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Growing up where you were born – A Comparison of Nursery Areas for Salmonids in River Stretches with and without Natural Spawning

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Summary

Ecosystems are significantly impacted by activities from human settlements. This is especially the case for aquatic ecosystems as many large cities sit on coastlines or along major rivers. Species like salmonids are especially affected since they migrate between freshwater and saltwater habitats during their lifetime. To study the relationship between human settlements and salmonids, the Oslo fjord in Norway is notable both as a destination for Atlantic salmon (*Salmo salar*) and sea trout (*S. trutta*) migration and as a major metropolitan area. Human activity in freshwater habitats affects the salmonids in particular since they use this environment for spawning and as a nursery. Sandviksvassdraget is one of the most important salmonid-carrying watercourses around the Inner Oslo fjord and the reported high catches of salmonids in Sandviksvassdraget are the result of continuous hatchery activity since 1857. However, there are characteristics that degrade the habitat of salmonids in the watercourse consisting of man-made dams, which reduce the available freshwater habitat for salmonids, as well as surrounding roads and construction sites that decrease coverage of riparian vegetation and introduce particle pollution.

The salmonids in the watercourse, their habitat, and their main food source, macroinvertebrates, have been studied in past years, but the variables that significantly impact the local population of salmonids and macroinvertebrates are still not well understood. Neither is the actual output of smolt to the Oslo fjord from the Sandviksvassdraget well known. This study found overall lower densities in the upstream stretches, where salmonid juveniles from the hatchery are released, than in the downstream stretches, where wild juvenile salmonids are found. Neither the tested environmental variables, nor the total abundance of macroinvertebrates had a significant effect on the salmonid densities. The macroinvertebrate diversity and abundance differed significantly between the rivers and upstream and downstream stretches and were influenced by allochthonous and autochthonous production in the stretches, but not by the salmonid densities. Mark-recapture data of adult trout showed that trout leaving Sandviksvassdraget into the Oslo fjord still reach the same parts of Oslo fjord as in 1949. In general, the distance from the capture point to the outlet from Sandviksvassdraget into the Inner Oslo fjord was larger for female trout than for males and increased with the total length of trout.

The significant effect of allochthonous production on macroinvertebrates indicates the importance of well-developed riparian vegetation along the watercourse. Even though no variables affected the juvenile salmonid density significantly, one can assume that the salmonids will benefit from the improvement of riparian vegetation, the decrease of particle input and the opening of non-accessible stretches. With increasing urban development in Sandviksvassdraget's catchment, the implementation of such measures will be necessary to ensure the preservation of the local salmonid population.

Sammendrag

Økosystemer er betydelig påvirket av aktiviteter fra menneskelig bosetninger. Spesielt akvatiske økosystemer er påvirket siden mange store byer ligger ved kysten og langs elver. Arter som laksefisker er spesielt truffet, siden de vandrer mellom ferskvanns og saltvanns habitater i løpet av livet. For å studere forholdet mellom menneskelige bosetninger og laksefisk er Oslofjorden i Norge kjent for laks (*Salmo salar*) og ørret (*S. trutta*) migrasjon, samtidig som et stort hovedstadsområde. Menneskelig aktivitet i ferskvanns habitater påvirker laksefisk spesielt, siden det blir brukt for gyting og som oppveksthabitat. Sandviksvassdraget er en av de viktigste laksefisk førende vassdrag rundt indre Oslofjord og de rapporterte høye laksefisk fangster i vassdraget er resultatet av kontinuerlig klekkeridrift siden 1857. Derimot er det kjennetegn i Sandviksvassdraget som ødelegger leveområdet til laksefisk som består av menneskeskapte demninger, som minker tilgjengelig ferskvanns habitat for laksefisk, samt veier og bygg og anlegg, som reduserer kantvegetasjon og introduserer partikkelforurensning.

Laksefisk i vassdraget, habitatet deres, og deres primære matkilde, bunndyr, har blitt studert i de siste årene, men variablene som påvirker lokale populasjonen av laksefisk og bunndyrene er fremdeles ikke godt forstått. Den egentlige produksjonen av smolt i vassdraget er heller ikke kjent. Dette studie fant generelt lavere tettheter i oppstrøms strekninger, hvor unge laksefisk fra klekkeriet blir satt ut, enn i nedstrøms strekninger, hvor man finner ville unge laksefisk. Ingen av de testete miljø variablene hadde en signifikant effekt på laksefisk tettheten og total bunndyr mangfold hadde heller ikke noe effekt. Bunndyr diversiteten og mangfoldet var forskjellig i de undersøkte elvene og oppstrøms og nedstrøms strekninger og var påvirket av både alloktont og autoktont produksjon i disse strekninger. Laksefisk tettheten hadde ingen signifikant effekt på bunndyr, verken på diversiteten eller mangfoldet. Merk-gjenfangst data av voksen ørret viste at ørret som vandrer ut fra Sandviksvassdraget inn i Oslofjorden, når fortsatt de samme områdene i fjorden som i 1949. Generelt var distansen fra fangststedet til utløpet av vassdraget inn i Indre Oslofjorden større for hunner enn for hanner og økte med total lengden av ørret.

Den signifikante effekten av alloktont produksjon på bunndyrene indikerer viktigheten av en godt utviklet kantvegetasjon langs elven. Selv om ingen av de miljø variablene hadde en signifikant effekt på laksefisk tettheten, kan man antar at laksefisk populasjonen vil få en nytte av tiltak, som utbedring av kantvegetasjonen, reduksjon av partikkelforurensning og åpning av ikke tilgjengelige strekninger. Med økende urbant utvikling i Sandviksvassdragets nedbørfelt vil gjennomføringen av slike tiltak være nødvendig for å bevare den lokale laksefisk populasjonen.

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Introduction

The human species is an indispensable part of all ecosystems and their activity, meaning the growth of their populations and settlements have a strong, and increasing impact on ecosystem health (Wetzel, 2001). Rising pressure on ecosystems, including their various habitats and species' composition, causes changes in habitat availability and quality, biodiversity, and population size (Sabater et al., 2018). An ecosystem's surroundings must meet many requirements to maintain its functioning (Allan & Castillo, 2009). Ecosystems around human settlements not only bring benefits for organisms using it as their habitat, but they also provide humans with several ecosystem services. The area around the Oslo fjord is the most densely populated in Norway, and it provides a number of ecosystem services, such as tourism, carbon storage, commercial fishing, and recreational activities like fishing and other outdoor activities (Chen et al., 2019). Some of the larger rivers around the Oslo fjord make it possible for anglers to fish salmonids in the fjord, representing a long tradition in Norway (Lamberg & Strand, 2019). Recreational activities contribute to the economic value of the Oslo fjord, but regulating such activities is necessary to ensure the sustainability of the fjord environment and the species that live there (Lewin et al., 2006).

The salmonids Atlantic salmon (*Salmo salar*) and brown/sea trout (*S. trutta*) use the Oslo fjord or even the open sea to feed before they return to their freshwater habitats where they spawn and/or remain over-winter (Jonsson & Jonsson, 2011). This behavioural trait is called anadromy, where juveniles stay in freshwater habitats for up to 8 years before migrating into the sea (Klemetsen et al., 2003). Open sea and fjord environments have greater food availability and quality for fish compared to their freshwater environments. Before migrating, the juvenile salmonids need to go through several physiological and behaviour changes, called smoltification, to adapt to saltwater. As smolts, the salmonids migrate out and feed until they return back to their natal rivers in following years (Jonsson & Jonsson, 2011; Klemetsen et al., 2003).

Even though it has been estimated that more than 6000 trout are taken by anglers in the Oslo fjord each year, the pressure put on the salmonids in the Oslo fjord by human activity is expected to be lower than in other fjord systems, mostly because there are no salmon aquaculture farms in the Oslo fjord (Halttunen et al., 2017; Haugen & Colman, 2020). Available mark-recapture data from trout tagged in Sandvikselva show that the Oslo fjord is still used to the same extent by trout in 2012 to 2019 as in 1949 (Bjørn Olav Rosseland, pers. comm.; Lamberg & Strand, 2019). This could indicate that there have been few critical changes in the saltwater habitat affecting the trout population, meaning changes in population size are most likely due to changes in their freshwater habitats in the rivers around Oslo fjord. Changes in freshwater habitats will mainly affect the survival of juvenile salmonids, which heavily relies on the availability of suitable spawning grounds, shelter to hide from predators after hatching as well as suitable and available food sources while growing and competing with other individuals (Jonsson & Jonsson, 2011).

In order to understand the number of juvenile salmonids a river can sustain, one has to investigate the entire framing of the river ecosystem, and how much food resources it can provide for fish production. A multitude of variables influence the quality of habitats for a river's fauna. Often, the different variables influence each other and have a combined effect (Armstrong et al., 2003). Vegetation, as allochthonous and autochthonous organic matter, the riverbed substrate, depth and water velocity influence food and shelter availability both for salmonids and other organisms (Heggenes et al., 1999; Jonsson & Jonsson, 2011; Kondolf & Wolman, 1993). The combination of the different environmental variables forms the environmental growth conditions for juvenile salmonids, and depending on the ecosystem, some variables will have more significant effects than others. The variables do not only influence the salmonids themselves, but also their prey, like macroinvertebrates, and their predators, making their combined impact on each individual through trophic interactions even stronger. Assessing these environmental variables and comparing several river stretches makes it possible to determine their effects on the salmonids, their food sources, and the river's potential as a salmonid spawning- and nursery habitat.

Macroinvertebrates and salmonids in the same river system have a strong impact on each other. Both bottom-up and top-down food web processes influence the species' and population composition and densities of both groups (Wallace & Webster, 1996; Williams & Taylor, 2003). Feeding on allochthonous and autochthonous organic matter and other macroinvertebrates, macroinvertebrates have an important role in the ecosystem connecting different trophic levels. Macroinvertebrates are an expansive and diverse group, including insect larvae, leeches, snails, and other invertebrates. These are separated into the following five functional feeding groups: scrapers, shredders, gatherers, filterers, and predators. They are the main food source for juvenile salmonids in freshwater. The larvae of Trichoptera, Plecoptera, Chironomidae and Simuliidae are especially eaten by juvenile salmonids (Elliott, 1994; Hynes, 1970; Klemetsen et al., 2003; Wallace & Webster, 1996; Wetzel, 2001). The composition and size of the macroinvertebrate populations in the different stretches of the watercourse links to the salmonid carrying capacity of these stretches. High densities of macroinvertebrates indicate a higher carrying capacity, and conversely low densities indicate either a low carrying capacity or an over exploration (high competition) of available resources by salmonids.

A river's production of salmonids is determined by the degree of functioning of its ecosystem. If vital components are lacking or are impaired, the number of juvenile salmonids surviving their first years can decrease drastically. A low survival rate during the first years will result in a low number of salmonid smolt migrating to the adjacent fjord system, providing lower catch prospects for the trout and salmon anglers, but more important, low numbers of returning adult individuals to the natal river for spawning, and potentially, low reproduction rates. In the Oslo fjord the Sandvikselva catchment area (Sandviksvassdraget) maintains salmonid populations, and provides the highest number of salmonid catches in the past years for the Inner Oslo fjord area (Statistisk sentralbyrå, 2020) (Appendix A).

Sandviksvassdraget is the longest anadrome river system in the Inner Oslo fjord and is an important trout and salmon carrying watercourse around the Inner Oslo fjord (Lamberg & Strand, 2019). Adult salmonids migrate into Sandviksvassdraget and move upstream to spawn. The salmonid population in the watercourse has decreased significantly in the past 20 years, but the reasons for this decline are not clearly known and likely result from a combination of several habitat degrading causes. Human-induced reductions of riparian vegetation and channelization of the river have imposed high pressure on Sandviksvassdraget's ecosystem. Sandvikselva, the lowest part of the watercourse, before it flows into the Inner Oslo fjord, flows through the city centre of Sandvika. This and other stretches are under increasing pressure from urban development and concreting of the catchment, causing a degradation of riparian zones and freshwater habitat for salmonids (Bækken et al., 2008).

The high catches of salmonids in Sandviksvassdraget can be traced back to the continuous activity at the Hamang hatchery in Sandvika. Since 1857, salmon (at first) and trout (since 1960) have been raised at the hatchery through winter and released in different parts of the watercourse during spring and early summer. To avoid interactions between hatchery juveniles and wild juveniles, the juveniles/alevins from the hatchery get released into parts of the watercourse that are not accessible for anadromous spawners. Several dams and natural migration obstacles in the watercourse cut off upstream river stretches from the downstream stretches and reduce the availability of potential spawning- and nursery habitat (Lamberg & Strand, 2019). The rivers Lomma and Isielva, that confluence to form the river Sandvikselva, are therefore only partly accessible for migrating salmonids (figure 1). Each spring in Isielva, salmon alevins from the hatchery are released upstream of the dam by Bjørumsaga. In the upper stretches of Lomma, upstream of the dam by Vøyen, trout alevins from the hatchery are released (Morten Merkesdal, Bærum municipality, pers. comm.).

The dams in the watercourse not only hinder migrating salmonids from spawning further upstream, but they also divide the rivers into different stretches. The species in the downstream stretch of the river have no access to the upstream stretch. While these two stretches are still part of the same river continuum, they can be sampled separately and compared for environmental variables, densities of juvenile salmonids and their abundance and diversity of macroinvertebrates. Since the nursery habitat for alevins from the hatchery do not overlap with the nursery habitat of wild alevins, comparing the juvenile salmonid densities can give insight into potential differences between these two salmonid groups and types of river stretches.

This study aims to [1] register and compare nursery habitat for juvenile salmonids in the upper stretches with alevins from the hatchery and the lower stretches with alevins from mostly natural spawning (we cannot be certain that those from above do not disperse to stretches below). Key environmental variables were sampled and tested against fish densities to analyse the variables that had a significant influence on the environmental growth conditions of juvenile salmonids. Furthermore, [2] which environmental variables, in combination with salmonid density, interact with the composition of macroinvertebrates, as a food source for salmonids. This provided the basis [3] for investigating which stretches supported most juveniles and why, which also relates to the overall output of smolt into the fjord.

The following questions and hypotheses were tested:

1.) Are there differences in the environmental variables at nursery habitats of juvenile salmonid in the upper and lower stretches that explain eventual differences in densities of alevins between these two types of stretches?
    - The upper stretches support higher juvenile salmonid densities than the lower stretches, due to less disturbed habitat, both in the riparian zone and the river course.
2.) Do any of the environmental variables and juvenile salmonid densities influence the diversity and the abundance of the macroinvertebrate community?
    - Riparian vegetation has a positive effect on the diversity and abundance of the macroinvertebrate community by providing food. Furthermore, increasing juvenile salmonid density may influence the macroinvertebrate by changing the abundance of selected species.
3.) Which stretches in the rivers (upper or lower) provide a higher smolt output into the Oslofjord?
    - The upper stretches have a higher smolt output, due to the higher availably of suitable habitat.

Methods

Study area

Sandviksvassdraget in Viken county has its outlet into the Inner Oslo fjord (UTM 32N 6639748 N, 585606 E). The river Sandvikselva, the lowest part of the watercourse, is formed at Vøyen by the rivers Isielva and Lomma, runs through Sandvika centre and is 4.5 km long from its formation point to the river delta (figure 1). Sandviksvassdraget is the largest watercourse running into the Inner Oslo fjord with an area of 225 km^2 and a catchment over 193 km^2. It is managed by Vestre Bærum Sportsfiskere and the Bærum municipality. The catchment consists of coniferous forest, cultivated land, urban development, and industry. High density of settlement, roads, and a high number of construction sites in the catchment are constant sources of particle pollution, which is nowadays the main problem in the watercourse. Sandvikselva has a dominating fall flood with a mean water flow at 60 m^3/s. The summer water flow in contrast is very low at 1 m^3/s (Bækken et al., 2008; Væringstad, 2003). In total, 11 different fish species inhabit the watercourse, including the two study species, Atlantic salmon and sea trout. From the outlet to the Oslo fjord to dams and natural migration obstacles, salmonids have up to a combined 15 km stretch that they can wander upstream to spawn. Every spring since 1857, salmon and trout alevins from the Hamang hatchery have been released into the surrounding tributaries of Sandvikselva to maintain the salmonid population. Adult salmonids along with their smolt counterparts migrate to the Oslo fjord, or further out into the sea, to feed and return to Sandvikselva following autumns to spawn or remain over-winter (Lamberg & Strand, 2019).

The Inner Oslo fjord consists of two basins, Bunnefjorden and Vestfjorden, and flows into the Outer Oslo fjord. It has a maximum depth of 164 m, but the depth throughout the entire fjord varies considerably. The entire Oslo fjord is an important resource for ecosystem services in Norway. Additionally, the increasing human activity trough population, agriculture, forestry and other industries have a significant impact on the ecosystems in and around the fjord (Chen et al., 2019). In particular, the Inner Oslo fjord is constantly under increasing high pressure from human activity (Anonym, 2018). For instance, runoff from the catchment caused anoxic conditions at the bottom of some areas in the Inner Oslo fjord, resulting in little to no benthic fauna below a certain depth (Baalsrud & Magnusson, 2002). Even though the Oslo fjord has been and still is a very popular place for recreational fishing, the state of the fish population in the fjord is not known. Trout is an important species in the Oslo fjord and one of the most studied species in the fjord. The trout population had an increasing density in the 1990s, mostly due to improved management of the freshwater habitat and regulations of the commercial catch in the fjord. Hatchery activity, reopening of suitable rivers and habitat improving measures have had positive effects on trout population (Thaulow & Faafeng, 2014).

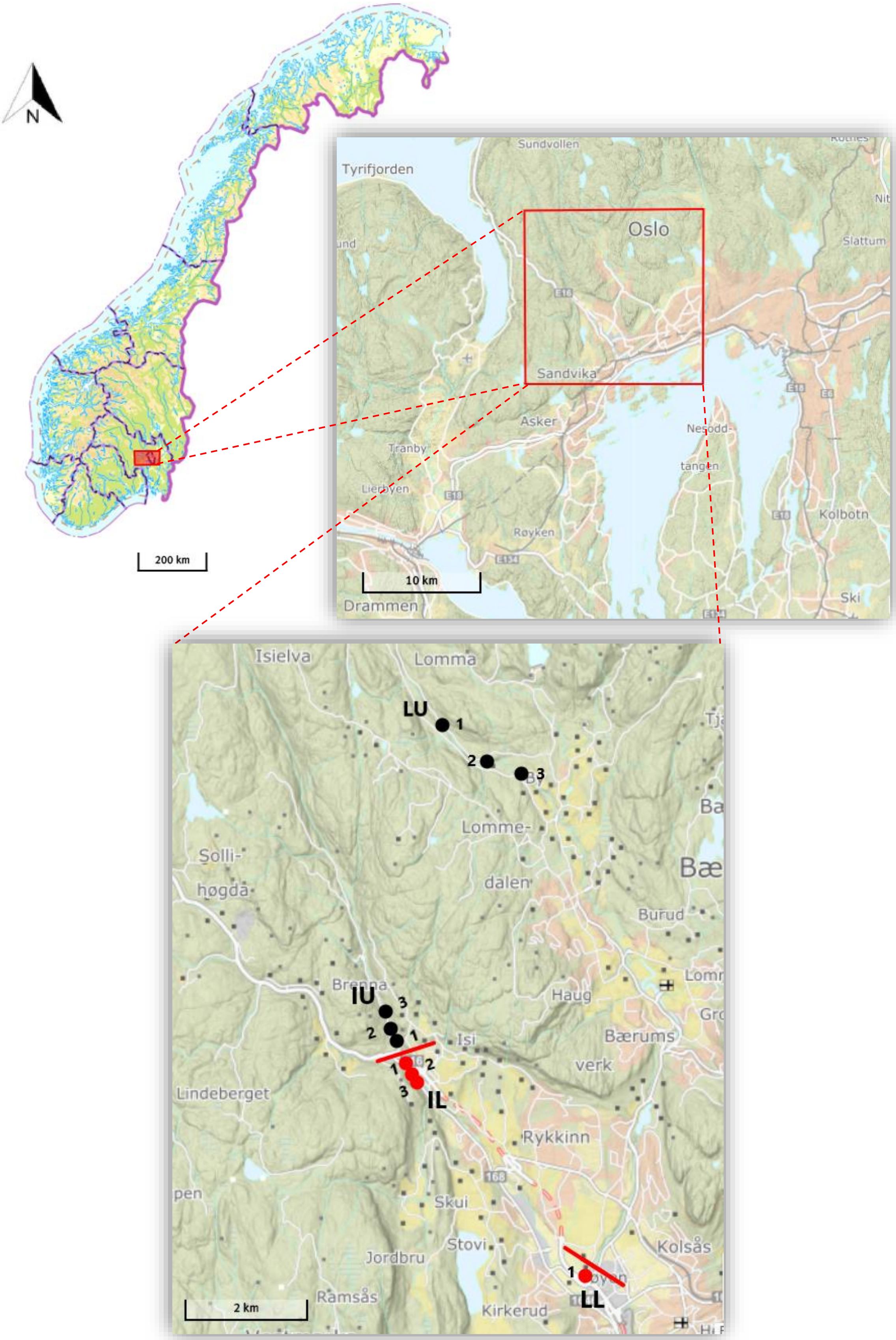

Figure 1: Maps showing the location of the study area in Norway, with the impassable dams (red lines), the upper sample sites (black dots) and lower sample sites (red dots) in Sandviksvassdraget © Kartverket (2020) (IU: Isielva-Upper stretch; IL: Isielva-Lower stretch; LU: Lomma-Upper stretch; LL: Lomma-Lower stretch).

Study species

Both Atlantic salmon and sea trout are native to Sandvikselva and use the river and its inflows naturally for spawning and nursery habitat. Salmon and trout are both anadromous salmonids and have overlapping, but slightly different requirements for their habitat and life cycles (Armstrong et al., 2003). The availability of suitable habitats in lotic ecosystems is crucial in determining the density of salmonids and the river capacity for salmonid populations. Variables like water depth and velocity, substrate composition and vegetation cover influence the habitat choice of salmon and trout and can cause inter- and intraspecific competition for the most suitable habitats (Heggenes et al., 1999).

Spawning occurs in autumn, where the female buries the fertilized eggs in the river substrate. The chosen spawning sites require certain conditions. A continuous and rapid water flow is essential to ensure the survival of the fish eggs, and later the alevins. Not only does this prevent dehydration, but also provides the eggs and alevins with dissolved oxygen and may reduce bacteria and parasite infections (Elliott, 1994). Salmon alevins prefer shallower and faster flowing waters than trout alevins (Heggenes et al., 1999; Jonsson & Jonsson, 2011). In the following spring, after emerging from within the substrate and consuming the yolk that the alevins carry in a sack, they start feeding primarily on drifting macroinvertebrate larvae (Elliott, 1994). The substrate at the spawning and nursery sites should preferably be coarse and composed of gravel, cobble, and larger stones, such as boulders, bank overhangs and dead woody material. This composition provides oxygen supply, heterogeneous structured micro niches with low water velocities for monitoring macroinvertebrate drift and shelter from predators (Armstrong et al., 2003; Heggenes et al., 1999). The trout population in rivers is usually size structured, where the depth and distance from the riverbank increases with increasing fish length (Heggenes et al., 1999). Juvenile salmon are better adapted to higher water velocities than trout due to phenotypic variables (Jonsson & Jonsson, 2011). Deeper pools and shadowed areas are often used as shelter to hide from predators by both salmon and trout (Armstrong et al., 2003).

Each year, since 2012, adult migrating salmonids are tagged, and their gender and body length noted. While tagging migrating salmon and trout each fall, fish eggs are fertilized by hand and kept at the Hamang hatchery. Both the eggs and the sperm are taken from fish that were caught in the river. The alevins are released into the river at approximately the same time in spring as the alevins from natural spawning emerge from within the substrate. In the early years, salmon was mostly cultivated, but nowadays, around 400 000 salmonid alevins, both salmon and trout, are cultivated in the hatchery and released in the Sandviksvassdraget (Lamberg & Strand, 2019; Morten Merkesdal, Bærum municipality, pers. comm.).

Salmon and trout, both cultivated and naturally hatched, migrate after smoltification from the Sandviksvassdraget into the Oslo fjord to feed. Sandviksvassdraget contributes with the highest number of salmonids to the Inner Oslo fjord (Lamberg & Strand, 2019). Recreational fishing on salmonids is an important ecosystem service provided by the Oslo fjord, but it also puts pressure on the salmonid populations (Liu et al., 2019). Salmon migrates through the fjord into the open sea while trout tend to use large areas of the Oslo fjord, which increases the risk of being caught by anglers (Dzadey, 2014). High mortality if caught and kept by anglers reduces the number of salmonids that can migrate back to their natal river and thus, influences the spawning activity in the rivers around the Oslo fjord.

Data sampling

The fieldwork was conducted from October 6th to November 8th, 2019. Until October 18th, 2019, the tagged adult fish included in this study were captured, tagged, and released for the last part of the study. Most of that work was carried out by Morten Merkesdal and volunteers from Bærum Fiskeforbund. Anglers that catch tagged salmonids from Sandviksvassdraget have the option to report their catches. The reported catches from 2012 to 2019 were used to analyse the usage of the Oslo fjord by trout.

For the comparison of spawning habitats, fieldwork was done from October 14th to November 8th, 2019, where most of the sampling was done in the last two weeks due to high water levels earlier in October. To compare the anadrome, natural (lower) spawning stretches against the above anadrome (upper) stretches of the river, suitable sample sites were chosen according to the local managers (Morten Merkesdal, Bærum municipality, pers. comm.). At those sample sites, electrofishing was carried out, macroinvertebrates were sampled, and environmental variables were logged. In total 10 samples sites (figure 1) were included in this study, which were around 25 to 30 meters long and at least 100 meters apart from each other. Six in Isielva, where three of them were in the lower stretch (anadrome) and three in the upper stretch (not anadrome), but where salmon alevins are released each spring. The remaining four sample sites were in Lomma, where three sites were in the upper and one was in the lower stretch. Trout alevins are released every year in the upper stretches in Lomma (Appendix B).

Electrofishing

To estimate the density of juvenile fish in the river stretches, electrofishing was carried out in all sample sites from the November 3rd to the November 8th, 2019 with an electric fishing apparatus (FA4, Terik). This was done with DC pulse, 70 Hz and 700V. Two or three people conducted the electrofishing, where all of them were catching the fish with dip nets, while one person handled the anode. At each sample site, three fishing passes were carried out, with at least 30 minutes in between each pass. At sites with low fish catches, only two passes were conducted. The "three pass system" was used to estimate the fish densities after the Zippin removal method (Bergan et al., 2011; Bohlin et al., 1989; Forseth & Forsgren, 2008; Zippin, 1958). The length for each sampled fish from each removal was measured and the species determined (figure 2).

Figure 2: A juvenile sea trout caught in Lomma.

Age Groups and fish densities

Based on the length distribution of sampled salmon and trout, the age groups were defined for each upper and lower river stretch. The densities for each age group and species were calculated after adjusting the data by changing the number of caught fish per fishing pass without changing the total number of caught fish. The densities are given as number of fish per 100 m². The calculated juvenile salmonid densities were used both as predictor and response data in the statistical analysis to analyse the effect of fish density on the macroinvertebrate community and the effect of the environmental variables and total macroinvertebrate abundance on the fish density.

Macroinvertebrates

Macroinvertebrates were sampled with the “kick-sampling method” along three transects at the beginning, the middle and the end of each sample site (Hynes, 1970). Each transect had three sub-transects, one at each riverside and one in the middle. A 25x25 cm net with a mesh size of 450 µm was placed at the bottom of the river. Upstream of the net, the bottom was kicked for 20 seconds and the net moved upstream. By kicking the river bottom, macroinvertebrates in the substrate were disturbed, loosened, and drifted with the current into the net. The samples were stored in plastic bags and preserved with ethanol 96 % until the macroinvertebrates were classified at the laboratory at the Norwegian University of Life Sciences. Ephemeroptera, Plecoptera and Trichoptera larvae were classified to species and all other orders were identified to the lowest taxonomic level possible.

The following literature has been used for the identification of sampled macroinvertebrates: “Limnofauna Norvegica” (Aagaard & Dolmen, 1996), “Guide to Freshwater Invertebrates” (Dobson et al., 2012), “Was lebt in Tümpel, Bach und Weiher?” (Engelhardt, 1989), “Insektslære for fluefiskere” (Krogvold & Sand, 2008), “Stoneflies (Plecoptera) of Fennoscandia and Denmark” (Lillehammer, 1988), “Aquatic Insects of North Europe” (Nilsson, 1996), “Insekter og småkryp i vann og vassdrag” (Raastad & Olsen, 1999), “Trichoptera larvae of Finland: A key to the Caddis Larvae of Finland and Nearby Countries” (Rinne & Wiberg-Larsen, 2017), and “Virvelløse dyr på land og i ferskvann” (Sømme, 1988).

Environmental variables

To test the quality of the habitat for trout and salmon, key environmental variables were registered for each site. After measuring the length, every site was divided into five cross-transects. At each transect, the width was measured, and the depth was measured at five points along the transect from riverbank to riverbank (10 %, 25 %, 50 %, 75 %, 90 %). The mean depth was calculated afterwards. Moss and algae cover, percentage of shadow covering the water surface and vegetation cover of the riparian zone and riverbank was visually estimated and given a percentage value. The substrate composition of the riverbed was classified by giving each substrate type (sand, gravel, cobbles, rocks, and boulders) a percentage value to calculate the mean substrate size afterwards. Water velocity was registered by measuring the time it takes for a leaf to flood 1 meter downstream. In addition, the number of pools and large woody debris (longer than 1 m and wider than 0.1 m) was counted for the entire length of the site (Appendix C).

Ecological classification

To compare the state of the salmonid populations in the different stretches of the watercourse, the estimated population size was used to classify the ecological state of each site sampled (Direktoratsgruppe Vanndirektivet, 2018). The method used in this study, described in more detail in the handbook by Direktoratsgruppe Vanndirektivet (2018), evaluates the ecological state of small, lowland rivers based on the estimated population size of juvenile salmonids without separating them into age groups and species. For each site, the habitat class was set for class 3, meaning the habitat was "well suited". The same class was used in earlier studies for the watercourse (Skrutvold et al., 2019a). A more detailed description of the habitat classes and class limits can be found in Appendix D. Anthropogenic influence on the fish population, like release of alevins and the lack of one or more age groups has to be taken into account when assessing the ecological state and the ecological state accordingly demoted. The aim of this study was to compare fish densities in the different stretches of the watercourse and to compare natural spawning sites with sites where alevins from the hatchery are released. Since it was not the aim to determine the actual ecological state of the river stretch, I decided, after consulting with my supervisors, not to demote the calculated states to make the sites more comparable.

A common procedure for the classification of the ecological state of rivers is to use macroinvertebrate samples. There are several indices listed in the handbook by Direktoratsgruppe Vanndirektivet (2018) that can be used to classify the ecological state of a river using the macroinvertebrate community. In this study, I decided, after consulting with my supervisors, not to use macroinvertebrate indices to classify the ecological state of the stretches. Sandviksvassdraget is characterized by stressors like channelization and riparian modification. For stressors of this type, no standardised indices are available in the handbook by Direktoratsgruppe Vanndirektivet (2018). The available indices classify the rivers and their macroinvertebrate community based on chemical parameters or on the degree of acidification and organic pollution. Furthermore, earlier studies have classified the overall watercourse based on the macroinvertebrate community and reported a "good" ecological state (Persson et al., 2014; Skrutvold et al., 2019b).

Shannon Wiener diversity index and Pielou evenness index

The Shannon Wiener diversity index (Heip et al., 1998) and the Pielou evenness index (Jost, 2010) were used to explore the effects of the location of the stretches in the river, the environmental variables, and fish density on the macroinvertebrate communities in linear models. Diversity indexes are used in ecological studies to get an estimate of the biological variability of a population that can be used to compare different communities (Heip et al., 1998). The Shannon Wiener diversity index is characterized by the number of individuals of each species and by the total number of species within one sample. The calculated Shannon Wiener index is a degree of uncertainty, as it describes the certainty of correctly predicting the species of the next individual in a community. The higher the uncertainty, the more difficult it is to predict the next individual correctly, and thus, the diversity of the studied community receives a higher score (Krebs, 1999). The "evenness" of a community describes how evenly the individuals of the different species in this community are distributed; simply if a population is dominated by a few species with high occurrence or is composed of a higher number of species with more or less even occurrence numbers. The closer the calculated score is to 1, the more even the species composition is in the studied area (Heip et al., 1998). The Pielou evenness index is calculated taking species diversity into account (Jost, 2010).

Statistical analyses

The statistical analyses were conducted with the software program R (R Development Core Team, 2019). The significant level of alpha was 0.05 for all conducted tests. For the visualization of some results Microsoft Excel was used, in addition to R.

The parameters river (Isielva and Lomma) and the location of the river stretch (upper and lower) were used as the main predictors in this study in combination with the environmental variables. The macroinvertebrate communities in the different river stretches were compared, regarding the number of taxons, diversity and evenness to access the "quality" of the community. When the macroinvertebrate data was the response data, juvenile salmonid density was included as a predictor and the total macroinvertebrate abundance was used as a predictor for the calculated juvenile salmonid densities.

Ordination

Ecological datasets are often complex and contain large differences in species composition and richness. There are many ways to organize and analyse a large multidimensional dataset, but testing each variable and sample on its own can lead to a higher amount of errors and misinterpretations, since the various variables can have a significant influence on each other (Šmilauer & Lepš, 2014). To reduce the chance of Type I errors (false positive) and to analyse the dataset in as few tests as possible, ordination was used in this study. Ordination is divided into unconstrained and constrained ordination. There again, the method differentiates between linear models and unimodal models. The heterogeneity of the data determinants the use of either a linear model or a unimodal model. For homogeneous data, linear ordination models are best fitted. To figure out if a linear or unimodal model should be used, a Detrended Correspondence Analysis (DCA) was conducted. The DCA accounts for the heterogeneity of the data by giving the length of the longest DCA axis in turn over units. A value above 3 indicates heterogeneous data (Šmilauer & Lepš, 2014).

An unconstrained ordination aims to find ordination axes that represent the most influential predictors for the sampled response data. For linear data, a Principal Components Analysis (PCA) can be used, and for unimodal data, a Correspondence Analysis (CA). If there are one or more predictors, in this study fish density and environmental variables, explaining the variation in the response data, macroinvertebrate abundance, a constrained ordination is used. For linear data, the redundancy analysis (RDA) and the canonical correspondence analysis (CCA) for unimodal data is used (Šmilauer & Lepš, 2014).

The given axes have eigenvalues that show to which degree the represented variables explain the variation in the response data. The higher the eigenvalue, the more variation is explained. Visualized in an ordination diagram, correlations are indicated by position of cases in the diagram and arrows with different directions and lengths. The closer the cases are in the diagram, the more variables they have in common. The length of an arrow indicates the effect on the response data, meaning the longer the arrow the stronger is the effect. Arrows pointing in the same direction indicate a positive correlation and vice versa (Šmilauer & Lepš, 2014).

The effects of environmental variables on the response data (macroinvertebrates or fish density) were analysed using the calculated principal component scores (PC) from the conducted PCA with the environmental variables as the response data. The number of PCs included depends on the cumulative proportion of the PC-axes. At least 50 % must be explained by the included axes. Eventually, calculated effects of the axes on the response data can be traced back to the environmental variables that are represented by the particular axis.

In this study, the R package “vegan” was used to carry out the ordination analyses. The package contains tools for descriptive community ecology and basic tools for diversity analysis, community ordination and dissimilarity analysis (Oksanen et al., 2019).

Model selection

To estimate the effect of environmental variables and fish density on the macroinvertebrate community, the Akaike’s Information Criterion (AIC) was used for model selection (Akaike, 1974). The aim is to estimate the balance between the precision and the bias of the model. The AIC for each model is the sum of the model’s deviance and twice the number of variables included in the fitted model. The lower the models AIC, the more can the respective response data be predicted by the included explanatory variables (predictors). The difference between the AIC for a given model and the one with the lowest AIC score is called ΔAIC. Models with a ΔAIC below 2 were considered as potential models (Anderson, 2008; Burnham & Anderson, 1998). In addition, a permutation test (999 permutations) and an Anova for linear models was performed to check if the predictors had a significant effect on the response data. If a predictor did not have a significant effect, the model that excluded this predictor was chosen, but only if the model still had an ΔAIC lower than 2.

Results

Fish

Size- and age structure and juvenile densities

Both trout and salmon alevins were larger in Lomma than in Isielva, but there were no differences within the species in the same river. With only 6.5 cm 0+ trout in the lower stretch in Isielva were the smallest, and 12 cm >1+ trout in the upper stretch in Lomma were the largest (table 1, figure 3 & 4). In the lower stretch in Lomma, only three trout were caught, belonging to the age group 0+. Therefore, no histogram for this species and this river stretch is presented in this study. The age limit for trout in the lower stretch in Lomma was set according to the age limit in the upper stretch.

Table 1: Length interval of sea trout and Atlantic salmon age groups in the different river stretches, measured in cm.

	River stretch	0+	1+	>1+
Sea trout				
Isielva	Lower	<6.5	6.6-11.5	>11.5
Lomma	Lower	<8.5		
Lomma	Upper	<8.5	8.6-12	>12
Atlantic salmon				
Isielva	Lower	<7	7.1-9.5	>9.5
Isielva	Upper	<7	7.1-9.5	>9.5
Lomma	Lower	<7.5	7.6-11	>11

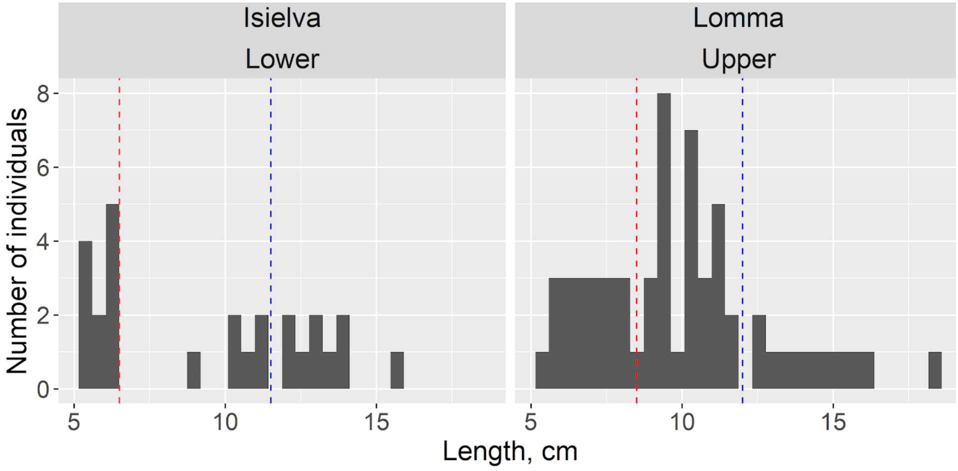

Figure 3: Histogram of the length distribution of age groups for sea trout in the lower stretch of Isielva and the upper stretch of Lomma. The 0+ age group is below the red dotted line, the 1+ age group is between the red dotted and the blue dotted line, the >1+ age group is above the blue dotted line.

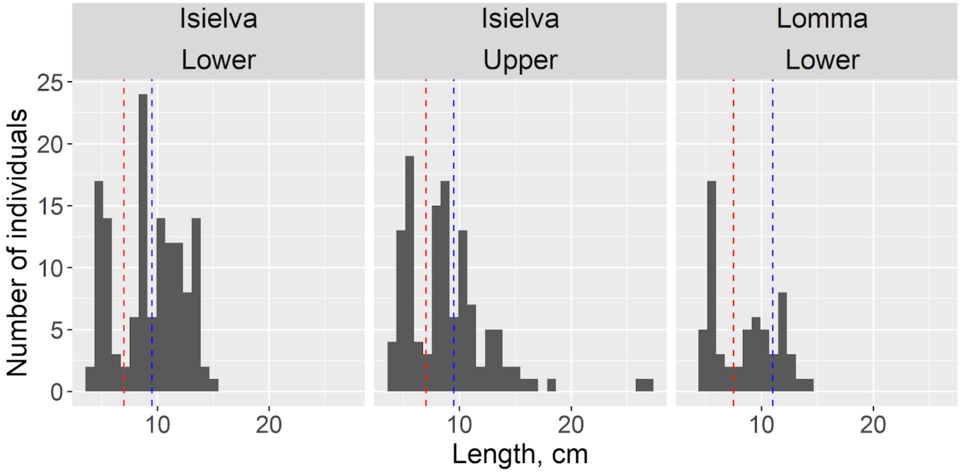

Figure 4: Histogram of the length distribution of age groups for Atlantic salmon in the upper and lower stretch of Isielva and lower stretch of Lomma. The 0+ age group is below the red dotted line, the 1+ age group is between the red dotted and the blue dotted line, the >1+ age group is above the blue dotted line.

In Isielva, salmon densities for all age groups were slightly higher (3.7 - 16.6 per 100 m^2) in the lower stretch than in the upper stretch (1.1 - 33.3 per 100 m^2), besides the one 0+ group with over 30 individuals in an upper stretch site. For all age groups, lower-stretch juvenile trout densities were much lower (0 - 4.3 per 100 m^2) than cooccurring juvenile salmon densities. As expected, no juvenile trout were caught in the upper stretches of Isielva, because only salmon are stocked in this part of the river and it is not accessible for naturally migrating trout. In the upper stretches of Lomma, only trout were caught for the same reason. In Lomma, at the lower stretch, salmon (5.0 - 9.0 per 100 m^2) had a higher density than trout (0 -1.0 per 100 m^2) for all age groups (figure 5). The catchability and density for each age group at every site is listed in Appendix E.

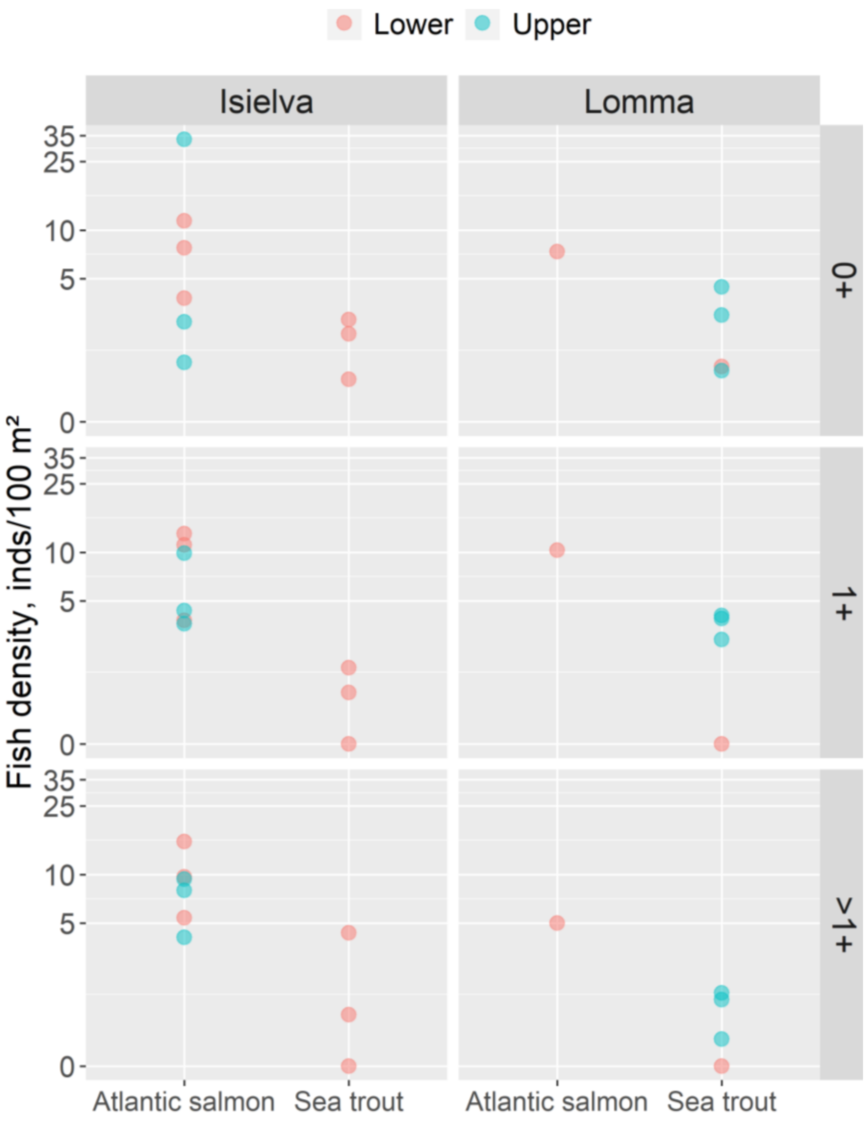

Figure 5: Juvenile Atlantic salmon and sea trout densities per 100 m^2, divided into age groups for the river stretches in Sandviksvassdraget. The y-axis is log-transformed.

Ecological classification

In general, upper-stretch sites had lower ecological state classes than the lower stretches when using anadromous fish densities for classification (figure 6). However, the site Isielva-Upper 1 had the highest density of salmonid juveniles and was the only site in the upper stretches classified as “excellent” with 52.6 salmonids per 100 m^2. The farther upstream the upper stretches were located, the lower were the densities and ecological state classifications in Isielva. In the lower stretch in Isielva, two sites were in an “excellent” state with 28.1 and 48.4 salmonids per 100 m^2 and one site was classified as “moderate”, having a density of 17.8 salmonids per 100 m^2, right below the class limit to “good” at 19 salmonids per 100 m^2. The estimated densities for all salmonid juveniles were overall lower in Lomma than in Isielva. All the upper sites in Lomma were in a “bad” ecological state, having densities of 6.2 and 9.7 salmonids per 100 m^2, and one site was even classified as “poor” with only 5.9 salmonids per 100 m^2. The lower stretch in Lomma was in a “good” state with 23.7 salmonids per 100 m^2.

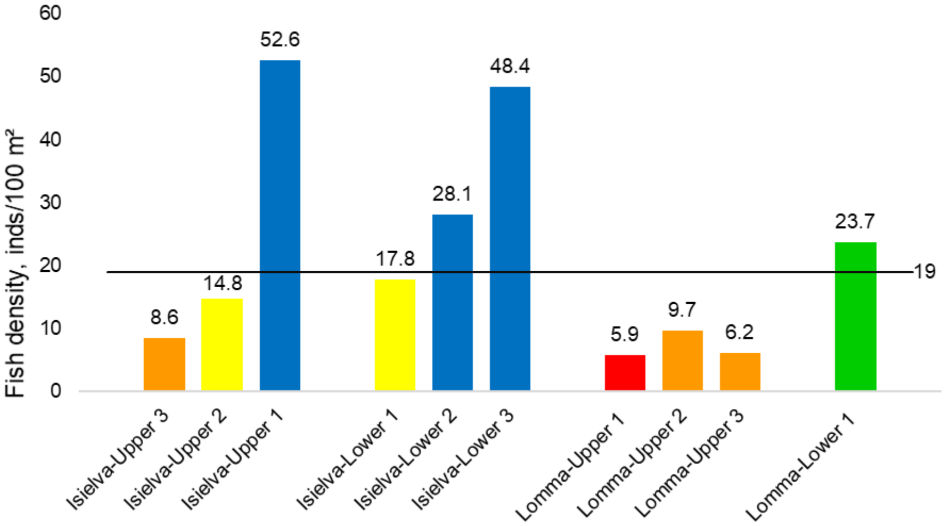

Figure 6: Ecological state for the sample sites in the stretches in Isielva and Lomma, defined after Direktoratsgruppe Vanndirektivet (2018). The class limit for a “good” ecological state is 19 salmonids per 100 m^2 (blue: “excellent” ecological state; green: “good” ecological state; yellow: “moderate” ecological state; orange: “bad” ecological state; red: “poor” ecological state).

Influence of environmental variables

For the environmental variables, the unconstrained Detrended Correspondence Analysis (DCA) calculated an axis length below 3 (axis length DCA1 = 0.785), therefore, linear ordination analysis was used for further analyses of these data (table 2). A principal component analysis (PCA) was conducted to analyse the environmental variables.

Table 2: Detrended correspondence analysis (DCA) was used to determine which model approach to use in the analysis of the environmental variables (linear or unimodal). An axis length lower than 3 supports a linear ordination approach.

	DCA1	**DCA2**	**DCA3**	**DCA4**
Eigenvalues	0.08	0.054	0.021	0.038
Decorana values	0.08	0.035	0.014	0.006
Axis lengths	0.785	0.666	0.412	0.684

The PCA of the environmental variables for both rivers showed that the percentage of shadowing of the water surface (shadow.water) and large woody debris (LWD) correlated positively with moss abundance. The axis PC2 in this study is associated mostly with autochthonous production and the PC1 axis with allochthonous production. Riverbank and flood zone vegetation (riparian vegetation) and algae showed a strong positive correlation to each other, along with LWD and the percentage of shadowing, but a negative correlation to moss. Average depth (depth.mean) correlated positively with mean substrate size (sub.mean) and number of pools, meaning the average substrate size and number of pools increased with increasing average depth (figure 7). The PC1, PC2 and PC3 scores accounted for 60 % of the variation in environmental variables and were used as predictors for fish density and macroinvertebrate data (table 3).

Table 3: PC1 to PC6 scores for environmental variables and the eigenvalues of the calculated PC axes.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
depth.mean	0.148	-0.336	0.544	-0.955	-0.846	0.228
sub.mean	0.662	-0.698	-0.289	0.689	-0.422	0.631
velocity	-0.328	-0.134	1.064	-0.092	0.565	0.744
shadow.water	-0.497	1.099	0.003	-0.587	-0.159	0.289
veg.flood	-0.897	-0.433	0.701	0.488	0.006	-0.129
veg.riverbank	-1.224	-0.399	0.328	0.023	-0.174	-0.192
moss	0.32	1.027	0.209	0.774	-0.153	0.329
algae	-1.087	-0.327	-0.606	0.486	-0.297	0.214
pools	-0.112	-0.619	-0.892	-0.646	0.461	0.403
LWD	-1.003	0.614	-0.665	-0.037	-0.081	0.242
Eigenvalue	2.449	1.849	1.698	1.46	0.723	0.684
Proportion Explained	0.245	0.185	0.17	0.146	0.072	0.068
Cumulative Proportion	0.245	0.43	0.6	0.746	0.818	0.886

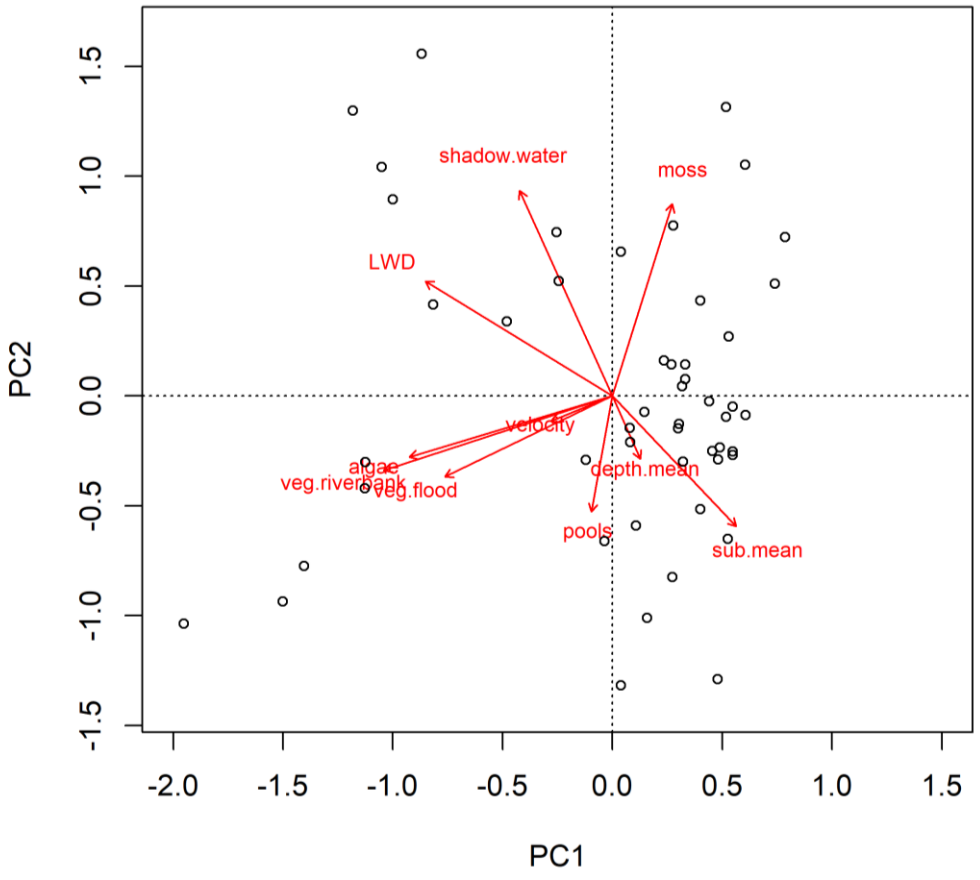

Figure 7: Biplot of PCA showing PC1 and PC2 scores for environmental variables (arrows) and site scores (dots).

The model selection procedure of the RDA favoured a model with the predictors “river” and “UpperLower” to explain the variation in environmental variables. The model including these two factors explained 14 % of the variation of the environmental variables (table 4). Figure 8 shows the position of each environmental variable in relation to the location of the stretches in the rivers. Pools, vegetation on the riverbank and the flood zone of the river were associated with the sites located in the upper stretches. Moss coverage and shadowing were higher in the lower stretches. LWD was more present in Lomma and in the lower stretches than in Isielva and the upper sites. However, the average depth and water velocity were higher in Isielva.

Table 4: Selection of model by a forward selection routine and permutation tests in constrained ordination for environmental variables (AIC = Akaike`s Information Criterion, ΔAIC = difference between AIC for a given model and the one with the lowest AIC score).

Predictor	**AIC**	**ΔAIC**	**F**	**Pr(>F)**
river + UpperLower	112.421	0	3.912	0.001
river	113.983	1.562		
UpperLower	115.227	2.806		
Intercept of river + UpperLower	116.119	3.698		

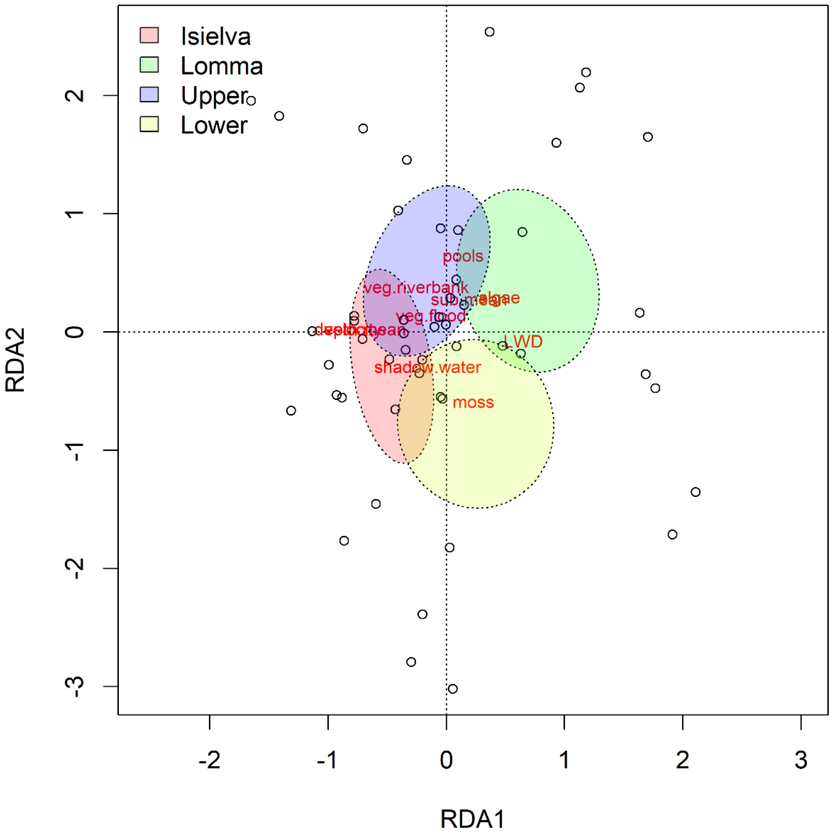

Figure 8: Biplot of the RDA of environmental variables. The position of the environmental variables indicates their correlation with the river stretches (ellipses). The dots represent the site scores.

Effect on fish density

The fish density in the rivers did not correlate significantly with PC1, PC2 or PC3 (table 5). A Pearson coefficient of -0.49 indicated a negative, but non-significant correlation between fish density and PC1 (figure 9). The Pearson coefficient was stronger for PC1 and fish density than for PC2 or PC3 and fish density. The negative correlation means that with a decreasing PC1 value, the fish density increases, but not significantly. Figure 7 and table 3 show that negative PC1 values represent the allochthonous production along the river. This indicates that increasing vegetation may increase the fish density.

Table 5: Effect of PC1 to PC3 on the juvenile salmonid density in Sandviksvassdraget.

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**	**Pearson coeff.**
PC1	1	612.68	612.68	2.490	0.153	- 0.49
Residuals	8	1968.16	246.02			
PC2	1	26.1	26.1	0.082	0.782	- 0.10
Residuals	8	2554.7	319.34			
PC3	1	208.95	208.95	0.705	0.426	0.28
Residuals	8	2371.89	296.49			

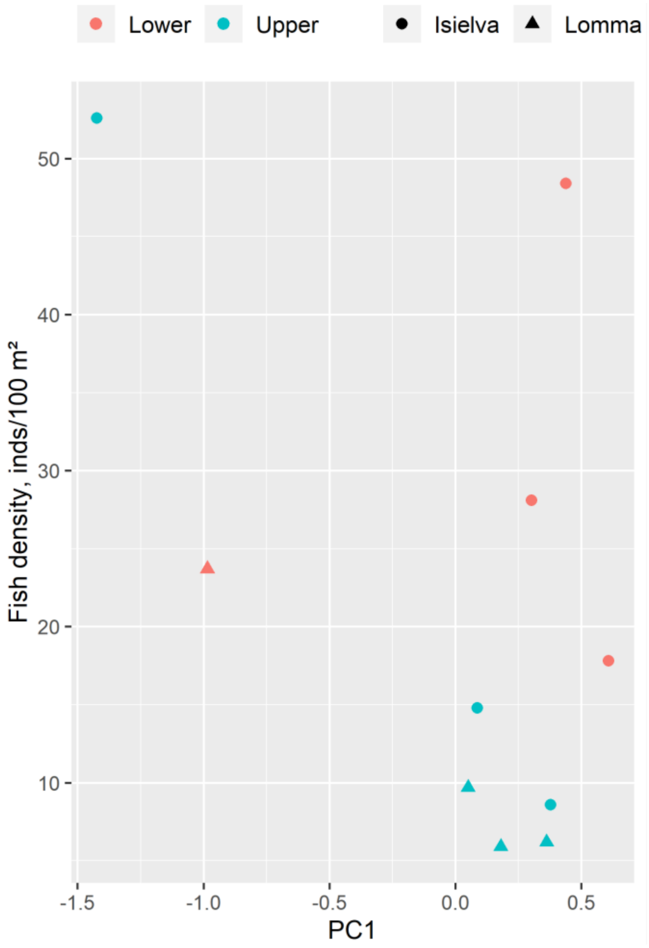

Figure 9: Correlation of juvenile salmonid densities in the different river stretches with PC1. No significant correlation is indicated.

Macroinvertebrates

Species composition

There were 50 taxa found in total in this study. Most of the sampled macroinvertebrates belonged to the orders Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies) and Diptera (true flies). The remaining taxa were identified as Coleoptera (beetles), Oligochaeta (worms), Acari (mites), Bivalvia (molluscs), Gastropoda (snails), Turbellaria (flatworms), Hirunidea (leeches), Amphipoda (crustacea) and Isopoda (crustacea). The lower site in Lomma had the highest abundance with 12 282 individuals. The other sites had much lower abundances between 1 135 to 3 803 individuals (figure 10).

Mayflies were the dominating group at all sites and the most common species within the mayflies with at least 51 % at all sites was *Baetis rhodani*, closely followed by *Baetis muticus*. At the sites in Isielva, only these two mayfly species were found. At all sites in Lomma at least one more mayfly species was registered. In total, 10 different species of stoneflies were sampled, and species from the two families *Amphinemura* and *Nemoura* were dominating. The site in the lower stretch of Lomma had, compared to the other sites, the lowest proportion of stoneflies. The composition of caddisflies varied between the sites. A total of 17 caddisfly species were identified. Two upper sites in Isielva and Lomma (Isielva-Upper 1 & 2, Lomma-Upper 1 & 2) had a more even distribution of caddisflies, with no dominating species. The species *Micrasema setiferum* and *Rhyacophila nubila* were found at all sites and *M. setiferum* was dominating within the caddisflies at the lower sites in Isielva and the upper site nr. 3 in Lomma. The upper site nr. 3 in Isielva was dominated by *Limnephilus coenosus* and the lower site in Lomma was dominated by *Hydropsyche siltalai*. Within the true flies, Chironomidae and Simuliidae were dominating at all sites. At the upper site nr.1 in Isielva and the lower site in Lomma Chironomidae were dominating, and at all the other sites Simuliidae were dominating. The species list for all sampled sites is presented in Appendix F.

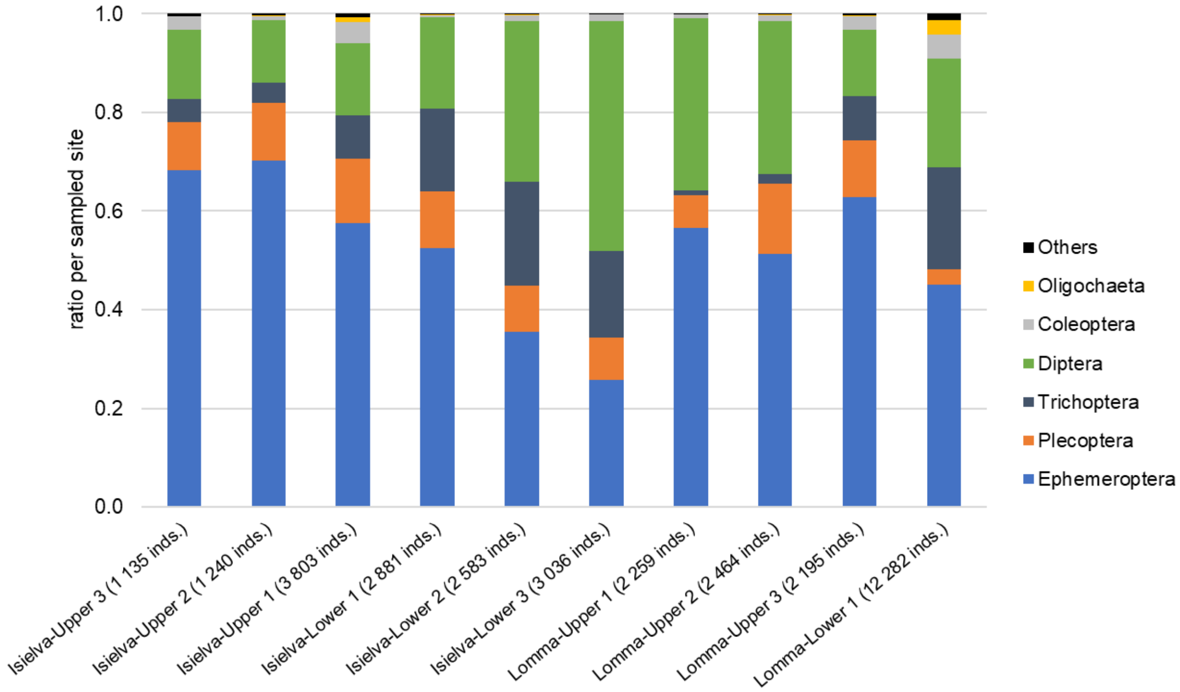

Figure 10: Total macroinvertebrate composition as ratio per sampled site at the different sample sites in Sandviksvassdraget.

Diversity and evenness

All stretches in the two rivers showed an increasing number of taxons with increasing number of sample sites (figure 11). The stretches in Lomma, both upper and lower, had a higher species diversity than the stretches in Isielva. The lower stretch in Lomma showed the highest number of taxons. The upper stretch of Lomma not only had a higher species diversity than Isielva, but also had a steeper increase of the number of taxons with increasing number of sample sites. In Isielva, the upper stretches had higher species diversities than the lower stretches, but the differences are small. Note that the confidence bounds of the four river stretches overlap significantly.

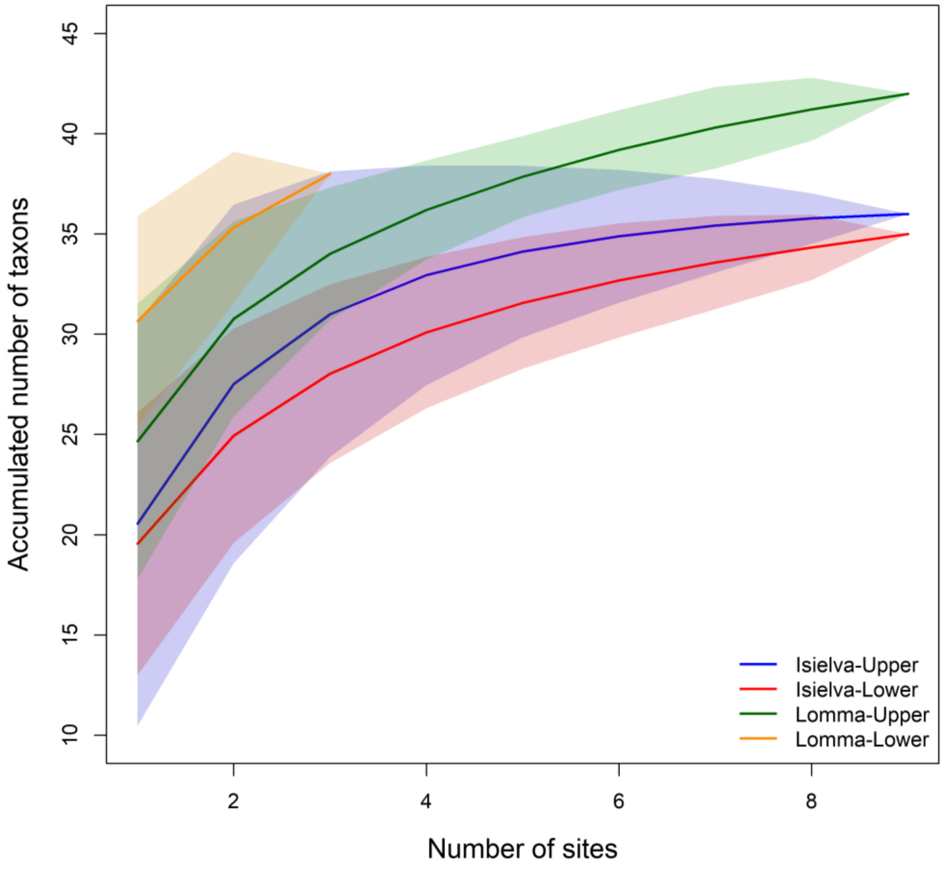

Figure 11: Accumulated number of taxons as a function of sample sites for the different stretches for each stretch. Shade shows the 95 % confidence bounds for the number of taxons. The stretches in Isielva and in the upper stretch in Lomma, had nine subsamples. The lower stretch in Lomma had only three subsamples.

The macroinvertebrate abundance regarding the evenness of the distribution of species abundance is shown in figure 12. In addition, an average Pielou evenness score was calculated for each river stretch (table 6; Appendix G). The sites in the lower river stretch of Isielva and the upper sites in Lomma had an average Pielou score of 0.553, meaning the sites had neither a very even distribution of the sampled species, nor were the sites significantly dominated by one or some macroinvertebrate species. The upper sites in Isielva had a slightly higher calculated evenness of 0.589. Figure 12 also shows a less steep slope, indicating a higher evenness for these sites. The calculated evenness of the lower river stretch in Lomma was highest with 0.684.

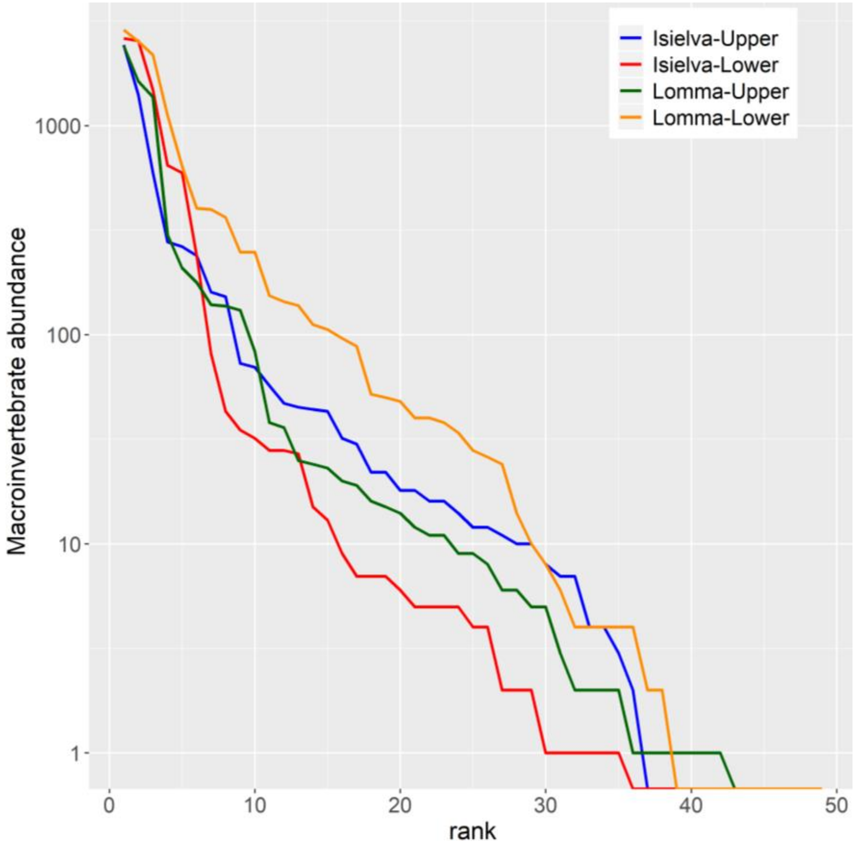

Figure 12: Rank abundance curve for macroinvertebrates in the different stretches in Lomma and Isielva.

Table 6: Calculated average Pielou Evenness and Shannon Wiener diversity indices for the four river stretches.

River stretch	**Pielou**		**Shannon Wiener**	
	mean	SD	mean	SD
Isielva - Upper	0.589	0.064	1.765	0.243
Isielva - Lower	0.553	0.044	1.638	0.175
Lomma - Upper	0.553	0.033	1.770	0.176
Lomma - Lower	0.684	0.030	2.337	0.052

The Shannon Wiener index for the four river stretches only showed the lower site in Lomma to be statistically significantly different from the other sites (figure 13; table 6). The lower stretch in Lomma had a significantly higher Shannon Wiener value, indicating a higher species diversity than the other river stretches. Model selection of linear candidate models of the Shannon Wiener values favoured the model with the predictors "river" and "UpperLower". An ANOVA (two-way) test for this model showed a statistically significant effect of these factors in an interaction model (table 7; Appendix H). An additional model selection of the Shannon Wiener values, substituting "river" and "UpperLower" as predictors with environmental variables, favoured a candidate model with PC1 and PC2 as predictors (table 8).

Table 7: Parameter estimates and corresponding test statistics for the selected linear model (river*UpperLower) fitted to predict Shannon Wiener values for macroinvertebrates. *** indicates a significance level of p < 0.001.

Parameter estimates				**Effect test**				
Term	Level	Estimate	SE	Effect	Df	SS	F	Pr(>F)
(Intercept)	Isielva	1.638	0.064	river	1	0.318	8.544	0.007
riverLomma	Lomma	0.699	0.129	UpperLower	1	0.074	1.985	0.171
UpperLower-Upper	Isielva-Upper	0.127	0.091	river: UpperLower	1	0.723	19.425	***
riverLomma: UpperLower-Upper	Lomma-Upper	-0.694	0.158					

Table 8: Ranked model selection table for candidate linear models fitted to predict Shannon Wiener values. Two model selections were conducted, one with "river" and "UpperLower" as predictors and one excluding "river" and "UpperLower" as predictors (K = number of fitted values, AIC = Akaike`s Information Criterion, ΔAIC = difference between AIC for a given model and the one with the lowest AIC score, AICWt = AIC weight (relative support), and LL = log likelihood value).

Predictor	**K**	**AIC**	**ΔAIC**	**AICWt**	**Cum.Wt**	**LL**
river*UpperLower	5	-5.39	0	0.86	0.86	8.95
PC1+PC2	4	1.29	0	0.21	0.21	4.15
PC1	3	1.46	0.17	0.20	0.41	2.73
PC1+PC2+PC3	5	1.57	0.27	0.19	0.60	5.47
PC1+PC3	4	1.97	0.68	0.15	0.75	3.81

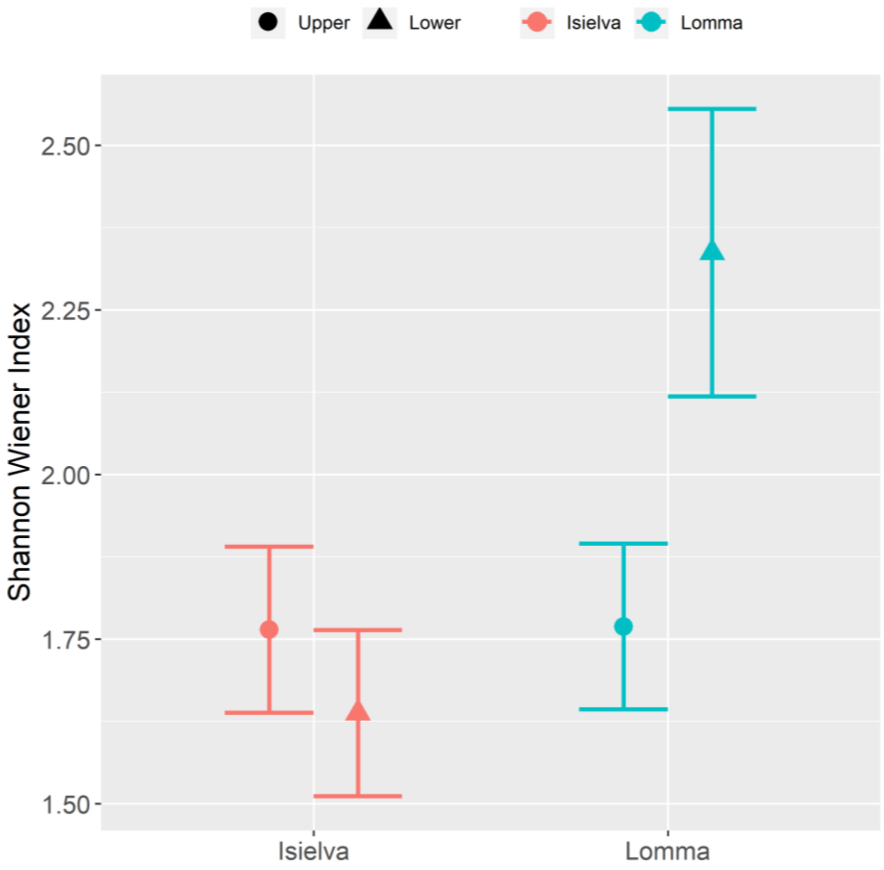

Figure 13: Average Shannon Wiener value for macroinvertebrates as a function of upper and lower stretches in Isielva and Lomma.

The measured environmental variables and the fish density did not have a significant additive effect on the beta diversity of the macroinvertebrates. A performed permutation test calculated a p-value of 0.236 ($r^2 = 0.077$, number of permutations = 999).

Abundance

For the macroinvertebrate abundance data, the DCA calculated a first axis length below 3 (axis length DCA1 = 1.427), therefore linear ordination analysis was used for these data (table 9).

Table 9: DCA to determine which model approach to use in the analysis of the macroinvertebrate data (linear or unimodal). An axis length lower than 3, supports a linear ordination approach.

	DCA1	**DCA2**	**DCA3**	**DCA4**
Eigenvalues	0.173	0.064	0.048	0.038
Decorana values	0.187	0.057	0.028	0.022
Axis lengths	1.427	1.448	1.036	0.880

The model selection procedure of macroinvertebrate data showed that the constrained RDA candidate model that included all predictors attained the lowest AIC value (table 10). However, only the predictors PC1, PC2, "river" and "UpperLower" had a significant statistical effect on the response data in a permutation test (Appendix I). Therefore, the model with the second-lowest AIC value and which excluded the non-significant predictors PC3 and "fish density" was chosen (table 10 & 11). About 60 % of the variation in the macroinvertebrate abundance are explained by the chosen model.

Table 10: Selection of model by a forward selection routine in constrained ordination for macroinvertebrate data (AIC = Akaike`s Information Criterion, ΔAIC = difference between AIC for a given model and the one with the lowest AIC score).

Predictor	**AIC**	**ΔAIC**
PC1 + PC2 + PC3 + fish density + river + UpperLower	97.242	0
PC1 + PC2 + river + UpperLower	97.250	0.008
PC1 + PC2 + fish density + river + UpperLower	97.652	0.410
PC1 + PC3 + fish density + river + UpperLower	98.674	1.432

Table 11: R^2 and effect p-values for the selected model fitted to explain variation in the macroinvertebrate data.

Predictor	**r^2**	**Pr(>r)**
PC1	0.585	0.001
PC2	0.199	0.045
river	0.105	0.032
UpperLower	0.344	0.001

The RDA of the macroinvertebrate abundance showed that most of the species were associated with the river Lomma and only a few were typical for Isielva. However, several species were not associated with any of the rivers, meaning they were found in both rivers in more or less the same amount. The stonefly *Nemoura cinerea* and black flies (Simuliidae) had a positive correlation to the sample sites in Isielva. Organic pollution tolerant macroinvertebrates like Oligochaetes, but also other less tolerant species like the caddisflies *Rhyacophila nubila* and *Lepidostoma hirtum* showed a negative correlation to PC1 and were associated with the sites in Lomma (figure 14). With decreasing PC1 the allochthonous production increased (figure 7). Only few species had a positive correlation to PC1, indicating that allochthonous production by riparian vegetation was an important variable for macroinvertebrate abundance. All in all, no species were typical for the upper stretches, but the caddisfly *Micrasema setiferum* had a strong positive correlation with the lower river stretches and PC2 (autochthonous production).

The beetle *Elmis aenea* and stonefly *Capnopsis schilleri* also showed a positive correlation with PC2. The upper sites in the rivers showed a negative correlation to PC2, indicating less moss and shadow coverage (figure 7). Because no macroinvertebrates were strongly associated with the upper sites, the influence of shadow cover and the amount of moss on the substrate seemed to be significant for macroinvertebrates, since the lower sites were correlated with shadow and moss coverage (figure 8). Most individuals of the functional feeding group “predators”, like the stonefly *Diura nanseni*, and the beetle *Agabus sp.* had a stronger positive correlation to the upper sites than to the lower sites. No other functional feeding group showed a correlation to either river or location of the stretches (Appendix J).

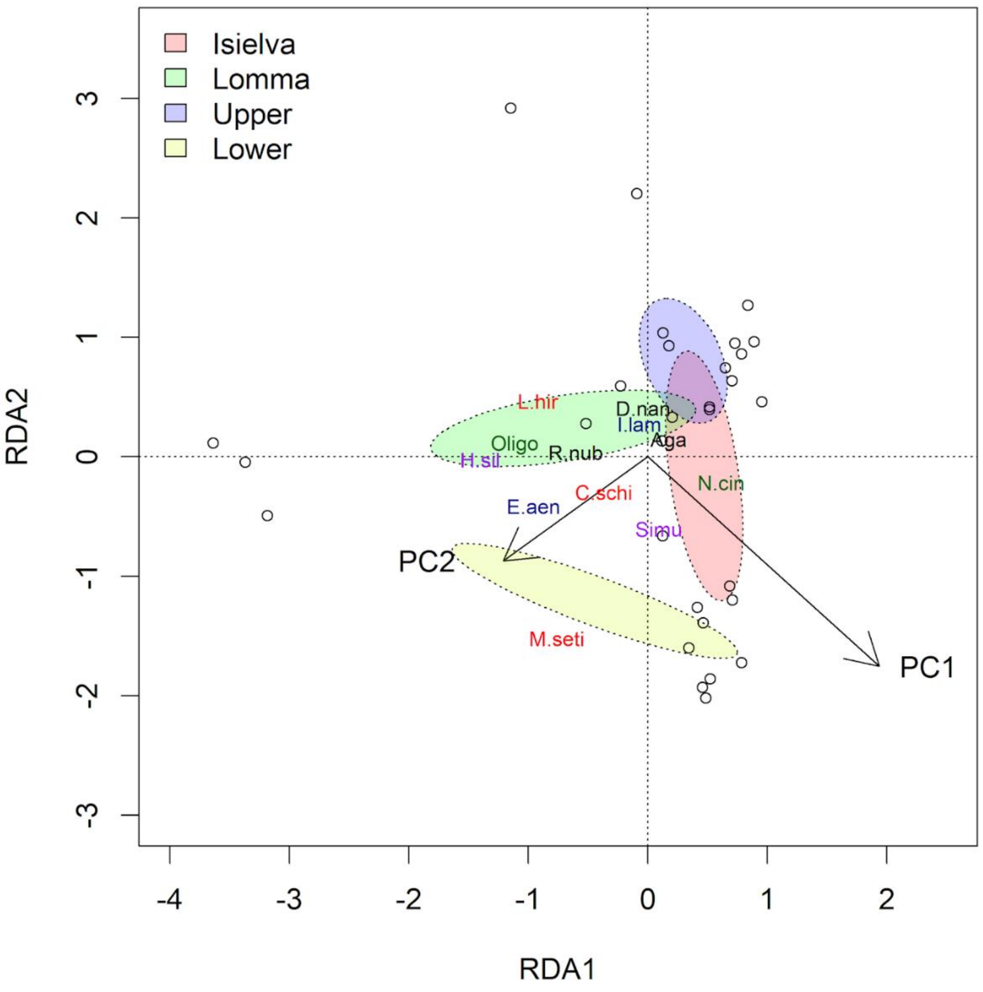

Figure 14: Biplot of the selected RDA, with PC1 and PC2, as continuous predictors, are shown as arrows and the river stretches as ellipses. 12 macroinvertebrate species are displayed, representing the five functional feeding groups with the highest influence in the RDA (M.seti: *Micrasema setiferum*; L.hir: *Lepidostoma hirtum*; H.sil: *Hydropsyche siltalai*; R.nub: *Rhyacophila nubila*; I.lam: *Ithytrichia lamellaris*; C.schi: *Capnopsis schilleri*; N.cin: *Nemoura cinerea*; D.nan: *Diura nanseni*; E.aen: *Elmis aenea*; Aga: *Agabus sp.*; Simu: Simuliidae; Oligo: Oligochaeta; red: shredder; blue: scraper; green: gatherer; violet: filterer; black: predator). The dots display the sample sites.

The average total abundance of macroinvertebrates per sample site did not correlate significantly with "fish density" (p-value = 0.53). However, the Pearson coefficient of 0.22 indicates a weak positive, non-significant relationship.

Mark-recapture data

There was a large degree of coherence between recapture locations of tagged trout from Sandvikselva in 1949 and the 2012-2019 period (figure16). The 1949 data had recapture distances up to 98 km away from the Sandvikselva river delta, whereas the maximum distance for the 2012-2019 data was 150 km. Model selection of linear candidate models fitted to recapture locations for the 2012-2019 data favoured an additive effect of gender and body length at tagging (table 12). This most supported model estimated recaptures to be further away from the Sandvikselva river delta for larger fish, and where females had larger recapture distances than males (figure 15).

Table 12: Effect of body length and gender of caught sea trout in the Oslo fjord on the distance from the recapture location to the Sandvikselva river delta. *** indicates a significance level of $p < 0.001$.

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
body length	1	22.585	22.585	17.477	***
gender	1	7.201	7.201	5.572	0.021
Residuals	83	107.262	1.292		

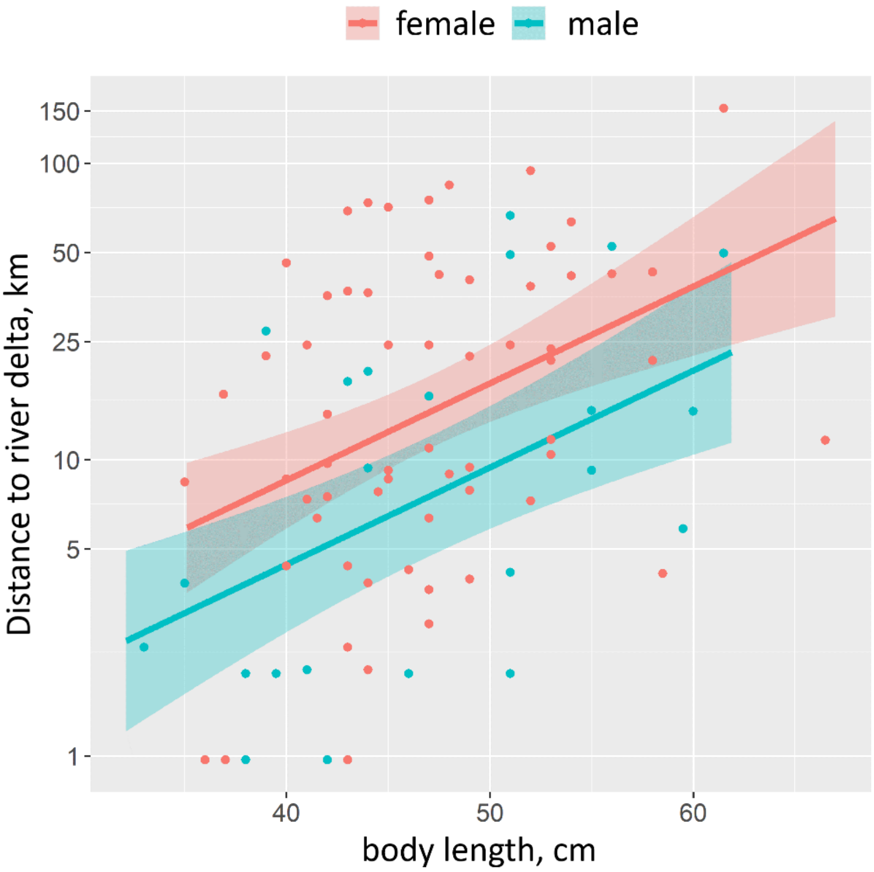

Figure 15: Prediction of linear model estimating recapture distance-to-river-delta for adult sea trout individuals captured and tagged in Sandvikselva during 2012-2019 as a function of gender and body length at tagging. Predictions were estimated from the model reported in table 12. Shaded areas indicate 95 % confidence bounds.

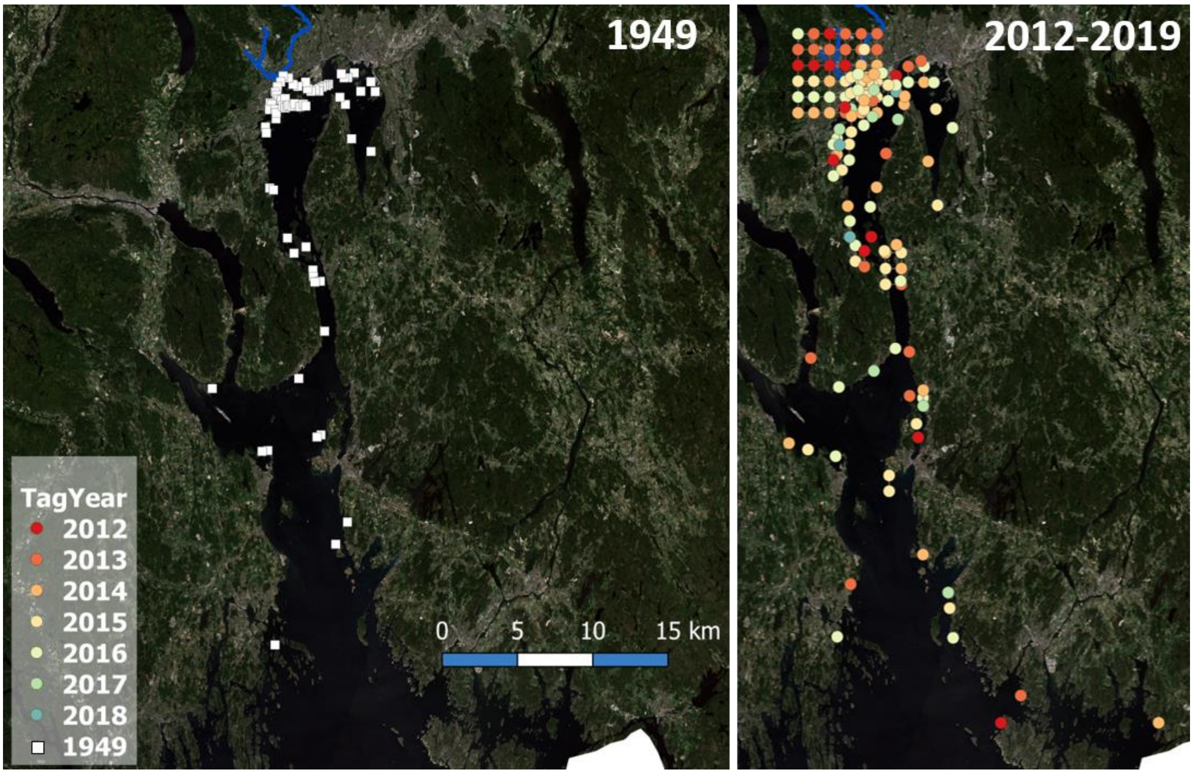

Figure 16: Recapture locations for sea trout from Sandvikselva in the Oslo fjord from 1949 and the period 2012 to 2019 (Bjørn Olav Rosseland, pers. comm.).

Discussion

Juvenile salmonid densities

In this study, juvenile salmonid densities were relatively low for all sampled stretches. The lower stretches had higher salmonid densities than the upper stretches, both in Lomma and in Isielva. The average density for lower stretches was 23 salmonids per 100 m^2 in Lomma and 31 salmonids per 100 m^2 in Isielva. The upper stretch in Lomma had the lowest average density of 7 salmonids per 100 m^2. The salmonid density in the upper stretch in Isielva decreased further upstream, and in the lower stretch, the densities increase further downstream. At all sampled stretches where salmon and trout were coexisting, salmon had higher densities. Even though each year thousands of salmonid alevins are released in the upper stretches in Lomma and Isielva, the densities were lower than the densities in the stretches with alevins from natural spawning. One reason for the overall low densities calculated for 2019 might the time of electrofishing. Electrofishing was carried out in early November at low temperatures and it is reported that the catchability of salmonids decreases significantly with decreasing temperature (Forseth & Forsgren, 2008).

Earlier studies in Sandviksvassdraget report varying densities. For early years, back in 1955 to 1961, Rosseland (1965) reported high juvenile densities in the watercourse, both in the upper stretches in Isielva and in stretches in Sandvikselva. Especially the reported juvenile densities for the upper stretch in Isielva indicated the success of the hatchery activity. The 9 km stretch upstream the dam at Bjørumsaga was expected to inhabit up to 20 000 juvenile salmon in 1961.Bremnes et al. (2007) reported salmonid densities at several sites in the watercourse for 2006. The sites in Isielva were located downstream of my study's lower sites in Isielva but can still be compared since they are nearby. The upper stretch in Isielva was only included in later studies in 2007 and 2008 (Bremnes et al., 2008; Bremnes et al., 2009). The salmonid densities reported for 2006 were higher compared with the densities calculated for 2019. Bremnes et al. (2009) reported salmonid densities up to 100 fish per 100 m^2 in the upper stretch in Isielva, where salmon had the highest densities. The salmonids in this river stretch hatched in the Hamang hatchery. Further downstream in the lower stretches in Isielva, were natural spawning occurs, around 70 salmonids per 100 m^2 were reported, where trout had the highest densities in 2006 and salmon in 2007 and 2008. In 2007, the densities were much lower for both salmon and trout in the lower stretch in Isielva (Bremnes et al., 2007; Bremnes et al., 2008; Bremnes et al., 2009). Higher salmonid densities than in my study were also reported in 2014. Lillelien (2014) reported 132 salmonids per 100 m^2 in the lower stretch of Isielva, but the sampled sites were downstream of our lower sites. Another study, conducted in 2018 by Skrutvold et al. (2019a), reported significantly higher salmonid densities in the lower stretch in Isielva. They calculated density of 307 salmonids per 100 m^2. 70 % of the caught salmonids were salmon and the ecological state for this river stretch was classified as “excellent”. Skrutvold et al. (2019a) explains the high densities for 2018 as partially due to high summer temperatures and low water flow. The low water flow largely forced the juveniles together on a smaller river cross section more so than during a normal water flow, resulting in higher densities per 100 m^2. Kirkemoen and Colman (2018) studied a stretch in Isielva, just downstream of the stretches studied in my study, and classified parts of the stretch as “excellent” based on the salmonid densities.

The lower site in Lomma was also studied by Bremnes et al. (2009). Other sites in Lomma studied by Bremnes et al. (2009) were located downstream of my upper sites in the river. The upper sites in Lomma had salmonid densities from around 30 to 70 fish per 100 m^2. In 2006, salmon had higher densities, while trout were more abundant both in 2007 and 2008. Lillelien (2014) estimated salmonid densities of almost 90 fish per 100 m^2 in the upper stretch in Lomma, but the location of these sampled sites differed from my upper sample sites. One of Lillelien’s sites was located halfway between our upper and lower stretch in Lomma and had a salmonid density of 41 fish per 100 m^2. None of the mentioned sites are accessible for migrating salmonids and natural spawning, and the caught juvenile salmonids have hatched in the Hamang hatchery and were released there as alevins. For the lower site in Lomma, Bremnes et al. (2009) calculated relatively high salmonid densities for all three years. Salmon were most abundant and in 2007, the fish densities were up to 130 fish per 100 m^2, with about 30 trout per 100 m^2.

Already Bremnes et al. (2009) mentioned high density variations between the years, which can be one explanation for the overall low densities calculated for 2019 in my study. The low densities can partially be traced back to late sampling time since temperature can have an effect on salmonid catchability during electrofishing. At temperatures close to 0 °C, salmonid juveniles decrease their activity and hide deeper in the substrate. This can influence the catchability negatively and result in low density estimates (Forseth & Forsgren, 2008). Compared to the year 2018, our densities were, however, really low. Forseth and Forsgren (2008) stated that the waterflow can influence the catchability significantly as well. Increasing water flow decreases the catchability, since the fish can use a larger area. The water velocity is stronger at higher water flow, which decreases the catchability and makes the fish less visible. The water flow in 2018 was exceptionally low, due to the high summer temperatures and limited precipitation, therefore is the catchability of juvenile salmonids expected to be higher than in 2019. Another reason for the low densities in my study can be higher mortality of juvenile salmonids after the high summer temperatures in 2018. High water temperature puts juvenile salmonids and salmonid embryos under stress and can decrease survival. Unusually low waterflow can add to increased mortality by reducing suitable habitat and food availably (macroinvertebrate drift)

(Jonsson & Jonsson, 2011; Root et al., 2015). Furthermore, the oxygen level can be critically low in warm water. Johansen et al. (2005) also suggested that increased water temperatures put juvenile salmonids under unusual stress conditions. High summer temperatures and low water flow can also increase the stress level on adult migrating salmonids, since more energy is needed for upstream migration in warmer water and make them more vulnerable for diseases, expose them to predators and reduce their egg quality (Jonsson & Jonsson, 2011; Root et al., 2015). Especially the low densities in the upper stretches, both in Isielva and Lomma, were unexpected. The upper stretches are located far upstream and are not under high pressure from human activities and the juvenile densities were therefore expected to be as high or even higher than in the lower/downstream stretches. Since these stretches are cut off from the downstream stretches of the watercourse, only juveniles from the hatchery use these areas as nursery habitat. The results of my study suggest that natural spawning lead to higher densities of juveniles in 2019.

The effect of environmental variables on the juvenile salmonid densities

Juvenile salmonids are influenced by their environment and differences in key environmental variables between habitats can therefore affect salmonid densities (Heggenes et al., 1999; Jonsson & Jonsson, 2011). I found significant differences in environmental variables between the studied stretches. Both between the two rivers in the watercourse (Isielva and Lomma) and between upper and lower stretches in these rivers. The upper stretches had more riparian vegetation cover along the river and pools, whereas the lower stretches were associated with moss cover, large woody debris, and shadowed water surface. Even though there were significant differences in the environmental variables between the river stretches, their effect was not significant enough to explain the different salmonid densities. In addition, were the juvenile salmonid densities very low at some sampling sites, and too low to conduct a meaningful model selection procedure. The results showed a non-significant effect of allochthonous (PC1) or autochthonous (PC2) production on the salmonid densities, which is in contrast to studies by Kondolf and Wolman (1993) and Degerman et al. (2004).

Riparian vegetation along a river is an important source for nutrients for the river's fauna, when entering the river system (allochthonous organic matter) (Abelho, 1999). Kondolf and Wolman (1993) found a positive correlation between riparian vegetation and fish density. By throwing shadow on the water surface, riparian vegetation allows the fish to be less visible to predators, keeps the water temperature low in summer and favours moss growth over algae growth. All this had a positive effect on fish density in the study by Kondolf and Wolman (1993). Johansen et al. (2005) also stated the importance of riparian vegetation in their study of Atlantic salmon in the river Tana in Norway, where it provided overhead cover, shade, and input of allochthonous material. Additionally, is riparian vegetation along the river also a source of terrestrial prey for salmonids. Cada et al. (1987) pointed out the importance of terrestrial prey for brown trout and rainbow trout in Tennessee and North Carolina. Especially older juvenile salmonids tend to have a significant proportion of terrestrial prey in their diet (Elliott, 1970). The importance of terrestrial prey for salmonids in Sandviksvassdraget was not included in my study, but should not be ignored, since it can contribute a significant amount of available food to the river. Degerman et al. (2004) mentioned that large woody debris positively correlates with the abundance of trout. Close to large woody debris, salmonids can find shelter from predators. Heggenes et al. (1999) studied the importance of different environmental variables for salmon and trout and pointed out several variables, which, however, did not show a significant effect on salmonid density in my study. Depth and velocity are listed as variables that can significantly influence the habitat use of juvenile salmonids. Trout juveniles tend to use deeper and slower-flowing areas in a river than salmon (Heggenes et al., 1999; Jonsson & Jonsson, 2011). In my study, neither velocity nor depth had a significant effect on fish density. Heggenes and Saltveit (2002) discussed the influence of moss on the density of salmon and trout and showed that different types of moss can have opposing effects on the density, but in my study, moss cover did not have a significant effect. Moss is also reported to be used by small trout juveniles as cover (Heggenes & Saltveit, 2002). Additionally, Johansen et al. (2005) found a positive correlation between Atlantic salmon parr and the proportion of moss cover. The river substrate can also have an effect on the river's fauna composition. A homogeneous substrate, especially fine substrate provides fewer micro niches than a riverbed with heterogeneous and coarser substrate. Juveniles find shelter behind, and under larger stones, where the water velocity is usually lower (Bohlin, 1977; Heggenes, 1988; Jonsson & Jonsson, 2011). The substrate did not seem to affect the salmonid densities in my study. Determining environmental variables that have a significant effect on fish density in this study was difficult, because of the low number of sampled sites and low number of caught fish. Since the importance of the named environmental variables has been proven in many studies before, future studies on juvenile salmonid population of Sandviksvassdraget should be conducted to determine the environmental variables that influence their respective densities.

Effects on the macroinvertebrate community

The analysis of the macroinvertebrate community indicates a significant difference between the different river stretches. The number of taxa, the Shannon Wiener diversity and the Pielou evenness were highest in the lower site in Lomma. In Isielva, the upper sites had a slightly higher diversity and evenness than the lower sites. The macroinvertebrate diversities in the river stretches were influenced by the allochthonous (PC1) and autochthonous (PC2) production. The macroinvertebrate abundance in the river stretches was also influenced by the river, the location and allochthonous and autochthonous production. Fish density did not seem to have a significant effect on the abundance of the macroinvertebrates in my study. The allochthonous production had the strongest effect on most of the species found in the samples. Increased riparian vegetation along the river correlated positively with most of the found macroinvertebrates, indicating higher species number and abundances with increasing riparian vegetation. Both tolerant macroinvertebrates like Oligochaetes and less tolerant species like caddisflies (Direktoratsgruppe Vanndirektivet, 2018; Oscoz et al., 2011) showed a positive correlation with riparian vegetation. This indicates that none of the river stretches are polluted with high amounts of organic input from their surroundings. A high number of macroinvertebrates were associated with the river Lomma. The caddisfly *Micrasema setiferum* was positive correlated both with the lower stretches and with autochthonous production. The lower stretches showed a high percentage autochthonous production, represented by PC2, which mostly consisted of moss in my study. *M. setiferum* is known to choose moss on the river substrate as habitat (Oscoz et al., 2011), to be sensitive for organic pollution and requires high oxygen supply (Direktoratsgruppe Vanndirektivet, 2018; Kjellberg et al., 2004; Viðinskienë, 2005). The high abundance of this species, especially in Isielva, indicates that the lower stretches have a low input of organic and inorganic particles, which would seal interstitial space, decrease the habitat availability, and cause anoxic conditions. The stonefly *Diura nanseni* is associated with springs and source water, which explains the positive correlation with the upper sites (Oscoz et al., 2011). Stoneflies and the coleoptera *Agabus sp.* are sensitive to pollution and are indicators for clean and well oxygenated water (Nilsson, 1996; Wetzel, 2001). Their correlation with the upper stretches indicates good water quality in these parts of the rivers.

The macroinvertebrate species found in my study match with reported species in earlier studies in the watercourse (Bremnes et al., 2007; Bremnes et al., 2008; Bremnes et al., 2009; Persson et al., 2014; Skrutvold et al., 2019b). For the years 2006 to 2008 Bremnes et al. (2009) reported that no macroinvertebrate family was dominating in Lomma. In 2013 Persson et al. (2014) found that Chironomids and mayflies, especially *Baetis sp*., were dominating the macroinvertebrate community in Lomma. Both in the upper and lower stretch, stoneflies, beetles and caddisflies were found, but with decreasing number of stoneflies downstream and increasing number of the caddisflies from the family *Hydropsyche sp.* (Bremnes et al., 2007). The caddisfly *Hydropsyche sp.* is known to be less sensitive for organic pollution than other caddisflies and high abundances can indicate a weak organic load (Direktoratsgruppe Vanndirektivet, 2018). However, the high diversity in the lower stretch in Lomma indicates that the macroinvertebrate community is not limited by the water quality (Bremnes et al., 2009).

In Isielva, Chironomids and mayflies dominated in all reported earlier years. Bremnes et al. (2009) reported for the years 2006 to 2008 that other macroinvertebrates families like caddisflies, stoneflies, blackflies, and beetles were abundant in significant numbers as well. Only in 2006, the caddisfly *M. setiferum* was abundant in high numbers in the lower stretch in Isielva. In 2018, only one individuum of *M. setiferum* was found in the lower stretch of Isielva (Skrutvold et al., 2019b). *M. setiferum* is known for having high variations in abundance between years, which can be the reason for the sudden high abundance in 2019 (Kjellberg et al., 2004).Note that in all reported years, the stretches in Isielva were in at least a good ecological state according to macroinvertebrates, with a slight decrease in species numbers downstream, but higher total abundance of macroinvertebrates. Bremnes et al. (2007) mentioned that the decreasing species' number downstream can be traced back to increased particle pollution. Isielva runs partly right next to a road, with no buffering vegetation on the riverbank, which could hold back parts of the runoff and fine particles. Another source for particle pollution is the highway E 16, which is furthermore under construction and expansion. Skrutvold et al. (2019b) mentioned ongoing construction activities and preparatory clearing of the woods by Bjørumsaga in fall 2018, where the old E16 bridge above Isielva will be replaced. The expansion of the E16, especially during construction, can change the macroinvertebrate community in the lower stretch of Isielva significantly. An increasing amount of particles in the runoff can decrease the substrate and habitat quality for macroinvertebrates. The community can switch to a simpler macroinvertebrate community with less sensitive species like Oligochaetes and Chironomids. Since macroinvertebrates are the main food source for juvenile salmonids, the expansion will likely affect the salmonid population as well. Not only will the decrease in suitable food influence the salmonids, but the increase in fine particles will also have a direct negative effect on salmonids by degrading the available spawning substrate. Furthermore, Kirkemoen and Colman (2018) reported a garbage dump draining further downstream into Isielva, periodically polluting the river and degrading the river habitat. The riparian vegetation in the watercourse has been under pressure from human activity in the catchment for centuries and was mentioned as one of the reasons for the salmonid decline in the watercourse (Bækken et al., 2008). The significant positive correlation of riparian vegetation with macroinvertebrates found in my study underlines this. Increasing allochthonous production from the riparian vegetation not only showed a positive effect on the diversity of macroinvertebrates, but also in the abundance of most found species. River stretches with high abundances of macroinvertebrates can support more juvenile salmonids and ensure their survival by providing enough food. But the macroinvertebrate community can also be influenced by top-down forces. However, the influence of fish density on macroinvertebrates is not clearly determined.

The salmonid density in my study did not have a significant effect on macroinvertebrate diversity or abundance, which indicates that the macroinvertebrate community is not under high pressure of predation by salmonids. Wallace and Webster (1996) mention that macroinvertebrates are not only are influences by bottom-up forces, but also by top-down forces from predators like fish. By removing fish as a predator on macroinvertebrates, Williams and Taylor (2003) demonstrated that predation by fish can have a significant effect on the macroinvertebrate assemblage when they are present, even though it did not have an effect on taxa richness. Gilinsky (1984) and Flecker (1984) stated that especially Chironomids are negatively influenced by fish predation, but no other macroinvertebrate groups showed significant effects of predation. In my study, neither Chironomids nor other macroinvertebrate groups seemed to be significantly affected by salmonid predation. This result matches with findings of studies by Allan (1982) and Nicola et al. (2010). Allan (1982) did not find major differences in macroinvertebrate density in the benthos after trout removal while Nicola et al. (2010) did not find any effect of fish predation on macroinvertebrates, but a significant effect of vegetation on some macroinvertebrates. The results of Johansen et al. (2005) match with my findings, where in their study the density of salmon did not influence the density of invertebrates. Furthermore, Englund et al. (1999) compared studies on the effects of vertebrate and macroinvertebrate predators on macroinvertebrates and found contradictory conclusions. They subsequently stated that study results can be influenced by the criteria used to select the studied data. The relationship between predator and prey is influenced by their environment and it can be difficult to detect whether they may have significant effects on each other (Johansen et al., 2005). The contradictory results of the named studies reflect the complexity of this relationship. The results in my study indicate that the composition of macroinvertebrates in the watercourse is determined by instream and riparian vegetation, rather than being affected by fish predation, which has been stated in literature as well. The non-significant effect of fish density can suggest that the river capacity has not been reached yet, and that with increasing fish density, the macroinvertebrate community can be more affected by predation.

Unexpectedly, I found little support for a positive correlation between total macroinvertebrate abundance and fish density. This was unexpected because macroinvertebrates are known to be the main food source for juvenile salmonids (Jonsson & Jonsson, 2011; Klemetsen et al., 2003; Wetzel, 2001). Food abundance is known to have significant effects on juvenile salmonids. In the study by Imre et al. (2004), where they analysed the effect of food abundance on the population density of juvenile steel trout, increasing food abundance led to increasing population density. In the Norwegian river Tana, Johansen et al. (2005) reported a positive correlation of Atlantic salmon parr with densities of benthic invertebrates. However, if the sample size were larger in my study the positive correlation might have been statistically significant due to its increased power.

Potential smolt production in Sandviksvassdraget

The mark-recapture data from 2012 to 2019 showed that the trout population from Sandviksvassdraget contributed to the whole Oslofjord and that larger individuals tend to travel greater distances. According to Thorpe et al. (1984), the number and size of salmon eggs positively correlates with their body length. This suggests that the salmonids, which migrate further into the Oslo fjord, have a higher number and larger size of eggs, increasing the number of juveniles and potential smolt output from Sandviksvassdraget. The actual number of smolt produced in the watercourse, and the proportion produced in the upper stretches from the hatchery is however not clearly known. Rosseland (1965) expected, based on mark-recapture data, that at least 10 % of the released juvenile salmon from the hatchery migrate as smolt from into the fjord in 1952 and 1956. For the month May in 2018 196 smolts were counted in a fish pass in Sandvikselva, where 72 of them were salmon smolt (Lamberg & Strand, 2019). It is unknow from which stretches in the watercourse the smolt was coming. The higher densities in the lower studied stretches in my study suggest a higher smolt production there, than in the upper stretches. However, the juvenile salmonids in the lower stretches are exposed to more stress caused by human activity in their surroundings, like construction sites, roads, urban development, and industrial activity (Lamberg & Strand, 2019). Furthermore, the decreasing coverage of riparian vegetation in the lower stretches degrades the habitat and food availability for salmonids. Another factor influencing the production of smolt can be the concurrence for food and habitat between the juveniles. Low densities in suitable habitats can increase the survival of juveniles by decreasing stress from intra- and interspecific concurrence and result in higher smolt production than stretches with higher densities. Flaten et al. (2016) reported for their study in a Norwegian fjord system, that larger juvenile trout will more likely migrate as smolt into the sea, whereas smaller trout will more likely stay in their freshwater habitat. Larger smolt did also migrate further into the sea than smaller smolt and the likelihood for returning to the river was higher for larger smolt. Juvenile trout from the upper stretches in Lomma were larger than from other stretches (table 1). The juveniles from this stretch can have an advantage over juveniles from lower stretches, since the concurrence for food and habitat between the juveniles might be lower in this stretch due to low densities, resulting in a longer body length and higher survival rate. Even though the salmonid densities differ between the lower and upper stretches, the smolt production might be the same or even higher in the upper stretches, because of lower exposure to the named stress factors. Furthermore, do the results of Flaten et al. (2016) suggest that more smolt from the upper stretch will return to Sandviksvassdraget than from the lower stretches. Considering the overall low densities of trout in the lower stretches, are the upper stretches in Lomma important for the trout population in the watercourse. Juvenile salmon did not show differences in body length between the upper and lower stretches, though juvenile salmon in the lower stretches are exposed to more stress, as mentioned above. The salmon smolt production might therefore be just as high in the upper stretches as in the lower stretches, or even higher. Besides the named stressors, can the number of returning salmonids for spawning have a significant effect on the total production of smolt. Almost 70 years ago Rosseland (1965) reported that between 29 to 168 salmon and 1930 to 3395 trout returned for spawning to Sandvikselva. Nowadays 102 to 839 salmon and 206 to 3333 trout were counted for the years between 2012 and 2018. Even though it seems like the number of returning salmonids is known to fluctuated, the number of returning salmonids, especially trout, in 2018 was very low. One reason for this could have been the high summer temperatures and low waterflow. A lower spawning activity than for other years can be expected for this year, underlining the importance of the hatchery activity in such years.

Potential sources of error

The low number of caught salmonids can be a result of the late sampling time. Electrofishing was conducted at temperatures close to 0 °C, which is reported to result in low catchability of juveniles (Forseth & Forsgren, 2008). The Zippin removal technique was used to estimate the densities, which requires a decreasing number of caught salmonids with increasing fishing pass in this study. At several sites, the second and/or third removal pass had higher catches than the pass before. Therefore, the data was corrected, before calculating the densities. This can, however, result in misleading densities. Another source of error can be inexperience in electrofishing in the beginning of the fieldwork. This might have led to lower numbers of caught salmonids at some sites. The assessment of environmental variables in this study is based on visual impressions and for some variables only the mean values were used in the statistical analyses, where information of microhabitats eventually got lost. Furthermore, the number of sampling sites in this study was too low to determine significant effects on the salmonid population.

The kick-sampling methods for macroinvertebrates is a semi-quantitative method and sampling might not reach all habitats and therefore not include all present species. Furthermore, inexperience in classifying macroinvertebrates can affect the diversity and ordination analyses. However, the species list was compared with earlier studies on macroinvertebrates in the watercourse, to reduce the possibility of misidentifications. In this study macroinvertebrates were only sampled in the fall and seasonal changes could not be detected. Seasonal changes of two sampling periods should be included, one in spring and one in fall (Hynes, 1970).

Suggestions for future management measures and studies

Riparian vegetation showed to be an important variable for macroinvertebrates, and the importance for salmonids is reported in several studies (Degerman et al., 2004; Johansen et al., 2005; Kondolf & Wolman, 1993). The riparian vegetation in Sandviksvassdraget has been under pressure for years and measures of improvement should be implemented at the stretches that lack vegetation covering the riverbank (Bækken et al., 2008). Increased riparian cover can also decrease the particle pollution from roads and ongoing construction in the catchment and keep the water temperature low during summer by throwing shadow (Johansen et al., 2005). Even though the salmonid densities in the upper stretches in my study were low, the smolt production from these stretches might be important for the total salmonid population of Sandviksvassdraget (Flaten et al., 2016; Thorpe et al., 1984). Since the juvenile salmonid population is reported to fluctuate from year to year, the juveniles from the Hamang hatchery can be crucial in preserving the salmonid population in the watercourse in years with low natural spawning activity. The increasing pressure from human activities in the catchment, especially in the downstream stretches, decreases suitable habitat availability for salmonids in these parts and increase the importance of the upstream stretches and the hatchery activity. A future tagging study of juveniles with PIT-tags can give more insight into the smolt production of the different stretches and will make it possible to compare the movement and survival of the juveniles in these stretches. With the now ongoing constructions of the E16 right above the dam in Isielva, this part of the watercourse will be under a lot of pressure and changes. This will decrease the available habitat for macroinvertebrates, juvenile and migrating salmonids and put the salmonid population under increased stress. The juveniles from the hatchery will be important in preventing a decrease in population size during this time. It is also suggested to remove the dam in Isielva, while the area is under construction. The dam, being a remnant of a sawmill, does not serve any purpose nowadays and the removal of it will increase the available anadrome spawning habitat for migrating salmonids after the construction time, which is also upstream of the increasing human activity.

Furthermore, sustainable management of salmonids in the Oslofjord is important for preserving the salmonid populations in the adjusting rivers. The mark-recapture data show that trout use the whole Oslofjord and it is known that salmon migrate through the fjord to reach the open sea. Changes in the fjord environment will therefore influence the trout and salmon populations in the rivers. Management of salmonids should therefore be conducted on a regional scale, including both habitats.

Conclusion

Overall had the upper stretches in Sandviksvassdraget lower salmonid densities than the lower stretches and thus worse ecological states. Neither had the tested key environmental variables, nor the total macroinvertebrate abundance a significant effect on the salmonid density, even though there were significant differences between the rivers and the upper and lower stretches. The differences in diversity and abundance of macroinvertebrates are results of the location in the rivers, and allochthonous and autochthonous production, but salmonid density did not have a significant effect. Especially the allochthonous production affected most of the macroinvertebrates in the stretches, suggesting that increased riparian vegetation increases the diversity and abundance.

Though the allochthonous production in this study did not affect the juvenile salmonid densities, the importance can be assumed due the importance for their main food source, macroinvertebrates. Macroinvertebrates play a crucial role in ecosystems, connecting different trophic levels. An improvement of their habitat, here an increase of riparian vegetation cover along the river, most likely will bring improvements of salmonid habitat and an increase in population densities.

Even if the lower stretches had higher salmonid densities one can assume that the actual smolt production is just as high or even higher in the upper stretches, since the salmonids in the lower stretches have a higher exposure to stress, induced by human activities or higher intra- and interspecific concurrence for habitat and food resources. Especially in Isielva, were a new bridge is under construction for the expansion of the highway E 16, the downstream stretches are expected to be under increased pressure. Affecting not only the salmonid population, but also the macroinvertebrate community. The upstream stretches become therefore an even more important habitat resource and the juveniles from the Hamang hatchery an even more important contribution to the total salmonid population of the watercourse. Monitoring the watercourse in the following years is important, to map out changes and prevent degradation of available habitat and decreases in salmonid densities.

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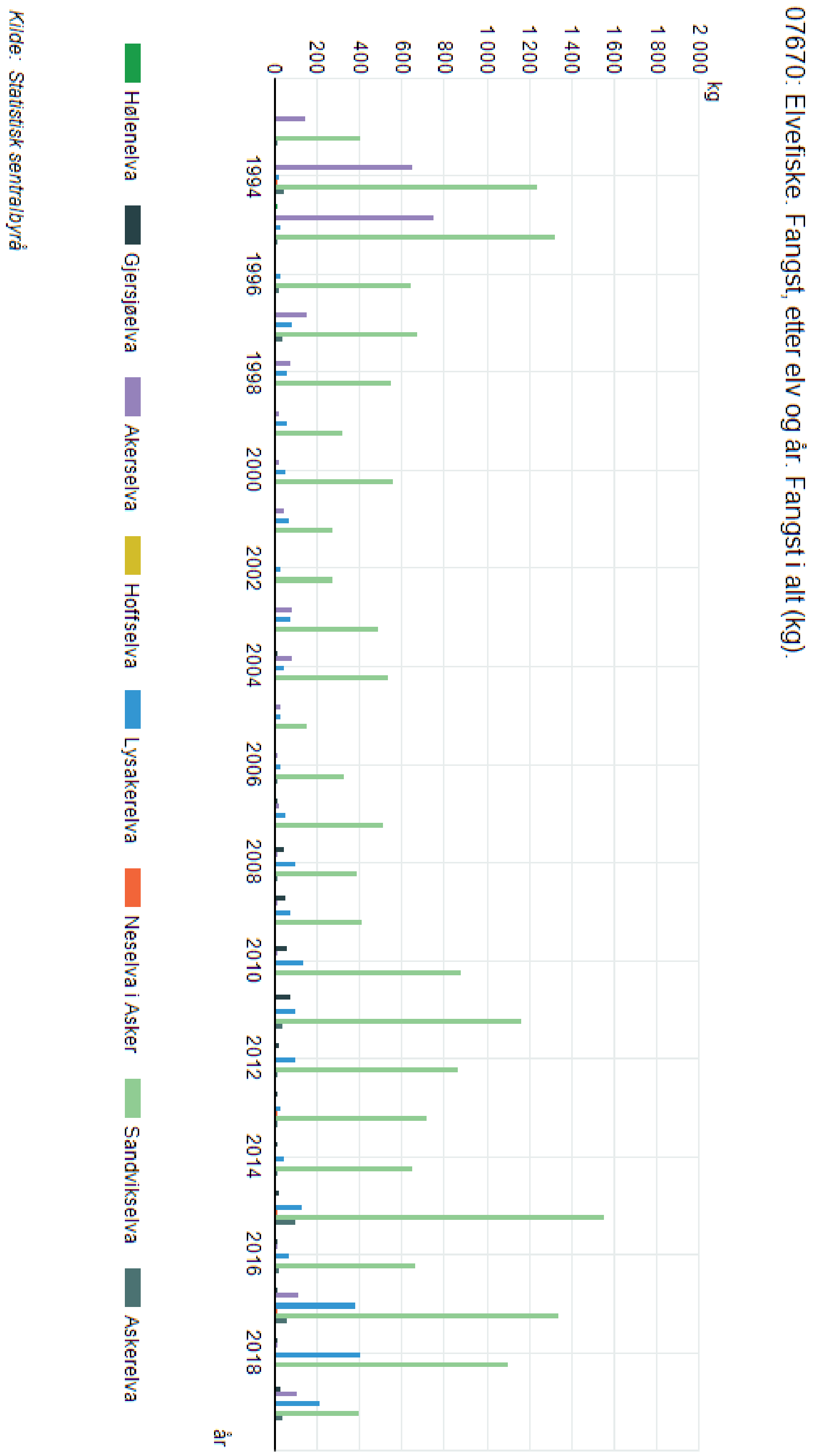
Appendices

Appendix A: Salmonid catches in kg in the rivers around the Oslo fjord from 1993 to 2019 (Statistisk sentralbyrå, 2020).



Kilde: Statistisk sentralbyrå

Appendix B: Coordinates for the sites in Isielva and Lomma in Sandviksvassdraget

Site	UTM-zone 32 N	UTM-zone 32 E
Isielva-Upper 1	6645650.43	579641.23
Isielva-Upper 2	6645837.81	579532.73
Isielva-Upper 3	6646117.74	579438.57
Isielva-Lower 1	6645298.41	579822.88
Isielva-Lower 2	6645140.54	579930.15
Isielva-Lower 3	6645053.7	580015.05
Lomma-Upper 1	6650817.14	579904.8
Lomma-Upper 2	6650289.69	580690.68
Lomma-Upper 3	6650199.07	581246.86
Lomma-Lower 1	6642123.26	583029.44

:

Appendix C: Environmental variables raw data for the studies rivers Isielva and Lomma in Sandviksvassdraget. (IU 1-1: Isielva -Upper 1, transect 1; IL 1-1: Isielva-Lower 1, transect 1; LU 1-1: Lomma-Upper 1, transect 1; LL 1-1: Lomma-Lower 1, transect 1; veg. flood zone: vegetation cover of the flood zone; veg. riverbank: vegetation cover of the riverbank; LWD: Large woody debris)

			Depth [cm]						Substrate [%]													
site - transect	length [m]	width [m]	10 %	25 %	50 %	75 %	90 %	mean	0-2 mm	2-20 mm	20-100 mm	100-250 mm	>250 mm	mean [mm]	velocity [m/s]	shadow [%]	veg. flood zone [%]	veg. river-bank [%]	moss [%]	algae [%]	pools	LWD
IU 1-1	28	10.2	10	23	20	25	44	24.4	0	2	50	30	18	195.22	0.79	45	33	63	16	16	2	4
IU 1-2	28	8.1	18	28	25	29	28	25.6	0	3	50	35	12	166.58	0.83	45	12	83	0	16	2	4
IU 1-3	28	7.5	23	45	51	31	25	35	0	10	50	30	10	146.1	0.74	35	33	83	0	16	2	4
IU 1-4	28	7.1	18	26	34	66	72	43.2	0	1	40	40	19	212.86	1.1	50	33	92	0	16	2	4
IU 1-5	28	8	26	14	12	38	53	28.6	0	1	50	30	19	201.36	1.33	30	63	92	16	16	2	4
IU 2-1	30	11.6	29	56	34	19	16	30.8	0	15	30	50	5	138.4	0.7	75	12	63	16	0	3	3
IU 2-2	30	8.9	13	24	40	15	18	22	2	18	60	15	5	95.5	0.53	80	12	33	16	0	3	3
IU 2-3	30	8.5	13	30	41	37	18	27.8	0.5	6	25	58.5	10	180.54	0.75	90	12	12	16	0	3	3
IU 2-4	30	6.46	17	25	51	69	82	48.8	1	2	30	30	37	301.98	0.85	60	0	12	16	0	3	3
IU 2-5	30	5.5	10	12	26	60	80	37.6	0.5	2.5	30	30	37	302.03	0.7	80	0	12	16	0	3	3
IU 3-1	26	8.56	16	39	34	25	13	25.4	3	5	30	31	31	266.58	0.33	30	12	12	16	0	2	3
IU 3-2	26	8.48	24	46	47	60	13	38	1	10	15	44	30	274.61	0.5	40	12	12	16	0	2	3
IU 3-3	26	5.17	37	77	94	54	18	56	10	35	0	45	10	145.2	0.6	40	12	12	16	0	2	3
IU 3-4	26	5.75	25	48	40	33	21	33.4	1	5	15	65	14	210.81	0.95	50	12	12	16	0	2	3
IU 3-5	26	7.2	6	20	19	42	28	23	0	5	40	30	25	233.3	1.4	50	12	12	50	0	2	3
IL 1-1	27	10.95	11	9	51	49	20	28	2	10	10	25	53	382.12	0.56	50	12	33	50	0	0	1
IL 1-2	27	8.95	15	41	37	32	22	29.4	2	4	14	70	10	193.86	0.63	50	12	12	50	0	0	1
IL 1-3	27	10.54	12	7	48	29	14	22	3	3	20	60	14	204.86	0.83	50	12	12	16	0	0	1
IL 1-4	27	10.16	7	38	33	25	13	23.2	2	1	44	43	10	164.28	0.53	60	12	12	50	0	0	1
IL 1-5	27	11.6	20	28	43	37	20	29.6	3	3	20	44	30	276.86	0.66	40	12	12	50	0	0	1
IL 2-1	30	7.55	43	44	38	42	36	40.6	4	10	36	20	30	245.24	0.55	45	12	33	16	0	2	2
IL 2-2	30	7.75	33	15	43	39	35	33	1	1	30	50	18	218.12	0.56	20	12	33	16	0	2	2
IL 2-3	30	7.55	29	34	37	23	16	27.8	0.5	4.5	40	35	20	210.75	1.04	50	12	12	16	0	2	2
IL 2-4	30	8.74	47	55	34	48	25	41.8	0	3	30	55	12	189.58	0.65	40	33	12	16	0	2	2
IL 2-5	30	8.32	29	38	38	32	31	33.6	0	10	35	30	25	230.85	0.62	20	12	12	16	0	2	2

		Depth [cm]							Substrate [%]													
site - transect	length [m]	width [m]	10 %	25 %	50 %	75 %	90 %	mean	0-2 mm	2-20 mm	20-100 mm	100-250 mm	>250 mm	mean [mm]	velocity [m/s]	shadow [%]	veg. flood zone [%]	veg. river-bank [%]	moss [%]	algae [%]	pools	LWD
IL 3-1	27	7.2	42	54	28	20	23	33.4	0	2	60	20	18	183.72	0.45	20	12	12	16	0	3	2
IL 3-2	27	9.3	18	23	45	16	9	22.2	1	4	50	25	20	199.2	0.63	15	12	12	16	0	3	2
IL 3-3	27	12.3	38	48	15	8	9	23.6	0	2	40	35	23	229.22	0.68	20	12	12	16	0	3	2
IL 3-4	27	7.6	25	20	33	25	5	21.6	0	2	40	40	18	206.72	0.62	50	12	12	16	0	3	2
IL 3-5	27	8.7	42	8	23	35	23	26.2	0	3	30	40	27	257.08	0.6	50	12	12	16	0	3	2
LU 1-1	25	10	19	28	35	27	15	24.8	0	2	20	28	50	373.72	0.37	20	12	33	16	16	4	2
LU 1-2	25	8	16	18	49	37	20	28	0	2	30	38	30	272.22	0.3	30	12	33	16	16	4	2
LU 1-3	25	9.2	21	40	46	48	30	37	0	5	15	40	40	329.55	0.4	20	12	33	0	16	4	2
LU 1-4	25	9.8	8	22	20	41	8	19.8	0	0	10	30	60	433.5	0.63	0	12	12	16	16	4	2
LU 1-5	25	7.6	5	22	22	17	5	14.2	0	2	10	60	28	286.22	0.33	0	12	12	16	16	4	2
LU 2-1	29	7.9	11	8	29	71	53	34.4	1	2	40	50	7	155.48	0.56	90	12	33	16	0	4	4
LU 2-2	29	9.25	9	20	54	67	48	39.6	0	1	45	50	4	139.61	0.45	45	12	33	0	0	4	4
LU 2-3	29	10.25	17	30	34	55	15	30.2	0	5	30	40	25	244.8	0.7	10	12	12	16	0	4	4
LU 2-4	29	11.75	14	19	30	27	12	20.4	1	4	20	65	10	188.7	0.87	30	12	12	16	0	4	4
LU 2-5	29	12.2	14	18	28	17	14	18.2	0	2	20	55	23	252.22	0.55	40	12	33	16	0	4	4
LU 3-1	27	11.9	8	17	37	16	10	17.6	0	4	35	45	16	200.19	0.75	15	12	33	16	0	1	1
LU 3-2	27	11.4	13	10	34	30	14	20.2	1	2	30	37	30	270.48	0.32	15	12	33	16	0	1	1
LU 3-3	27	10.95	14	33	35	32	17	26.2	1	1	25	40	32	285.12	0.85	20	33	33	16	0	1	1
LU 3-4	27	12.15	16	31	25	45	27	28.8	1	2	15	42	40	332.73	0.5	15	33	12	16	0	1	1
LU 3-5	27	11.75	17	25	24	31	22	23.8	2	4	40	34	20	208.96	0.45	36	12	33	16	0	1	1
LL 1-1	23	14.1	12	20	5	17	15	13.8	5	3	50	25	17	180.38	0.45	70	33	33	50	16	2	10
LL 1-2	23	11.8	12	28	20	20	12	18.4	3	5	40	40	12	169.58	0.4	85	12	33	16	16	2	10
LL 1-3	23	12.6	12	42	27	16	9	21.2	1	3	60	20	16	171.34	0.4	75	12	33	16	16	2	10
LL 1-4	23	10.9	26	36	18	21	14	23	1	3	55	30	11	154.59	0.38	75	12	33	50	16	2	10
LL 1-5	23	12.3	32	30	19	12	11	20.8	0.5	1.5	50	20	28	240.17	0.55	50	12	33	16	16	2	10

Appendix D: Habitat class description and class limits for ecological state of lowland rivers with salmonids (fish per 100 m^2) (Direktoratsgruppe Vanndirektivet, 2018).

Habitat class 1: “less suitable habitat”, neither good spawning habitat nor good hiding possibilities

Habitat class 2: “Suitable habitat”, moderate spawning habitat and some hiding possibilities

Habitat class 3: “Well suited habitat”, Both good spawning habitat and good hiding possibilities

Species composition	**excellent**	**good**	**moderate**	**bad**	**poor**
Anadrome sympatric, habitat class 3	>25	24-19	18-13	12-6	<6

Appendix E: Salmonid densities and catchability for each age group at every site, calculated after Bohlin et al. (1989).

Species	**Age**	**Site**	**Estimated catchability**	**Density per 100 m2**	**Standard Error**
Atlantic salmon	0+	Isielva-Upper 1	0.1	33.3	87.3
Atlantic salmon	1+	Isielva-Upper 1	0.4	8.7	3.1
Atlantic salmon	>1+	Isielva-Upper 1	0.3	10.5	5.7
Atlantic salmon	0+	Isielva-Upper 2	0.4	2.5	1.3
Atlantic salmon	1+	Isielva-Upper 2	0.4	4.3	1.4
Atlantic salmon	>1+	Isielva-Upper 2	0.2	8.0	10.8
Atlantic salmon	0+	Isielva-Upper 3	0.6	1.1	0.4
Atlantic salmon	1+	Isielva-Upper 3	0.6	3.5	0.5
Atlantic salmon	>1+	Isielva-Upper 3	0.8	4.0	0.2
Atlantic salmon	0+	Isielva-Lower 1	0.3	3.7	3.2
Atlantic salmon	1+	Isielva-Lower 1	0.2	3.7	6.9
Atlantic salmon	>1+	Isielva-Lower 1	0.3	9.7	5.8
Sea trout	0+	Isielva-Lower 1	0.6	0.7	0.3
Sea trout	1+	Isielva-Lower 1	0	0	
Sea trout	>1+	Isielva-Lower 1	0	0	
Atlantic salmon	0+	Isielva-Lower 2	0.3	7.8	4.5
Atlantic salmon	1+	Isielva-Lower 2	0.2	11.1	17.9
Atlantic salmon	>1+	Isielva-Lower 2	0.5	5.4	1.1
Sea trout	0+	Isielva-Lower 2	0.3	2.0	2.0
Sea trout	1+	Isielva-Lower 2	0.6	0.9	0.3
Sea trout	>1+	Isielva-Lower 2	0.6	0.9	0.3

Species	Age	Site	Estimated catchability	Density per 100 m2	Standard Error
Atlantic salmon	0+	Isielva-Lower 3	0.3	4.9	4.8
Atlantic salmon	1+	Isielva-Lower 3	0.2	7.2	9.1
Atlantic salmon	>1+	Isielva-Lower 3	0.2	16.6	22.4
Sea trout	0+	Isielva-Lower 3	0.3	2.6	3.5
Sea trout	1+	Isielva-Lower 3	0.6	1.6	0.4
Sea trout	>1+	Isielva-Lower 3	0.2	4.3	8.0
Sea trout	0+	Lomma-Upper 1	0.8	2.8	0.3
Sea trout	1+	Lomma-Upper 1	1.0	2.7	
Sea trout	>1+	Lomma-Upper 1	1.0	0.4	
Sea trout	0+	Lomma-Upper 2	0.3	3.9	2.2
Sea trout	1+	Lomma-Upper 2	0.3	4.9	3.3
Sea trout	>1+	Lomma-Upper 2	0.8	1.3	0.1
Sea trout	0+	Lomma-Upper 3	0.3	1.5	1.6
Sea trout	1+	Lomma-Upper 3	0.3	3.7	2.1
Sea trout	>1+	Lomma-Upper 3	0.3	2.0	2.7
Atlantic salmon	0+	Lomma-Lower	0.3	7.0	3.2
Atlantic salmon	1+	Lomma-Lower	0.4	9.5	2.9
Atlantic salmon	>1+	Lomma-Lower	0.5	5.0	1.1
Sea trout	0+	Lomma-Lower	0.7	1.0	0.1
Sea trout	1+	Lomma-Lower	0	0.0	
Sea trout	>1+	Lomma-Lower	0	0.0	

Appendix F: Macroinvertebrate species list. Feeding group information gather from Schmidt-Kloiber and Hering (2015).

site	**Feeding group**	**Isielva-Upper 1**			**Isielva-Upper 2**			**Isielva-Upper 3**			**Isielva-Lower 1**			**Isielva-Lower 2**			**Isielva-Lower 3**		
transect		1	3	5	1	3	5	1	3	5	1	3	5	1	3	5	1	3	5
Ephemeroptera																			
Baetis rhodani	scraper/gatherer	600	402	286	321	140	119	338	63	163	194	532	513	251	220	226	325	163	191
Baetis muticus	scraper/gatherer	356	360	187	129	66	95	156	9	46	41	102	129	53	69	99	61	25	16
Heptagenia sulphurea	scraper/gatherer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heptagenia fuscogrisea	scraper/gatherer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caenis horaria	gatherer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plecoptera																			
Diura nanseni	predator	20	20	2	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Amphinemura sulcicollis	gatherer	160	44	15	15	5	4	16	3	2	3	3	13	4	13	16	9	15	5
Amphinemura borealis	scraper	88	14	11	13	4	5	13	0	4	1	3	5	2	5	7	4	5	0
Nemoura cinerea	gatherer	44	22	20	68	11	12	48	1	13	6	123	151	31	82	65	79	59	49
Nemoura avicularis	shredder	0	2	2	0	0	0	0	0	0	0	1	2	0	0	0	3	0	0
Protonemura meyeri	shredder	0	0	1	5	0	0	1	0	1	2	2	4	0	5	3	3	9	0
Taeniopteryx nebulosa	gatherer	0	2	1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Capnopsis schilleri	shredder/gatherer	0	4	4	0	1	1	1	3	0	2	5	3	3	1	3	9	3	6
Capnia bifrons	shredder	0	10	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1
Leuctra hippopus	gatherer	8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichoptera																			
Polycentropus flavomaculatus	predator	56	10	3	0	0	4	0	0	0	0	0	0	0	0	0	1	1	0
Apatania sp.	scraper/gatherer	16	8	1	0	7	4	0	9	0	0	1	1	5	0	3	2	1	2
Limnephilus coenosus	shredder	0	16	6	0	1	3	3	18	0	0	0	0	2	0	2	1	2	0
Lepidostoma hirtum	scraper/shredder	28	18	10	0	5	5	0	4	0	0	0	0	0	0	0	0	0	0
Agapetus ochripes	scraper	24	0	1	1	3	0	1	0	2	1	5	0	1	0	0	1	0	5
Hydropsyche pellucidula	filterer	12	6	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Hydropsyche angustipennis	filterer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydropsyche siltalai	filterer	8	4	0	4	0	0	0	0	0	2	0	2	0	0	0	0	0	1
Rhyacophila nubila	predator	32	4	5	2	4	1	5	0	4	2	3	7	1	4	3	4	4	0
Ithytrichia lamellaris	scraper	12	0	3	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0
Oxyethria frici		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mystacides azurea	gatherer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

site	**Feeding group**	**Isielva-Upper 1**			**Isielva-Upper 2**			**Isielva-Upper 3**			**Isielva-Lower 1**			**Isielva-Lower 2**			**Isielva-Lower 3**		
transect		1	3	5	1	3	5	1	3	5	1	3	5	1	3	5	1	3	5
Trichoptera																			
Agraylea multipunctata		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrasema setiferum	scraper/shredder	4	0	4	0	1	0	2	0	1	67	234	157	97	292	130	141	279	86
Sericostoma personatum	shredder	4	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Silo pallipes	scraper	12	2	3	1	1	0	0	1	2	0	1	1	0	0	1	1	0	0
Chaetopteryx villosa	shredder	12	6	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	0
Coleoptera																			
Limnius volckmari	scraper	8	0	1	0	0	1	0	1	0	2	0	2	0	1	1	0	2	1
Hydraena gracilis	scraper/predator	12	0	1	1	0	0	0	0	2	0	0	0	0	2	2	1	0	0
Elmis aenea	scraper	8	0	2	0	0	1	1	0	0	0	4	3	6	3	8	8	10	1
Agabus sp.	predator	124	0	4	0	1	4	27	0	0	0	0	1	2	9	1	9	5	0
Diptera																			
Chironomidae	gatherer	364	86	27	23	17	5	59	8	6	5	13	26	15	64	20	14	70	11
Simuliidae	filterer	0	34	45	79	8	26	47	12	27	39	260	187	35	583	120	39	970	313
Dicranota sp.	predator	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antocha sp.		0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1
Helius sp.		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pericoma sp.		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Other																			
Acari	predator	20	0	3	1	0	2	1	2	1	0	0	0	0	0	3	2	2	0
Oligochaeta	gatherer	32	4	3	2	1	0	0	1	0	1	3	1	0	1	0	1	0	0
Bivalvia	filterer	0	2	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Gastropoda	scraper	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Amphipoda		0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Asellus aquaticus		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Turbellaria	predator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hirunidae	predator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

site	**Feeding group**	**Lomma-Upper 1**			**Lomma-Upper 2**			**Lomma-Upper 3**			**Lomma-Lower 1**		
transect		1	3	5	1	3	5	1	3	5	1	3	5
Ephemeroptera													
Baetis rhodani	scraper/gatherer	239	153	273	227	290	299	319	248	361	900	1040	930
Baetis muticus	scraper/gatherer	97	100	331	91	160	166	138	90	198	708	708	764
Heptagenia sulphurea	scraper/gatherer	18	6	59	8	7	18	7	8	8	100	184	114
Heptagenia fuscogrisea	scraper/gatherer	0	0	0	0	0	0	0	0	0	0	0	2
Caenis horaria	gatherer	0	0	0	0	0	0	1	1	0	28	32	28
Plecoptera													
Diura nanseni	predator	1	1	8	0	0	1	1	0	3	0	0	2
Amphinemura sulcicollis	gatherer	18	6	10	19	37	38	16	12	22	48	64	42
Amphinemura borealis	scraper	12	4	26	5	16	22	12	17	17	24	56	26
Nemoura cinerea	gatherer	20	6	15	23	49	77	63	10	38	0	0	4
Nemoura avicularis	shredder	6	3	9	11	13	17	12	2	10	8	12	20
Protonemura meyeri	shredder	1	0	0	2	5	2	2	1	3	0	0	6
Taeniopteryx nebulosa	gatherer	0	1	1	2	2	0	1	0	2	0	0	0
Capnopsis schilleri	shredder/gatherer	1	1	1	1	2	0	3	1	1	20	16	4
Capnia bifrons	shredder	0	0	0	0	2	1	2	0	0	0	8	2
Leuctra hippopus	gatherer	0	0	1	0	0	0	0	0	0	4	0	4
Trichoptera													
Polycentropus flavomaculatus	predator	1	1	4	0	3	2	1	6	2	0	4	0
Apatania sp.	scraper/gatherer	0	0	0	1	1	4	0	0	0	0	4	10
Limnephilus coenosus	shredder	0	0	0	0	1	2	0	0	9	20	0	4
Lepidostoma hirtum	scraper/shredder	0	1	3	0	0	0	2	8	10	48	128	72
Agapetus ochripes	scraper	0	0	0	1	1	1	0	2	1	44	28	40
Hydropsyche pellucidula	filterer	0	0	0	0	1	1	1	1	1	132	80	36
Hydropsyche angustipennis	filterer	1	0	0	0	0	0	0	0	0	0	0	0
Hydropsyche siltalai	filterer	1	0	1	1	0	4	0	0	4	340	424	356
Rhyacophila nubila	predator	2	0	2	2	2	8	1	1	7	36	28	32
Ithytrichia lamellaris	scraper	0	1	1	0	0	5	3	3	10	0	4	0
Oxyethria frici		1	0	0	0	0	0	0	0	0	0	0	0
Mystacides azurea	gatherer	0	0	0	0	0	0	0	1	0	0	0	0

site	**Feeding group**	**Lomma-Upper 1**			**Lomma-Upper 2**			**Lomma-Upper 3**			**Lomma-Lower 1**		
transect		1	3	5	1	3	5	1	3	5	1	3	5
Trichoptera													
Agraylea multipunctata		0	0	0	0	0	0	0	1	0	0	0	0
Micrasema setiferum	scraper/shredder	1	1	2	3	5	2	57	27	39	184	208	248
Sericostoma personatum	shredder	0	0	0	0	0	0	0	0	0	0	0	0
Silo pallipes	scraper	0	0	0	0	0	0	1	0	1	8	20	0
Chaetopteryx villosa	shredder	0	0	0	0	0	0	0	0	0	0	4	0
Coleoptera													
Limnius volckmari	scraper	4	0	2	2	2	9	9	2	8	28	68	42
Hydraena gracilis	scraper/predator	0	1	1	1	1	4	0	1	5	24	12	16
Elmis aenea	scraper	1	0	1	0	2	4	8	4	16	96	152	154
Agabus sp.	predator	1	2	4	0	0	3	1	6	2	0	4	0
Diptera													
Chironomidae	gatherer	8	4	17	4	70	56	9	13	27	624	1020	888
Simuliidae	filterer	296	35	426	29	47	555	156	47	40	20	56	68
Dicranota sp.	predator	0	0	0	0	0	0	0	0	1	12	24	2
Antocha sp.		0	0	1	0	1	0	0	0	0	0	0	0
Helius sp.		0	0	0	0	0	0	0	0	0	0	0	0
Pericoma sp.		0	0	0	0	0	0	0	0	0	0	0	0
Other													
Acari	predator	0	0	0	1	0	2	1	3	1	28	12	8
Oligochaeta	gatherer	0	0	0	0	1	4	0	0	4	104	164	96
Bivalvia	filterer	0	0	1	0	0	1	0	0	0	0	20	6
Gastropoda	scraper	0	2	0	1	0	0	0	0	0	24	8	18
Amphipoda		0	0	0	0	0	0	1	0	0	0	0	0
Asellus aquaticus		0	0	0	0	0	0	0	0	0	0	0	0
Turbellaria	predator	0	0	0	0	0	0	0	0	0	0	0	0
Hirunidae	predator	0	0	0	0	0	0	0	0	0	12	16	6

Appendix G: Pielou Evenness index and Shannon Wiener index for the sites in Isielva and Lomma.

site	transect	Shannon Wiener diversity index	Pielou Evenness index
Isielva-Upper 1	1	0.699	2.277
Isielva-Upper 1	3	0.576	1.853
Isielva-Upper 1	5	0.533	1.814
Isielva-Upper 2	1	0.555	1.603
Isielva-Upper 2	3	0.567	1.640
Isielva-Upper 2	5	0.587	1.727
Isielva-Upper 3	1	0.566	1.695
Isielva-Upper 3	3	0.694	1.879
Isielva-Upper 3	5	0.528	1.394
Isielva-Lower 1	1	0.541	1.499
Isielva-Lower 1	3	0.537	1.635
Isielva-Lower 1	5	0.550	1.726
Isielva-Lower 2	1	0.590	1.625
Isielva-Lower 2	3	0.559	1.645
Isielva-Lower 2	5	0.630	1.948
Isielva-Lower 3	1	0.558	1.796
Isielva-Lower 3	3	0.464	1.365
Isielva-Lower 3	5	0.551	1.492
Lomma-Upper 1	1	0.517	1.572
Lomma-Upper 1	3	0.519	1.529
Lomma-Upper 1	5	0.513	1.654
Lomma-Upper 2	1	0.536	1.631
Lomma-Upper 2	3	0.589	1.900
Lomma-Upper 2	5	0.546	1.818
Lomma-Upper 3	1	0.579	1.909
Lomma-Upper 3	3	0.580	1.890
Lomma-Upper 3	5	0.596	2.026
Lomma-Lower 1	1	0.711	2.343
Lomma-Lower 1	3	0.688	2.385
Lomma-Lower 1	5	0.653	2.281

Appendix H: 10 most supported AIC-based model selections statistics for candidate model to predict the Shannon Winer index for the four stretches in Isielva and Lomma (AIC = Akaike`s Information Criterion, ΔAIC = difference between AIC for a given model and the one with the lowest AIC score, K= number of estimated parameters; AICWt= the model AIC weight; LL= model log-likelihood).

No.	Predictor	K	AIC	ΔAIC	AICWt	LL
1	river * UpperLower	5	-5.39	0	0.86	8.95
2	PC1 + PC2	4	1.29	6.68	0.03	4.15
3	PC1	3	1.46	6.85	0.03	2.73
4	PC1 + PC2 + PC3	5	1.57	6.96	0.03	5.47
5	PC1 + PC3	4	1.97	7.36	0.02	3.81
6	PC1 + fish density	4	3.26	8.65	0.01	3.17
7	PC1 + PC2 + fish density	5	3.59	8.98	0.01	4.45
8	PC1 + PC3 + fish density	5	4.5	9.89	0.01	4.0
9	PC1 + PC2 + PC3 + fish density	6	4.57	9.96	0.01	5.54
10	PC2	3	10.54	15.93	0	-1.81

Appendix I 1: 10 most supported AIC-based model selections statistics for candidate model to predict the abundance of macroinvertebrates for the four stretches in Isielva and Lomma (AIC = Akaike`s Information Criterion, ΔAIC = difference between AIC for a given model and the one with the lowest AIC score).

No.	Predictors	AIC	ΔAIC
1	PC1 + PC2 + PC3 + river + UpperLower + fish density	97.242	0
2	PC1 + PC2 + river + UpperLower	97.250	0.008
3	PC1 + PC2 + river + UpperLower + fish density	97.652	0.41
4	PC1 + PC3 + river + UpperLower + fish density	98.674	1.432
5	PC1 + PC3 + river + UpperLower	99.412	2.170
6	PC1 + PC2 + river + fish density	100.461	3.219
7	PC1 + PC3 + UpperLower + fish density	100.617	3.375
8	PC1 + PC2 + PC3 + UpperLower	101.400	4.154
9	PC1 + PC2 + UpperLower + fish density	102.613	5.371
10	PC1 + PC3 + UpperLower	103.069	5.827

Appendix I 2: R2 and effect p-values for the first model fitted to explain variation in the macroinvertebrate abundance data.

Predictor	r^2	Pr(>r)
PC1	0.585	0.001
PC2	0.199	0.047
PC3	0.136	0.148
fish density	0.024	0.714
UpperLower	0.344	0.001
river	0.105	0.048

Appendix J: PC1 and PC2 scores for macroinvertebrates, indicating the correlation between each species and the axes.

Species	**PC1**	**PC2**
Baetis rhodani	-0.433	0.090
Baetis muticus	-0.697	-0.183
Heptagenia sulphurea	-1.094	0.125
Heptagenia fuscogrisea	-0.084	0.028
Caenis horaria	-0.837	0.176
Diura nanseni	-0.163	-0.437
Amphinemura sulcicollis	-0.598	-0.190
Amphinemura borealis	-0.624	-0.293
Nemoura cinerea	0.631	0.296
Nemoura avicularis	-0.531	0.093
Protonemura meyeri	0.058	0.365
Taeniopteryx nebulosa	0.055	-0.135
Capnopsis schilleri	-0.331	0.304
Capnia bifrons	-0.239	0.054
Leuctra hippopus	-0.328	-0.149
Polycentropus flavomaculatus	-0.229	-0.519
Apatania sp.	-0.213	-0.268
Limnephilus coenosus	-0.239	-0.204
Lepidostoma hirtum	-1.113	-0.471
Agapetus ochripes	-0.839	-0.009
Hydropsyche pellucidula	-1.146	-0.169
Hydropsyche angustipennis	0.01	-0.003
Hydropsyche siltalai	-1.485	0.058
Rhyacophila nubila	-0.716	-0.027
Ithytrichia lamellaris	-0.211	-0.252
Oxyethria frici	0.01	-0.003
Mystacides azurea	0.002	-0.002
Agraylea multipunctata	0.002	-0.002
Micrasema setiferum	-0.671	1.584
Sericostoma personatum	-0.052	-0.208
Silo pallipes	-0.456	-0.206
Chaetopteryx villosa	-0.21	-0.224
Limnius volckmari	-0.892	0.133
Hydraena gracilis	-0.727	-0.056
Elmis aenea	-1.092	0.487
Agabus sp.	-0.088	-0.291
Chironomidae	-1.154	0.001
Simuliidae	0.256	0.872
Dicranota sp.	-0.595	0.004
Antocha sp.	0.057	0.094
Helius sp.	0.057	0.094
Pericoma sp.	0.009	0.021
Acari	-0.653	-0.144
Oligochaeta	-1.242	-0.101
Bivalvia	-0.409	0.035
Gastropoda	-0.617	0.102
Amphipoda	0.019	0.071
Asellus aquaticus	0.007	0.029
Turbellaria	0.008	0.021
Hirunidae	-0.609	0.110

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