The 12 streams were located in three geological areas - Luleå, Sundsvall and South (Skinnskatteberg, Surahammar and Örebro).

Table 2. All 12 streams studied were categorized according to geographical location, age and size. Special indicates that the pond is old and big but there is another small young pond before the downstream site where macroinvertebrate sampling took place.

Stream ID	Geo group	Age group	Size group
BD_01	Luleå	young	small
BD_02	Luleå	medium	medium
BD_03	Luleå	young	small
BD_11	Sundsvall	old	large
BD_13	Sundsvall	old	large
BD_14	Sundsvall	old	large
BD_21	South	old	medium
BD_22	South	young	small
BD_23	South	special	special
BD_24	South	special	special
BD_25	South	medium	large
BD_26	South	young	small

2.2 Macroinvertebrate sampling

The 12 streams were quantitatively sampled for benthic macroinvertebrates between October 15 and November 15, 2012 using a Hess sampler (Fig. 3). The Hess sampler used had a height of 40 cm and a mesh size of 500 µm and covered a bottom area of 0.086 m^2. Four replicates were sampled approximately 100 meters upstream and 100 meters downstream of the beaver dams, respectively. The upstream replicates were used as controls when investigating the effect of beaver dams on macroinvertebrate assemblage of the stream. The organisms collected were preserved in 0.5 liter containers with 99 % ethanol. The water level was higher than normal (*personal observation*) for many of the streams but it was still possible to sample them for macroinvertebrates. For one of the streams in Skinnskatteberg, the water level was far above normal and it was only possible to take two samples in the upstream and the downstream site respectively.

Fig. 3. Hess sampler used for sampling of macroinvertebrates in streams with a sandy/rocky substrate.

2.3 Sorting and identification of macroinvertebrates

2.3.1 Sorting and subsampling

When processing the samples the macroinvertebrates were removed from the debris and re-preserved in vials containing 99 % ethanol. All organisms were identified to the lowest taxonomic level possible. Samples that contained high numbers of Chironomidae (>200 individuals/sample) were subsampled by sorting at least 300 individuals in a fraction of the total sample. Due to the high number of Simuliidae in the southernmost streams (>1000 individuals/sample) I subsampled both Chironomidae and Simuliidae in these streams. For both groups the cut-off for sub-sampling was set at 200 individuals.

2.3.2 Sorting species into functional feeding groups

After the macroinvertebrates had been determined to the lowest taxonomic level possible, all taxa were sorted into FFG's. The keys provided by Meritt and Cummins (2007) and Nilsson (1996, 1997) were used for identification of the FFG's. In addition to the groups defined in Cummins and Klug (1979), I added the FFG omnivores (see Appendix 1).

2.4 Coarse particulate organic matter (CPOM) and water chemistry

In addition to sorting the macroinvertebrates from the samples, coarse particulate organic matter (CPOM) was removed from the samples for quantification. Three categories of CPOM were collected from the samples. The CPOM categories were woody debris (W), deciduous leaves (D) and needles (N). The CPOM was then oven dried (105°C for 48 hours) before weighed to nearest 0.001 g. All pieces of material with a size of less than 0.5 × 0.5 cm (for leaves), or a length of 0.5 cm (for branches and pieces of needles) was considered to be fragments and was not included in the measurement. At all sites water samples were collected for analysis of water chemistry variables – tot-N (total nitrogen), NO_2/NO_3, TOC, DOC, and MeHG. The water chemistry was sampled using flasks attached on 4 meter long rods. The samples were collected in the middle of the water column. Chemical analysis were performed by Department of environmental analysis, SLU, according to their standard accredited methods.

2.5 Data analysis and calculations

2.5.1 Software

I chose to use non-parametric tests when analyzing the data since it did not have a normal distribution. For analysis of the data I used Statistica v.9.0. For calculations of diversity, evenness/equitability and similarity indices I used Microsoft Excel 2007.

2.5.2 α- diversity

I used two different approaches when calculating the species diversity of the stream (α-diversity). These were Shannon's diversity index and Simpsons index of diversity (1-D). The reason for using two different indices for calculating the diversity was that the indices calculate the diversity in different ways. Simpson's index of diversity (1-D) is for example less affected by the presence of rare species. Shannon's diversity index is one of the most popular ways of measuring species diversity. This index increases as the diversity increases but biological systems seem to never exceed a value of 5.0. Shannon's diversity index measures the amount of order in the sample by using four types of information: 1) the number of species, 2) the total number of individuals in each species, 3) the places that individuals of each species occupy and 4) the places occupied by individuals as separate individuals (i.e. not taking into consideration that the individuals are part of a species community) (Krebs 1999). When doing the calculations I counted Chironomidae as one species and Oligochaeta as one species in the data set since I lacked species data for these orders.

$$H' = \sum_{i=1}^{s} (p_i)(log_2 p_i)$$

H' = Shannon's diversity index
s = number of species
p_i = proportion of total sample that belongs to the i-th species

(Krebs 1999)

The second way of calculating species diversity that I used was Simpson's index of diversity (1-D). This is a complement to Simpson's original measure (D). The original measure (D) gives an index that ranges from 0 to 1 where 0 represents infinite diversity while 1 equals no diversity. Since this is counterintuitive I instead used Simpson's index of diversity (1-D). With this index the diversity increases as the value of the index increases, i.e. 0 represents no diversity while 1 equals infinite diversity. Simpson's index of diversity (1-D) is relatively unaffected by rare species in the dataset (Krebs 1999).

$$1 - D = 1 - \sum_{i=1}^{s} \left[\frac{n_i(n_i - 1)}{N(N - 1)} \right]$$

1 - D	= Simpson's index of diversity
n_i	= number of individuals of species i in the sample
N	= the total number of individuals in the sample
s	= number of species in the samples

(Krebs 1999)

Simpson's index of diversity gives a higher weight to abundant species and is therefore quite resilient against addition of rare species. My estimates of both Shannon's diversity and Simpson's index of diversity are probably underestimated since many specimens were only determined to higher taxonomic levels. The diversity indices are still useful for comparisons of relative trends between sites of this study.

2.5.3 β-diversity

I also compared the similarity in species composition between the upstream and downstream reaches (β-diversity) and to do so I used Sørensen's similarity index. The index ranges from 0 (no species overlap) to 1 (complete species overlap).

$$S_s = \frac{2a}{2a + b + c}$$

S_s	= Sørensen's similarity coefficient
a	= number of species that occurs in both sample A and sample B
b	= number of species that only occurs in sample B but not in A
c	= number of species that only occurs in sample A but not in B

(Krebs 1999)

Sørensen's coefficient weights the matches in species composition more heavily than mismatches for the two compared samples (Krebs 1999).

2.5.4 Evenness

In addition I calculated the evenness, or equitability, of the samples. Evenness is a measure of how similar the abundance of species is. I.e., a community with all species having roughly the same abundance has a higher evenness than a community with few dominant species (Krebs 1999). Simpson's index of diversity takes evenness into account when calculating the diversity. I used Shannon's equitability as a measure of the evenness of species for the streams.

$$E_H = \frac{H}{lnS}$$

E_H = Shannon's equitability
H = Shannon's diversity index
S = total number of species in the community

2.5.5 Species richness

Species richness, the total number of species, was calculated for all upstream and downstream sites. The information was then used to investigate if the beaver ponds affected the species richness of the downstream reaches. The pond factors that were investigated, in addition to the upstream/downstream comparison of species richness, were pond age, size and geographical location.

3 RESULTS

A summary of the species found at each site can be found in Appendix 4.

3.1 Diversity, evenness and species richness

3.1.1 Upstream/downstream comparison

There was a trend for higher Shannon's and Simpson's diversity downstream (D) of the beaver ponds compared to upstream (U), when including samples from all three geographical groups (Wilcoxon Matched Pairs Test, n=45, t=430 z= 0.99, p>0.05, and n=45, t=424, z=1.06, p>0.05 respectively) (Fig. 4A and B).

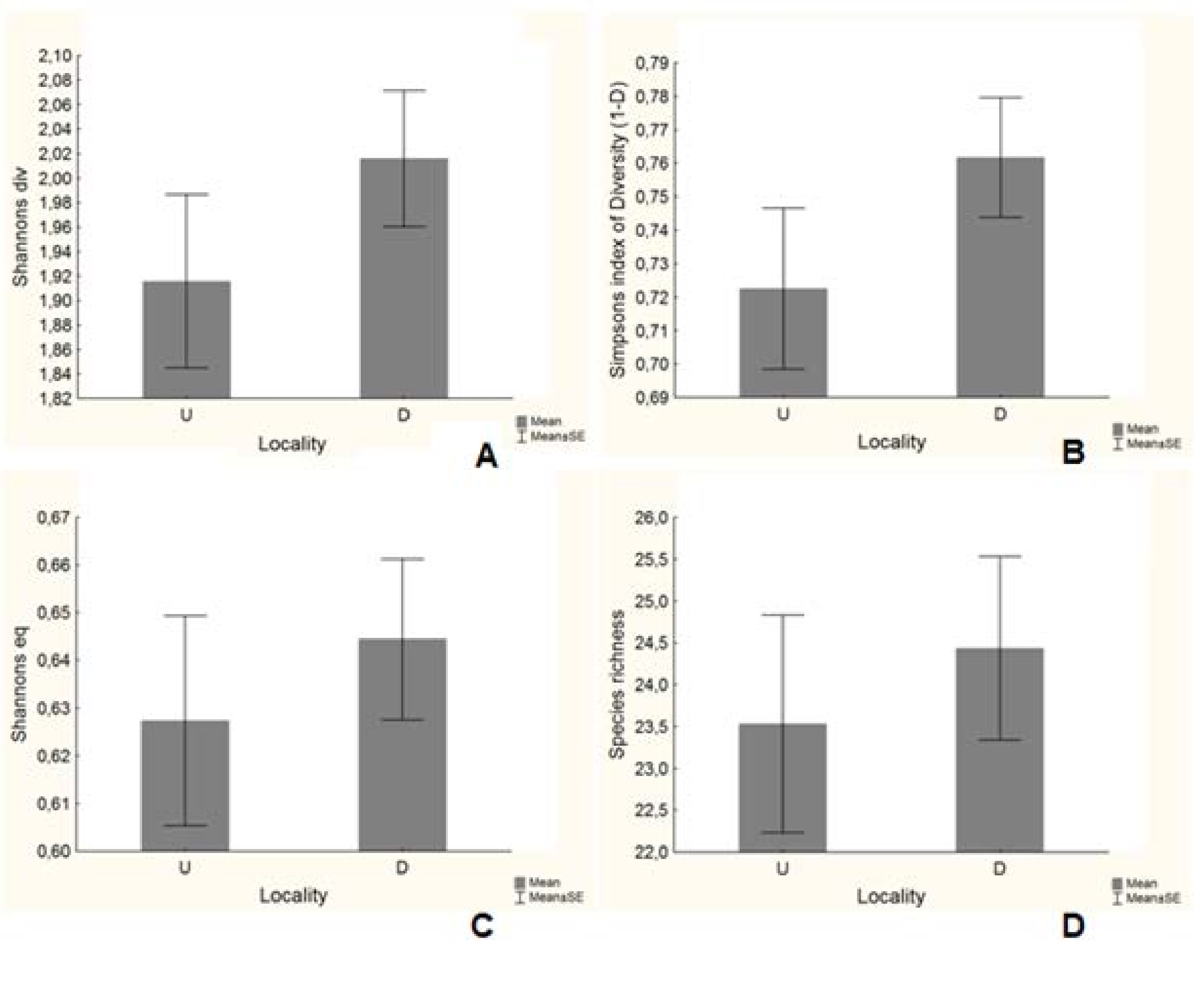

Fig. 4. Comparison of upstream (U) and downstream (D) reaches for A) Shannon's diversity, B) Simpson's index of diversity (1-D), C) Shannon's equitability (evenness), and species richness (D).

A similar pattern was seen for Shannon's equitability (evenness) and the species richness which showed no difference between the U and D reaches (Wilcoxon Matched Pairs Test, n=45, t=503, z=0.16, p=0.87, and n=45, t=471, z=0.52, p>0.05, respectively) (Fig. 4C and D).

3.1.2 Pond age

Shannon's diversity and Simpson's diversity downstream of the pond differed significantly between the different age groups (Kruskal-Wallis test, $H(3, n= 46) =13.8$, $p <0.01$, and $H(3, n= 46) =14,0$, $p <0.01$, respectively). The downstream sites had a significantly higher Shannon's diversity downstream of young ponds compared to sites downstream of medium aged ponds (Multiple Comparisons p values (2-tailed), $p<0.01$) (Fig. 5a). One could also see a none-significant trend towards a lower diversity as the pond ages. Sites downstream of young ponds had a higher Simpson's diversity compared to sites below medium-aged ponds (Multiple Comparisons p values (2-tailed), $p=0.01$) and had a tendency towards a lower species diversity for older ponds (Fig. 5b).

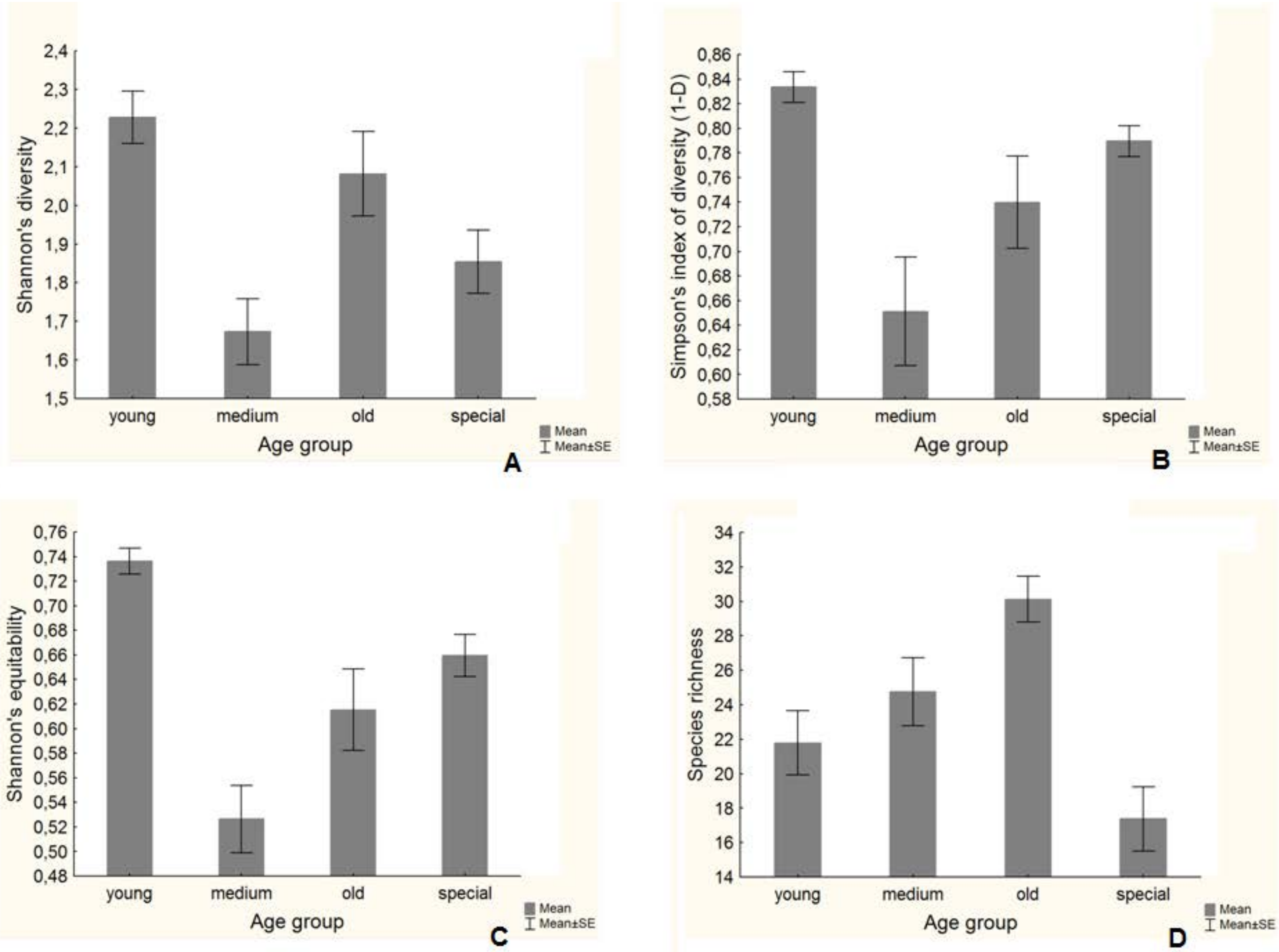

Fig 5. Comparison of A) Shannon's diversity index, B) Simpson's index of diversity (1-D), C) Shannon's equitability, and D) species richness between sites below ponds of the four different age groups young, medium, old and special (special=an old pond with a young pond located between it and the downstream site).

Shannon's equitability was significantly higher downstream of young ponds compared to sites located downstream medium-age ($p <0.0001$) and old ponds ($p =0.01$) (Kruskal-Wallis test, $H(3, n= 46) =22.1$ $p =0.0001$) (Fig. 5C). The species richness was highest for the sites downstream of old ponds when compared to young (p <0.01) and special ponds (p <0.0001) (Kruskal-Wallis test, (3,n=46)=19.6, p<0.001).

3.1.3 Pond size

The pond size did not have any significant effect on Shannon's diversity index (Kruskal-Wallis test, H(3, N= 46) =7.3, p =0.06) (Fig. 6A) but it did influence Simpson's index of diversity. Sites below small ponds had higher Simpson's diversity compared to sites downstream of medium-sized ponds (Kruskal-Wallis test, $H(3, n= 46) =9.85$ $p <0.05$) (Fig. 6B). Shannon's equitability did vary significantly due to pond size (Kruskal-Wallis test, $H(3, n= 46) =19.1$, $p <0.001$) with the sites downstream of small ponds having significantly higher evenness compared to the medium-sized (p <0.0001) and large ponds (p <0.01) (Fig. 6C). For the species richness both the medium-sized (p <0.01) and large ponds (p <0.01) had higher species richness than the sites downstream of small ponds (Kruskal-Wallis test, $H(3, n= 46) = 16.6$, p<0.001).

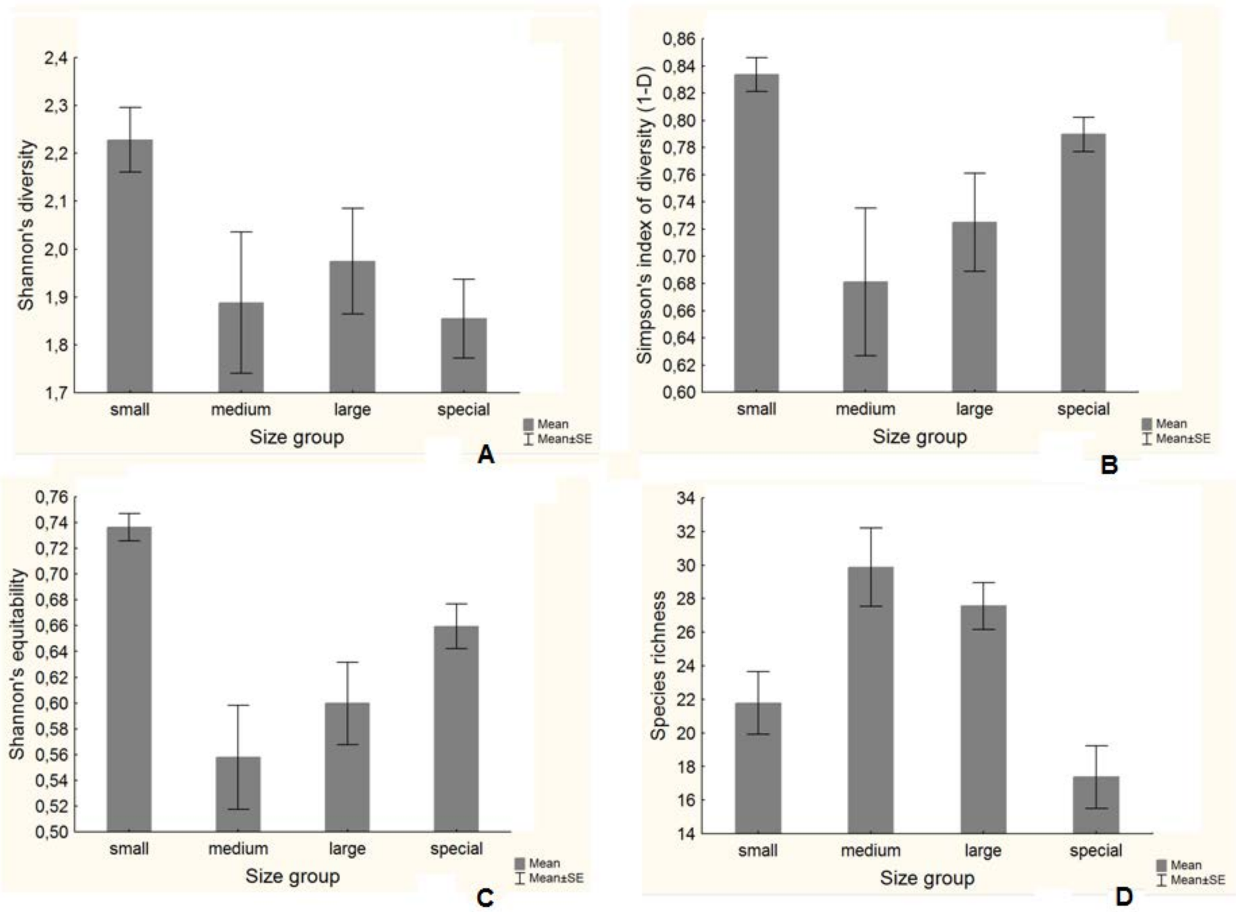

Fig 6. Comparison of A) Shannon's diversity index, B) Simpson's index of diversity (1-D), C) Shannon's equitability (evenness), and D) Species richness, between sites downstream of small, medium-sized, large and special ponds (special= a large pond with a small pond located between it and the downstream site).

Table 3. All the young beaver ponds were categorized as small. The older ponds tended to be larger, e.g. the ponds that were categorized as large were either medium-aged or old.

		AGE GROUP			
SIZE GROUP		**Young**	**Medium**	**Old**	**Special**
	Small	BD_01 BD_03 BD_22 BD_26			
	Medium		BD_02	BD_21	
	Large		BD_25	BD_11 BD_13 BD_14	
	Special				BD_23 BD_24

3.1.4 Geographical location

No significant difference in diversity or evenness was found between the geographical groups (Luleå, Sundsvall and South). This was true for both Shannon's diversity index (Kruskal-Wallis test, $H(2, N= 46) = 0.11$, $p = 0.95$), Simpson's index of diversity (1-D) (Kruskal-Wallis test, $H(2, N= 46) = 0.60$, $p = 0.74$) and Shannon's equitability (Kruskal-Wallis test, $H(2, n= 46) = 0.97$, $p > 0.05$).

3.2 Sørensen's similarity index (β-diversity)

3.2.1 Difference between streams

Sørensen's similarity index (Table 4) did not differ significantly between the streams (Kruskal-Wallis test, $H(11, N= 12) = 11.0$, $p = 0.44$) (Fig. 11).

Table 4. Sørensen's similarity index (β-diversity).

Stream	Sørensen's similarity
BD_01	0,676
BD_02	0,705
BD_03	0,821
BD_11	0,692
BD_13	0,750
BD_14	0,686
BD_21	0,740
BD_22	0,615
BD_23	0,426
BD_24	0,545
BD_25	0,675
BD_26	0,606

Sørensen's similarity index (β-diversity) has a non-significant trend towards lower beta diversity as you go from north to south. The similarity index did not display any significant differences for age or geographical location. In addition, there was no difference when comparing the similarity of streams.

3.2.2 Pond age and size

No effect of pond age could be seen for Sørensen's similarity index (Kruskal-Wallis test, $H(3, n= 12) =5.83$, $p >0.05$) and the same was true for pond size (Kruskal-Wallis test, $H(3, n= 12) =5.73$ $p >0.05$).

3.2.3 Geographical location

The geographical location of the streams did not have any significant impact on the β-diversity (Sørensen's similarity index) (Kruskal-Wallis test, $H(2, N= 12) =5.04$, $p =0.08$) but did display a tendency towards a lower β-diversity southwards (Fig. 7).

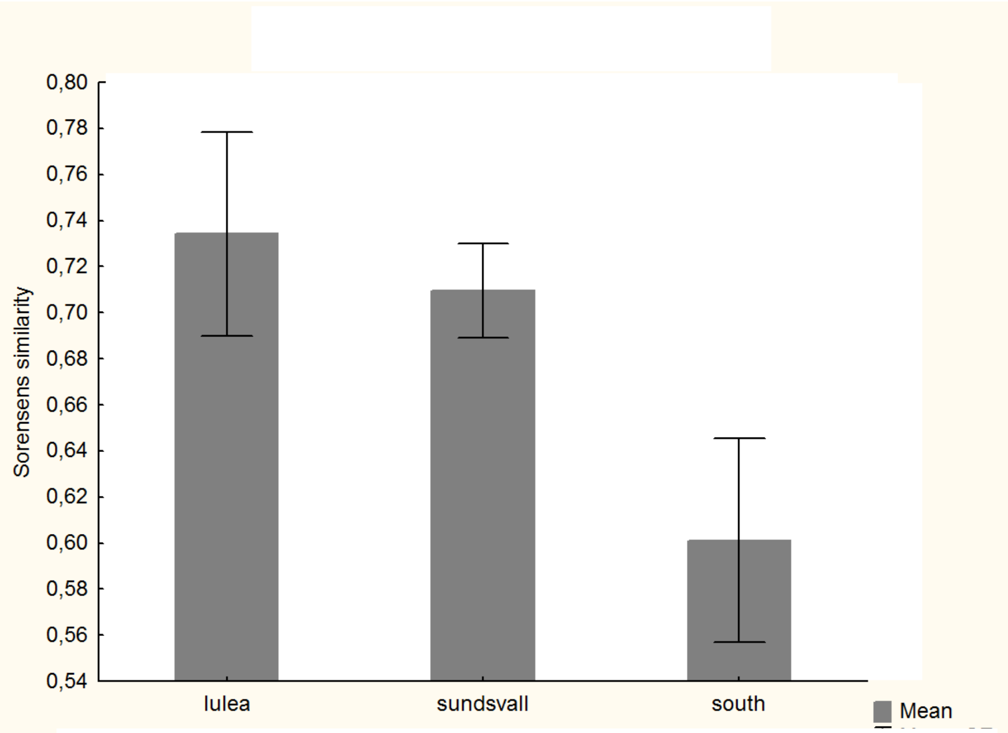

Fig. 7. Sørensen's similarity index (β-diversity) for the three geographical groups – Luleå, Sundsvall and South.

3.3 Functional feeding groups

Out of the eight FFG categories only the three predator groups (predator, suctorial predator and piercing predator) displayed any differences in abundance between the upstream and downstream areas (Fig. 8). The predator and the suctorial predator group both had a higher abundance downstream of the beaver ponds (Wilcoxon Matched Pairs Test, n =44, t =288.5, z = 2.41, p <0.05, and n =33, t =120.5, z = 2.86, p <0.01, respectively). The piercing predators however were more abundant upstream compared to the downstream sites (Wilcoxon Matched Pairs Test, n =35, t =168.0, z = 2.41, p <0.05). None of the other FFG categories displayed any differences in abundance between the upstream and downstream reaches (Wilcoxon Matched pairs test, $p>0.05$ for the filtering collector, gathering collector, shredder, scraper, omnivore groups).

When comparing the upstream and downstream proportions of the FFG's I did not find any significant difference in proportion for any of the FFG's (Wilcoxon Matched pairs test , $p>0.05$).

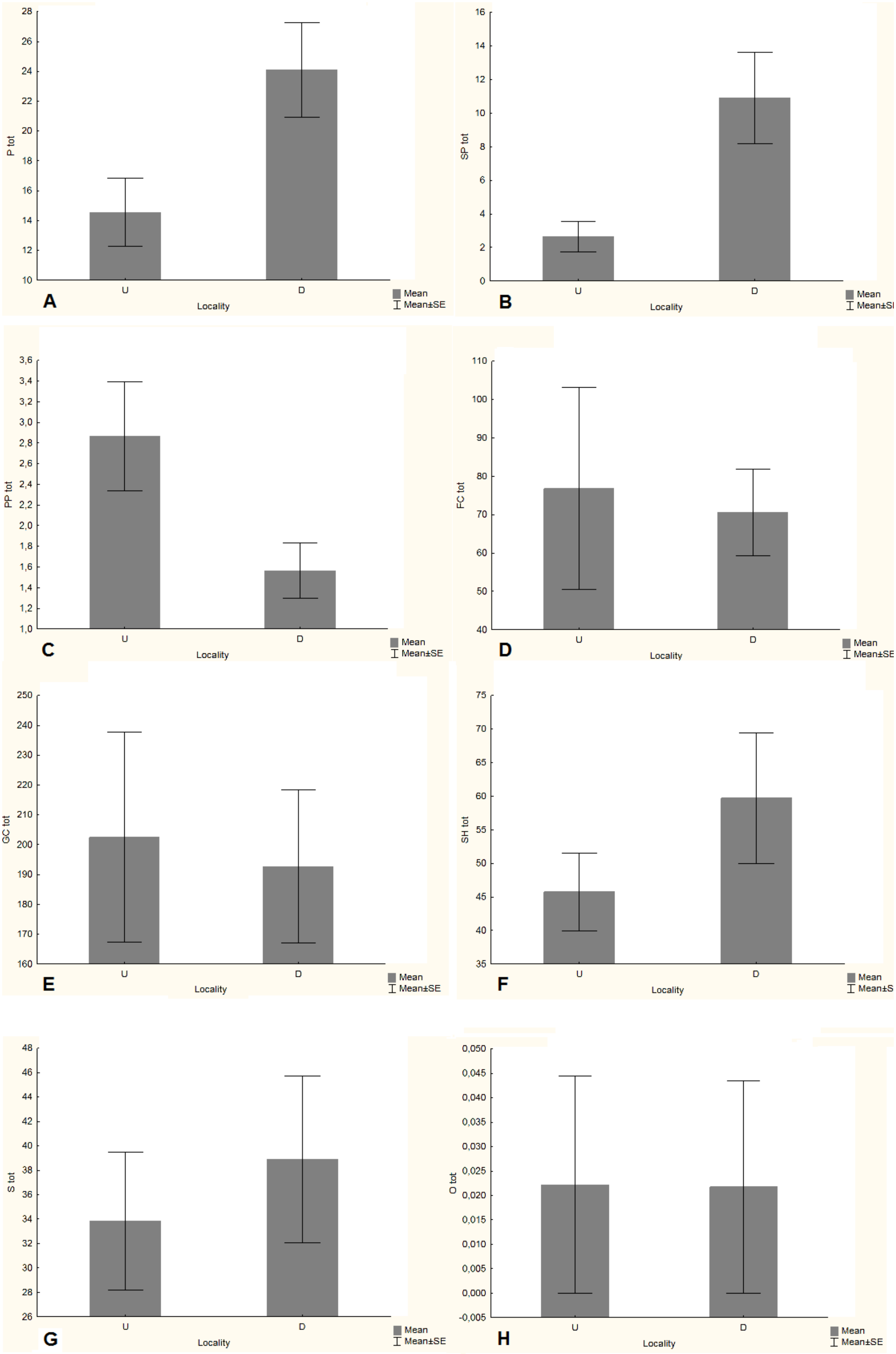

Fig. 8. The abundance of predators (A) and suctorial predators (B) with a higher abundance downstream (denoted D in each graph) than upstream (denoted U). The opposite is seen for the piercing predators (C) that are more abundant upstream than downstream. None of the other functional groups (D-H) display any difference in abundance between upstream and downstream reaches (D=Filtering collector, E=Gathering collector, F=Shredder, G=Scraper, H=Omnivore).

3.4 CPOM

None of the three CPOM categories; woody debris (Wilcoxon Matched Pairs Test, n=45, t=485.5, z=0.36, p>0.05), deciduous debris (Wilcoxon Matched Pairs Test, n=39, t=285, z=1.47, p>0.05) and needles (Wilcoxon Matched Pairs Test, n=42, t=336, z=1.44, p>0.05) differed significantly in dry weight between the upstream and downstream reaches (Table 5).

Table 5. Results of the coarse particulate organic matter (CPOM) collected upstream and downstream of beaver ponds. The data displayed no significant difference between upstream and downstream reaches (Mean ± Standard deviation).

	Woody debris (g)	Deciduous debris (g)	Needles (g)
Upstream (n=45)	2,1 ± 3,8	0,4 ± 0,5	0,2 ± 0,4
Downstream (n=46)	1,9 ± 2,8	0,2 ± 0,4	0,4 ± 0,6

n = number of samples

3.5 Water chemistry

The results of the water chemistry analysis (Table 6) showed that the concentrations of several substances differed between the water flowing into the pond and the water leaving it. The concentration of MeHg downstream of beaver ponds was significantly higher than the upstream concentration (Wilcoxon Matched Pairs test, n=12, t=3.0, z=2.8, p <0.01). The same pattern could be seen for both the DOC concentration and for the tot-P concentration which both had higher values below the ponds (Wilcoxon Matched Pairs Test, n=12, t=11, z=2.2, p<0.05 and n=11. t=4.5, z=2.53, p=0.01 respectively). Tot-N was also significantly higher at the downstream sites (Wilcoxon Matched Pairs Test, n=12, t=7, z=2.51, p=0.01) while TOC (p=0.06), NO_2/NO_3 (p=0.46) showed no significant difference between upstream and downstream reaches.

Table 6. A comparison of water chemistry between the water upstream and downstream of beaver ponds displayed differences in concentration for several variables. MeHg, DOC, tot-P and tot-N were all found at higher concentrations downstream of the beaver ponds. The data is presented as mean (standard deviation).

	MeHg (ng/L)	**TOC (mg/L)**	**DOC (mg/L)**	**tot-P (µg/L)**	**tot-N (µg/L)**	**NO_2/NO_3 (µg/L)**	**Cl (mekv/L)**	**F (mg/L)**
Upstream	0.36 (0.24)	16.0 (10.5)	15.4 (10.2)	14.8 (8.2)	519 (267)	59.5 (80.8)	0.08 (0.10)	0.23 (0.23)
Downstream	0.54 (0.35)	17.8 (12.9)	17.4 (12.4)	24.7 (25.5)	693 (594)	72.7 (84.7)	0.08 (0.10)	0.23 (0.26)

4 DISCUSSION

Neither Shannon's diversity index nor Simpson's index of diversity (1-D) displayed a significant difference in diversity between the upstream and downstream sites. This is in line with the results from Margolis *et al.* (2001b) who also did not see any difference in diversity between upstream and downstream reaches. Both Shannon's diversity and Simpson's index of diversity (1-D) did however show a non-significant trend towards a higher diversity downstream than upstream. According to McDowell and Naiman (1986) Shannon's diversity in autumn differed between stream and pond localities. In contrast, when only looking at the stream I found no significant difference in macroinvertebrate assemblage between the upstream and downstream reaches.

When looking at the differences in diversity between sites downstream of ponds of different age and size I found a significant result for both these categories. For the pond size however, the difference was only significant for Simpson's index of diversity (1-D). Since pond size is connected to pond age (see Table 3, all ponds classified as small were also classified as young, and large ponds were either old or medium-aged) similar results for these two factors was expected. Both Shannon's diversity index and Simpson's index of diversity was significantly higher at sites located downstream of young ponds compared to medium-aged ponds. The areas below young ponds did not differ significantly from that of the old or special group. The same significant pattern could be seen for Simpson's index of diversity. Young ponds also had the highest evenness compared to all other age categories except the 'special' group (an old dam with a young dam constructed between it and the downstream sampling site). This is quite interesting since I have found no previous studies on this subject - that species diversity seem to decrease with pond age/size. I theorize that newly established ponds may offer a new habitat for arriving species with "intermediate disturbance", no species is favoured to begin with, and this may explain why the species diversity was higher downstream of young ponds compared to medium-aged ponds. During the succession of the beaver ponds some species are outcompeted while others tend to become dominating. The evenness seem to partly support my assumption about species competitions, with a higher evenness of species at the sites downstream of young ponds. When the pond is still young the evenness is high but as the pond grows older the evenness decreases i.e. some species become dominant while others are outcompeted resulting in a lower evenness.

Fuller and Peckarsky (2011a) did not find any differences between upstream and downstream abundances of FFG's of macroinvertebrates. I could confirm this for all groups except the three predator groups – predators, piercing predators and suctorial predators – which all differed between the upstream and downstream sites. The abundance of predators and suctorial predators was significantly higher at the downstream sites and was consistent with the results of Smith *et al.* (1991). In contrast, the piercing predators were more abundant upstream of the pond. Smith *et al.* (1991) also found that gathering-collectors were more abundant downstream but I did not see this difference. The higher number of two of the three predator groups might be due to a higher number of preys at the downstream site compared to the upstream site earlier in the season. One example is Chironomidae, of which many had reached the pupal stage at the time of the sampling (*personal observation*). The higher abundance of piercing predators upstream is probably related to their food preferences, although I have not found any support in the literature regarding this. The CPOM of the downstream and upstream reaches did not differ significantly and so it seems natural that the shredder and collector abundance did not differ either. Since the pond contains as much as 10 times more carbon in the water table than the stream I had expected a higher number of species of e.g. filtering collectors downstream of the dam (due to e.g. increased algal production caused by the higher carbon levels downstream) but this was not the case. The streams of this study differed in both depth and width (see Appendix 3) but this would not affect the beaver activity and influx of beaver-collected material. Beavers are known to be equally active in both smaller and larger streams when it comes to the mass of wood cut by the beaver (Naiman *et al.* 1986).

Since the water column of the pond can contain as much as 37 times more N than the stream reaches (Naiman and Melillo 1984) it is not surprising that the tot-N level was significantly higher downstream of the pond than upstream (Table 6). The higher MeHg levels downstream of the pond confirm that beaver dams are sources of MeHg. Both DOC and tot-P had higher concentrations downstream of the ponds. Cl and F concentrations were not affected by the pond.

Margolis *et al.* (2001b) theorized that the influence of beaver dams on the invertebrate assemblage may be influenced by a seasonal component. It would therefore be interesting to sample the streams at several time periods throughout the year to see if the effects of the beaver dams differ during different seasons. According to McDowell and Naiman (1986) Shannon's diversity in autumn differed between stream and pond localities. My study was conducted in late autumn and in order to get as a complete picture as possible of beaver-induced effects on macroinvertebrates I would suggest sampling throughout different seasons. Fuller and Peckarsky (2011a) found that the annual variation in hydrology can strongly influence rare systematic effects and the effects such as that of pond morphology on downstream ecosystems. For several of the streams the water flow was higher than normal (*personal observation*) and collecting data throughout high-flow as well as low-flow seasons would generate interesting additional information. By repeating the investigations during several seasons one can detect potential effects of e.g. change in flow as well as seasonal variations.

When looking at species richness I could not detect a difference between the upstream and downstream macroinvertebrate assemblages. What I would suggest for future studies on this topic is to instead investigate if there is any differences in species assemblage between the respective sites. For this study time was an ever limiting factor and therefore this comparison could not be done.

The geographical location of the pond did not affect the species diversity downstream of the pond and there was no significant difference in evenness between the geographical regions. Since the geographical regions displayed no differences in species diversity and evenness it should be possible to choose suitable streams without regards of geographical location in future studies, and consider them as replicates.

5 CONCLUSION

The conclusion from previous studies, of no difference in macroinvertebrate species diversity upstream and downstream of ponds, is confirmed by my results. In addition, I found that the predator FFG was significantly more abundant downstream of the ponds. What caused this difference will need to be investigated further in future studies.

There was no evidence showing that beaver ponds do affect downstream macroinvertebrate diversity. It is possible that if looking at the entire stream system, including both the pond and the stream, the construction of a beaver pond may affect the macroinvertebrate diversity. But for the downstream reaches the diversity of macroinvertebrates are not affected.

The most interesting result from my study was that pond age and size have an effect on species diversity, with a higher diversity downstream of young ponds. This has, to my knowledge, not been described before in the literature and may be an important component affecting the species diversity of the reaches downstream of beaver ponds. For future studies it would be important investigate to what extent pond age and size may affect the macroinvertebrate species diversity downstream of the pond and what variables, connected to age and size of the pond, that may cause this effect.

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8 APPENDIX 1 - Functional Feeding Groups

Collectors (Gathering collectors and filtering collectors)
Collectors are consumers of fine particulate organic matter (FPOM) and have a variety of adaptations for acquiring fine particulate detritus and can collect particle of varies different sizes. Unlike the scrapers the collectors prefer organic material with a size of < 1 mm. (Cummins and Klug 1979). The collectors can be divided into two different groups. The filtering collectors mainly feed on fine particulate detritus that is in suspension while the gathering collectors primarily feed on detritus that is deposited and sediment-related. There is however an overlap between these two groups. Some lotic invertebrates that live in burrows in the sediment can maintain a current through their burrows and in that way feed on detritus from transport even though that they mainly feed on sediment-related detritus. Species that belong to the filtering collectors can be found in Ephemeroptera (mayflies) and Diptera (mostly Simuliidae) while species that belong to the gathering collectors can be found in Diptera (Nematocera) and Trichoptera (Cummins and Klug 1979).

Shredders
Shredders are also known as detrivores. Through their feeding activities they are responsible for the conversion of CPOM (coarse particulate organic matter) to FPOM (fine particulate organic matter). Examples of CPOM can be needles, leaves and woody debris, and they seem to prefer CPOM that is well-colonized by microorganisms (Cummins and Klug 1979). Species belonging to the shredder functional group can be found in nonpredaceous stoneflies, caddisflies (especially the family Limnephilidae and craneflies (Diptera), Trichoptera (Cummins and Klug 1979).

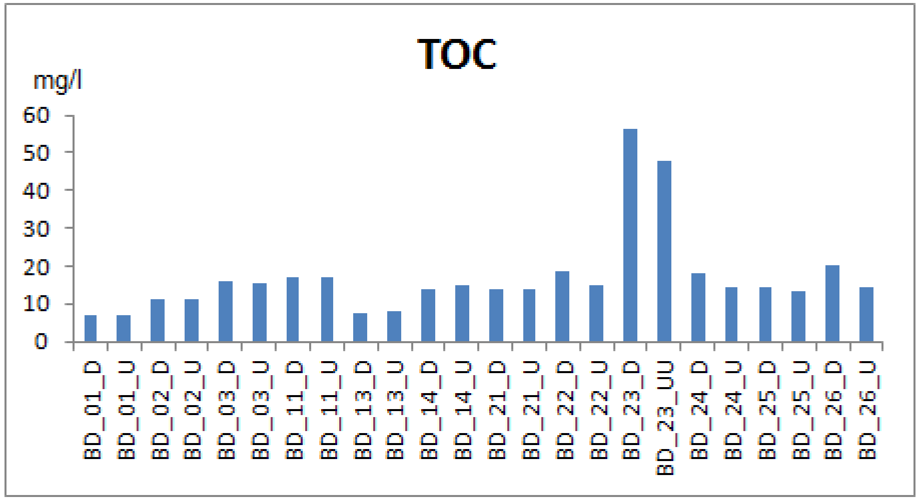
Predators
Predator species are adapted to catch live prey. The behavior of predators, such as activity, is affected by the supply of prey. When the supply of prey is scarce the activity of the predators is reduced. Also processes like morphological growth are reduced when the supply of prey is scarce (Cummins and Klug 1979).
From the general predator group I separated two additional predatory groups. These were:
Suctorial predators – with sucking mouthparts, e.g. species of the family Tabanidae (Horse-flies).
Piercing predators - with mouthparts developed for piercing their prey, e.g. species of the family Limoniidae (Crane flies).

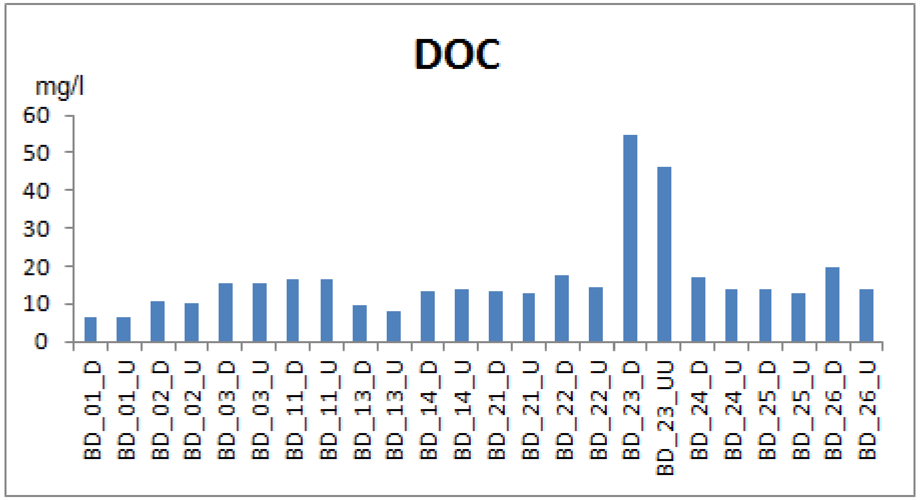
Scrapers
Scrapers have adaptations which makes it possible for them to graze on food that have gathered on surfaces. They can colonize exposed surfaces thanks to their adaptations for coping with high stream velocity (gills that can work as suction gills to maintain their position on the exposed surface) (Cummins and Klug 1979). Species of this group can be found among mayflies (Ephemeroptera) and Trichoptera families (Cummins and Klug 1979).

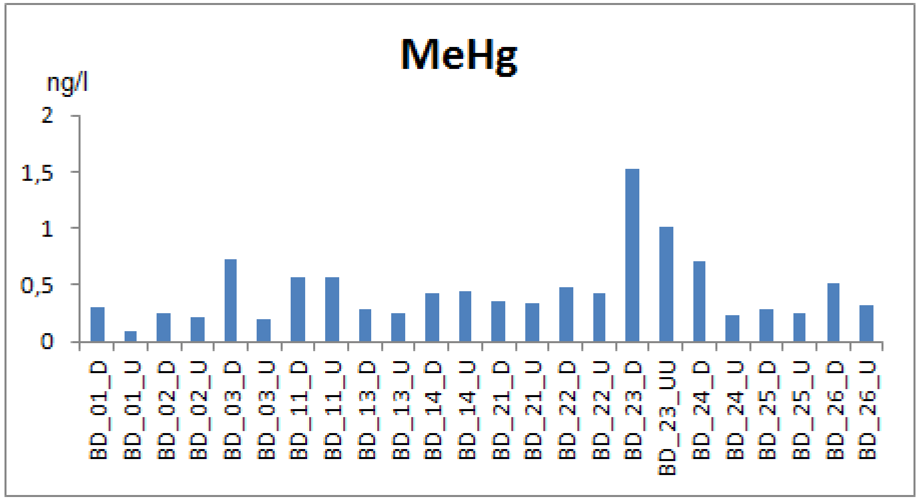
Omnivores
This group have a variety of different food sources. The group omnivore was added for the species *Hydraena riparia*. This species was only found at two locations with one individual per location.

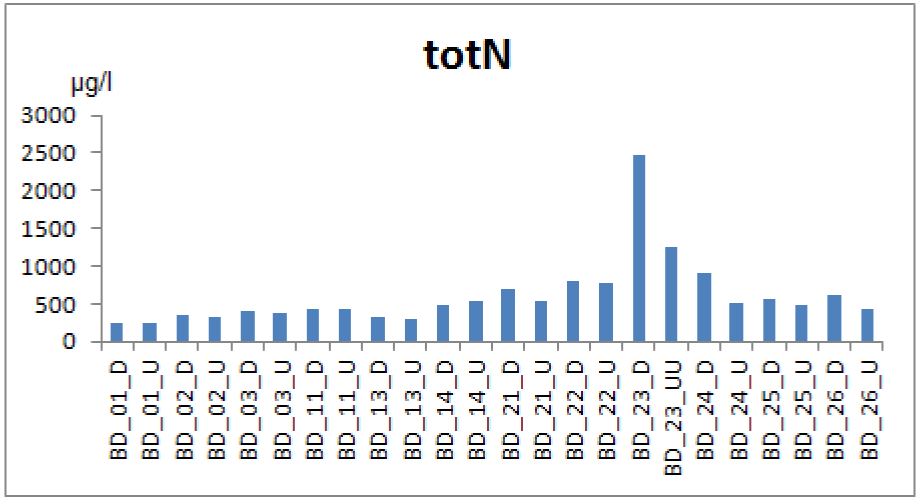
9 APPENDIX 2 - Water chemistry tables

Mean values for the water chemistry data, sampled upstream and downstream beaver dams at 12 locations, between years 2012-2013.









10 APPENDIX 3 - Stream characteristics

Stream characteristics for macroinvertebrate sampling sites. All streams were located in one of three of the following geological groups (GeoGroups) - from north to south - Luleå, Sundsvall, South. The U and D in the stream designation indicates sites located upstream (U) or downstream (D) of a beaver dam (BD). The substrate types were estimated by visual observation.

		Substrate (%)						
Stream	**GeoGroup**	**Boulders >40 cm**	**Cobbles**	**Pebbles**	**Sand/Mud**	**Silt/Clay**	**Mean width (m)**	**Mean depth (cm)**
BD_01_U	Luleå	80			20		4.2	41
BD_01_D	Luleå	70	10		20		4.1	30
BD_02_U	Luleå	70	30				4.1	38
BD_02_D	Luleå	100					7.9	32
BD_03_U	Luleå	100					2.5	50
BD_03_D	Luleå	95	5				2.6	30
BD_11_U	Sundsvall	40	30	20	10		4.2	48
BD_11_D	Sundsvall	40	30	20	10		3.7	50
BD_13_U	Sundsvall	10	30	30	30		3.9	35
BD_13_D	Sundsvall	80	10		10		2.8	44
BD_14_U	Sundsvall	70	20	5	5		4.9	31
BD_14_D	Sundsvall	80	20				6.2	34
BD_21_U	South	20		40	40		4.1	29
BD_21_D	South	45	15	15	25		5.0	19
BD_22_U	South	35		30	35		4.3	22
BD_22_D	South			20	80		4.4	24
BD_23_UU*	South	30			70		1.5	18
BD_23_D	South		10		90		2.2	30
BD_24_U	South	20	30	30	10		1.9	39
BD_24_D	South	5	40	35	20		2.0	37
BD_25_U	South	20				80	2.0	70
BD_25_D	South					100	4.5	65
BD_26_U	South	20	20	40	20		4.6	19
BD_26_D	South	40	25	25	10		4.8	9

* BD_23_UU was sampled for macroinvertebrates further upstream from the pond compared to the water chemistry data since the BD_23_U site proved to be unsuitable for macroinvertebrate sampling

11 APPENDIX 4 - Species list

List of the species collected during the study. Abundance of each species is given as a sum of the total number of individuals included in the four samples collected the upstream (U) sites and the downstream (D) sites. The Geo Group is the geographical region in which they were collected (Lu=Luleå, Su=Sundsvall, So=South).

Stream ID	**01_U**	**01_D**	**02_U**	**02_D**	**03_U**	**03_D**	**11_U**	**11_D**	**13_U**	**13_D**	**14_U**	**14_D**	**21_U**	**21_D**	**22_U**	**22_D**	**23_UU**	**23_D**	**24_U**	**24_D**	**25_U**	**25_D**	**26_U**	**26_D**
Geo Group	**Lu**	**Lu**	**Lu**	**Lu**	**Lu**	**Lu**	**Su**	**Su**	**Su**	**Su**	**Su**	**Su**	**So**	**So**	**So**	**So**	**So**	**So**	**So**	**So**	**So**	**So**	**So**	**So**
Polycelis sp.													1											
Dugesia sp							3												2	28		1		
Planaria torva																				1				
Dendrocoelum lacteum			1																					
Nematoda			1																					
Ancylus fluviatilis													28		1									
Bathyomphalus contortus																			3	81				
Gyraulus acronicus											3	8												
Lymnaea stagnalis																				2				
Radix balthica				2								1								2				
Radix labiata																				1				
Pisidium sp.			11	2	4	6	2	2	15		2	43	4	2	5	45	37	188	52	51		6	7	7
Sphaerium sp.			1														3	3						
Eiseniella tetraedra																						1		
Lumbriculidae																	1			1				
Tubificidae		1													1			1	2	2				
Spirosperma ferox																		1	1					
Enchytraeidae									1										1	1	1			
Naididae		2	1	1	1	2		1	1	1	3	2	2	3					1	4				
Stylaria lacustris					1	1														1				
Glossiphonia complanata																		5	4	34				
Helobdella stagnalis																				1		2		
Erpobdella sp.																		1	6	24		4		

Erpobdella octoculata																				47	1			
Hydrachnidia	3	40	4	39	8	60	35	7	25	40	29	77	6	43	2	6	1			2	4	5		
Asellus aquaticus				2					1		1	4				1	131	211	122	309		9	6	35
Gammarus lacustris			2										5	4	5	27								
Alainites muticus	3	1					6		25	8														
Nigrobaetis digitatus									9	2					1									
Nigrobaetis niger	19	30		1			60	13	55	35	8		2	12	4	47					13	126		9
Baetis rhodani	215	195	7	10			51	49	52	192	3	5	59	257	18	8					217	242		
Centroptilum luteolum											2													
Siphlonuridae	1					2		4				3		1							2	13		
Heptagenia dalecarlica	1		1				2	1																
Heptagenia sulphurea							2	8	137	47			8	26	4									
Leptophlebia sp.				1			1		34	14	1	2		7		2			1					
Leptophlebia marginata			1	13	6		9	3	4	8	21	1				4			3			2	1	
Leptophlebia vespertina												3							3					1
Ephemera danica														2	2	1								
Diura nanseni					1	3																		
Perlodes dispar															1									
Isoperla sp.	2		86	44			2		2	28	20	61	6	5							1	4		
Isoperla grammatica			29	3					4	8		10									1			
Isoperla difformis			1				2						3		1	2					2	1		
Siphonoperla burmeisteri	4	1					1		2	1		5		5	2	2								
Taeniopteryx nebulosa		4		2	12	47				1	6	6				2								
Brachyptera sp.							1	4		4		1	10	27	9	7					14	10		
Amphinemura sp.	5	39	18	4			19	17	194	177	163	47	25	13	2	1					1			

Amphinemura sulcicollis							3		17	3	12	8	6	7										
Nemoura sp.		1	7		18				2													8		
Nemoura avicularis				1	6			3			5	3		1		20								
Nemoura cinerea	2	17	15	13	43	33	6	13			5	8		6		9	113	12	267	538	5	339	1	1
Nemoura flexuosa						1		1			1													
Protonemura meyeri	7	2					18		12	50	1	7	38	9	2	9					5			
Capnia sp.														3										
Capnopsis schilleri							41	29			1		1	2	25	100								
Leuctra sp.			13	1	33	6	1	4		3	15	8	3	42	1						5	2		
Leuctra hippopus	6	14	23	12	4	3	11	14	1	3	37	95	13	4	1	31			1		127	5		
Leuctra nigra					12	4	1																	
Calopteryx virgo										1									1					
Cordulegaster boltoni	1		1	2						2		1				1								
Sialis fuliginosa	1		1	1	3		9	2		1	36	1			1						1			
Sialis lutaria																		12	4					1
Haliplus sp.																								1
Platambus maculatus							1																	
Hydraena gracilis	1	3					2	4	4	9			2	1	1						7	4		
Hydraena riparia									1			1												
Elmis aenea	26	102	3				71	9	61	42	2	4	100	81	4	2								
Oulimnius tuberculatus	7	1	8	3						3		4	8	9	35	3			1					
Limnius volckmari	7	8	9						18	19			72	157	14	2					20	16		
Cyphon sp.																					1			
Elodes sp.																			1			1		
Ceratopsyche silfvenii							2	1				1												
Hydropsyche pellucidula							1	1	1	2			10						6	1				1
Hydropsyche		11	1												1						3	6		

saxonica																								
Hydropsyche siltalai	2	36		2			2	1	74	17			14	4							1	28		
Neureclipsis bimaculata									1		3													
Plectrocnemia sp.							1									1	3							
Polycentropus sp.			1	1	2	2	4		11		24	9					1							
Polycentropus flavomaculatus	2		127	20	40	21	14	13	25	20	102	74		10		3						5		
Polycentropus irroratus									1		24	13				2						1	2	
Lype phaeopa									1		1					1			1			1		
Philopotamus montanus									4															
Agapetus ochripes	4						4	4		1			134	55	13				1		3	1		
Hydroptila sp.	1						2					1	1	5										
Ithytrichia sp.														1										
Oxyethira sp.				1						6		2												
Rhyacophila fasciata									2				1								1	1		
Rhyacophila nubila	2	16	29	13	2	4	5	1	23	22	4	8	12	10	1						9	3		
Silo sp.		2						3					21											
Limnephilidae			4	18	7	3	23	1	5	2	21	1	2			7		1	3	4	5			1
Glyphotaelius pellucidus									1									13		1				
Limnephilus centralis																	1							
Limnephilus fuscicornis																				1				
Limnephilus rhombicus							1											7		3				
Halesus sp.																3								
Micropterna lateralis																	2							
Micropterna sequax																	13							
Potamophylax sp.							5				12					2				2				
Potamophylax							7		1		1													

latipennis																								
Lepidostoma hirtum	2			1			39	6	12	6	15		5			1					1			
Oligostomis reticulata																		2		1				
Athripsodes sp.							1		3	1			7	8	4	2			1					
Athripsodes cinereus													11	2	3	1								
Ceraclea sp.														1										
Mystacides azurea			5	1																				
Oecetis sp.																3								
Beraeodes minutus																1		15		42				
Sericostoma personatum			1	1			52	5	3	14	5		1								8	38		
Chionea sp.		1																						
Dicranota sp.	1	1	6	1		7		7	7	2		4	41	14	15	7	10		3	1	17	3		5
Eloeophila sp.					4	6		1		2			1	2	6	2	3	1	2			1		
Pedicia sp.																	4							
Phylidorea sp.							1																	
Pilaria sp.																		1						
Rhypholophus sp.				1		1	1	1									7							
Psychodidae	11	11					1	3		1	2	2	2			1								
Ptychoptera sp.																2								
Simuliidae	18	131	53	129	103	63	88	141	105	94	139	315	94	89	11	26	96		1427	249	247	948	4	12
Simulium argyreatum		5		16			7	29	5	18	2		9	5					23	16	14	42		2
Simulium monticola			1	17			2	2	2	1	2	4	2						8		6	11		1
Simulium ornatum-Grp							1						4											
Simulium rotundatum/frigidum													8											
Simulium rostratum				3								2							5		3			
Simulium trifasciatum		3		10			1	2		1	4		1						1			25		
Simulium vernum	1	10	1	5		21	14	10	7	4		5	31	17	7	52	117	1	90	1	21	29	1	3

Ceratopogonidae	4	30	4	10	1	63	5	4	15	14	12	34	18	8	6	9		1		12	4	5	17	1
Culicoides sp.		11	7	10	17	38	11		5	4	13	45	4	5	8	16	6	1	5	20		4	21	
Chironomidae	33	257	1014	949	281	339	1213	221	606	466	2581	2113	555	866	184	271	206	182	312	743	209	518	203	19
Tanypodinae.			3			1			2		4	3		3			1		1	1	1			
Orthocladiinae		4	2	4	2	5	2		3	1	8		5	3	1				1	9	2	6	1	1
Micropsectra sp.							1					5					1	1						
Rheotanytarsus sp.		2	1	1			5		4	5	3	1	1	4					1					
Stempellina sp.																1								
Stenochironomus sp.	1						1				1			1		1								
Tanytarsus sp.			8		2	1	5				11	1			1	1	1			1	1		1	1
Tabanidae															1	1				1				
Hemerodromia-Gr. Gen. sp.	15	210	12	47	5	121	5	7	5	9	1	15	59	75	4						9	5		
Chelifera-Gr. Gen. sp.				1								8					1							
Dolichopodidae																1								
Ephydridae											1							1					1	
Oligochaeta	87	232	263	31	66	72	37	33	212	59	52	93	181	265	49	83	127	112	211	526	64	32	38	4