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The effect of hydropeaking on density, diversity and species richness of mayflies (Ephemeroptera) and stoneflies (Plecoptera) in two river systems

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Biology
Submission date: June 2012
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ACKNOWLEDGEMENTS

This master thesis was performed at the Department of Biology, NTNU, in connection to the project Environmental Impacts of Hydropeaking (EnviPEAK), which is connected to the Centre for Environmental Design of Renewable Energy (CEDREN).

I would like to thank my supervisor Jo Vegar Arnekleiv for introducing me to this interesting thesis, for guidance along the way and for helping me in the field. Gaute Kjæstad deserves a big thank you for helping me in the field, for good advice and for being so patient in teaching me the species of Ephemeroptera and Plecoptera. For helping me in the field I also want to thank Aslak Sjursen and Lars Rønning. Next I particularly want to thank Christophe Pelabon for helping me conducting my statistical analyses, for good advice and for always keeping an open door. For help with my statistics I also want to thank Sigurd Einum and Ivar Herfindal, I really appreciate you taking the time to help me. Furthermore, I want to thank Morten Stickler for the sincere feedback and for taking the time to read my thesis, I can't thank you enough. Thank you Tania Zakowski for your advice and useful discussions. For providing me with temperature and water discharge data I want to thank Tyler King, Knut Alfredsen, and Roser Casas-Mulet. For helping me with information regarding my two rivers I want to thank Viggo Finset (Trønder Energi Kraft AS) and Vidar Fossøy (Statkraft AS).

I would like to thank my friends and classmates at NTNU Gløshaugen for support, discussions and for enjoyable lunch breaks. Thanks to Marianne, Helle and Ida for proofreading at the very end. Furthermore, I would really like to thank my wonderful family for encouragement and support through all these years. Last but not least I would like to thank Lasse. You have been of great help with Excel and Word. And thank you for keeping up with me these last months and for always being there for me.

ABSTRACT

Hydropeaking corresponds to the management of hydropower resources where electricity is produced in accordance with prices and demand. Although fully justified economically, hydropeaking may have adverse consequences for the aquatic ecosystem. Due to frequent and rapid fluctuations in water discharge hydropeaking could generate negative effects on the ecosystem downstream the outlet of the hydropower station. Frequent fluctuations in water discharge, altered temperature regime, substrate composition and vegetation cover can result in reduced macroinvertebrate density and variety downstream the outlet of hydropower stations. Furthermore, macroinvertebrates inhabiting the shallow zone could be exposed to stranding as a consequence of frequent dewatering of the river-margin.

In order to provide environmental guidelines for the hydropower industry, it is essential to understand how changes brought upon hydropeaked rivers affect the aquatic ecosystem.

We studied the effect of hydropeaking on the total macroinvertebrate density and on the density, diversity and species richness of the orders Ephemeroptera and Plecoptera in two hydropeaked rivers, the Bævra River and the Lundesokna River, in central Norway.

Findings from the given study demonstrated negative effects on the macroinvertebrates, likely caused by hydropeaking. The results showed a lowered total density and a lowered density, diversity and species richness of Ephemeroptera and Plecoptera in the zones exposed to frequent dewatering. In the permanently water covered zone, however, there was less indication of a hydropeaking effect. These findings suggest that hydropeaking prevent establishment of normal benthic macroinvertebrate communities in the exposed shallow zone, while the macroinvertebrate fauna in the permanently water covered zone are less affected.

SAMMENDRAG

Effektkjøring innebærer en drift av vannkraftverk hvor elektrisitet produseres i samsvar med pris og etterspørsel. Selv om dette er økonomisk forsvarlig vil det kunne ha uheldige konsekvenser for det akvatiske økosystemet. Effektkjøring vil som en følge av hyppige og raske fluktuasjoner i vannføring kunne føre til at økosystemet nedstrøms utløpet til kraftverket blir negativt påvirket. Hyppige fluktuasjoner i vannføring, endret temperatur regime, substratsammensetning og vegetasjonsdekke kan resultere i redusert tetthet og diversitet av makroinvertebrater nedstrøms utløpet av kraftverket. Samtidig vil makroinvertebrater som holder til i den grunne sonen kunne bli eksponert for stranding som en følge av hyppig tørrlegging av elvebredden.

For å kunne sette miljømessige retningslinjer for kraftindustrien er det viktig å ha forståelse for hvordan forandringer i effektkjørte elver påvirker det akvatiske økosystemet.

Virkningen av effektkjøring på den totale tettheten av makroinvertebrater og på tetthet, diversitet og artsantall av Ephemeroptera og Plecoptera ble undersøkt i to effektkjørte elver, Bævra og Lundesokna, Midt-Norge.

Funn fra dette studiet indikerer at makroinvertebrater blir negativt påvirket av effektkjøring. Resultatene viste en reduksjon i total tetthet og en reduksjon i tetthet, diversitet og artsantall av Ephemeroptera og Plecoptera i sonen eksponert for hyppig tørrlegging. I den permanent vanndekte sonen var det imidlertid mindre indikasjon på at makroinvertebrat-faunaen ble negativt påvirket av effektkjøring. Disse resultatene antyder at effektkjøring forhindrer opprettelse av et normalt samfunn av makroinvertebrater i den eksponerte, grunne sonen. Makroinvertebratene i den permanent vanndekte sonen derimot, er påvirket i mindre grad.

TABLE OF CONTENTS

1 INTRODUCTION

1.1 Hydropower production and hydropeaking

Energy efficiency and increased energy production from renewable energy sources like hydropower, are today two central means to meet the challenges of climate change (Harrison and Whittington, 2001). Efficient use of energy can largely be achieved by increasing the amount of energy produced in accordance with demand. Neither thermal power stations nor renewable energy sources like solar and wind power have this opportunity. Furthermore, increased energy production from renewable sources will result in increased production by solar and wind power stations. However, both solar and wind power are vulnerable to variation in sun and wind supply, thus a backup system is therefore needed to cover the electricity demand when sun and wind are absent. A possible solution to both these challenges is hydropeaking. By being regulative, hydropeaking could increase the energy efficiency and additionally function as a renewable back-up system for solar and wind power (Energy Creative Group AS, 2007).

In recent years hydropeaking, as a strategy for managing hydropower stations to maximize energy production, has caused challenging interests due to potential social and environmental effects. The hydropeaking strategy entails the opportunity to change the energy production quickly, in accordance with energy prices and demand (Norwegian water resources and energy directorate, 2010). As a regulative renewable energy source, this strategy is gaining increasing attention in Europe (The European Wind Energy Association, 2011).

In Norway, hydropeaking as a managing strategy was actualized with the implementation of the new energy act in 1991. The new act implies that power prices no longer are fixed by local authorities, but instead set by the market based on production, transmission and consumption conditions in the Nordic countries (Lier, 2003; Ministry of petroleum and energy, 2007). By employing peaking operations, price differences are utilized by increasing the energy production in relation to energy consumption and prices (Norwegian water resources and energy directorate, 2010). However, although this mode of operating the hydropower stations is climate friendly, it is not necessary environmentally friendly.

The quick and frequent alterations in water discharge caused by hydropeaking will affect the lotic ecosystem, and thereby alter the habitat for freshwater biota (Harby et al., 2004). The focus of this thesis is to examine the effect of frequent and quick alterations in discharge on the fauna of the orders Epehemeroptera and Plecoptera.

1.2 Effects of altered abiotic factors on the river biota

Natural water flow in rivers varies between hours, days, seasons and years. In regions with marked seasonal variation, as Norway, rivers are affected by seasonal patterns of high flows caused by precipitation and snow melting. Aquatic species are adapted to these changes in water flow, and some species even depend on the predictability of flow events to complete their life cycle (Poff et al., 1997). Compared to natural variation, anthropogenic alterations of the flow due to hydropeaking can be more rapid and unpredictable for the aquatic organisms (Harby et al., 2004). Aquatic organisms inhabiting rivers managed by hydropeaking can be exposed to physiological stress and potential mortality caused by washing-out during high flows or stranding of organisms living in the littoral zone (Perry and Perry, 1986; Cereghino et al., 2002). Furthermore, rapid fluctuation in flow may also alter abiotic factors in the river downstream of the hydropower station. Changes in abiotic factors like water velocity, water depth, wetted area, water temperature, erosion, sedimentation processes and thereby the quality of the substrate could adversely affect fish (Young et al., 2011), vegetation (Johansen, 2000) and the macroinvertebrate fauna (Cushman, 1985; Bruno et al., 2010).

1.2.1 Hydropeaking and the effects on macroinvertebrates

Alterations in wetted perimeter caused by fluctuating flow is considered one of the most important factors affecting density and diversity of macroinvertebrates (Raddum et al., 2006). In general rivers could be divided into two zones: (1) The deep zone which is permanently covered with water and (2) the shallow zone which is fluctuating in accordance with water discharge (Fjellheim, 1996). In a hydropeaked river the shallow zone is frequently dewatered and inundated in correlation with the management of the hydropower station (McKinney et al., 1999). In these zones the risk of stranding is therefore high, and the most common species are highly mobile and/or have the opportunity to use the interstitial space (i.e. the hyporheic zone) as refuge (Fjellheim, 1996). This shallow zone could be referred to as the ramping zone. The effect of frequent alterations in discharge on the macroinvertebrate fauna was investigated by Arnekleiv et al. (1994) in the Nidelva River, Norway. To study how macroinvertebrates were distributed from shallow to deep areas in the river, samples were taken in a cross section divided into three zones where zone 1 and 2 were exposed to drying caused by hydropeaking operations, while zone 3 was permanently wetted. The results revealed that the amount of macroinvertebrates in zone 1, which were most frequently exposed to drying, was 90 % less compared to zone 3 which was permanently wetted. The study also documented a clear negative correlation between the number of drying episodes and the amount of macroinvertebrates. A severe diversity decline in the zones exposed to drying was also detected (Arnekleiv et al., 1994). In another study implemented in two regulated rivers with daily fluctuating flows, little recolonization of macroinvertebrates to shallow areas exposed to drying was observed, and most of the invertebrates were restricted to the constant water covered area (Perry and Perry, 1986). Nevertheless, recolonization of the shallow area is possible. The main sources of recolonization are shown to be drift, oviposition by flying insects, upstream mitigation within the water and movement of individuals from the substrate and the hyporheic zone (Williams and Hynes, 1976). However, recolonization from the hyporheic zone is determined by the substrate composition. It is essential that the substrate is porous enough to allow small and flexible larvae to use the hyporheic zone as a refuge from frequent and fast flow (Bruno et al., 2009).

In hydropeaked rivers, though, substrate composition could be altered due to continual cycles of deposition and erosion (Cushman, 1985). Low water velocity will increase sedimentation of fine particles, while high water velocity generates a larger proportion of coarse sediments (Saltveit, 2006). By filling up interstitial spaces and covering of surfaces, increased sedimentation, as an effect of reduced water velocity and sediment release from the dam, yields a more homogenous habitat and reduces the availability of refuges from high flow (Rabeni et al., 2005; Bruno et al., 2009). For some functional feeding groups increased sedimentation could result in disruption of respiration and feeding activity (Rabeni et al., 2005). Moreover, increased water velocity, resulting from peaking events, could have severe effects on the macroinvertebrate fauna by increasing scoring and movement of the streambed. This could in turn lead to catastrophic drift of macroinvertebrates (Fuller et al., 2011). Catastrophic drift occurs as a direct effect of large floods, and is intensified by movement of streambed and transport of sediments (Gibbins et al., 2007). In a study from France, Cereghino et al. (2004) demonstrated that the mayfly larva of *Rhithrogena semicolorata* (Heptageniidae) was able to control its entry into drift under natural flow regime, while during peaking operations the flushing action of each peak flow forced the larvae into the drift. In the same study, macroinvertebrate density was measured upstream and downstream of the hydropower station outlet. Most of the downstream sites showed decreased density compared to the upstream reference site. Catastrophic drift was indicated to be one of the factors responsible for this pattern (Cereghino et al., 2004).

Changed discharge regime has also appeared to alter species composition of aquatic vegetation downstream the hydropower station in hydropeaked rivers. As an effect of frequent sediment movement and subsequent covering of the bryophytes, both the ramping zone and the permanent water covered zone have shown a reduction in the bryophyte cover. Moreover, reduction in green alga and macrophytes have also been observed in the ramping zone. These effects have been assigned to high flow and frequent dewatering (Johansen, 2000). Since macrophytes, periphyton and other surface layer complexes are important food sources and could function as shelter from high flow and predators, alterations in the aquatic vegetation could negatively affect the benthic fauna (Allan, 1995). Bryophytes could also function as shelter in addition to accumulate organic detritus and provide substrate for alga (Turetsky, 2003; Rosa et al., 2011). In a study examining macroinvertebrate diversity in relation to disturbance of primary production, high flow disturbance of the streambed and associated scour of periphyton resulted in a reduced number of macroinvertebrate species. However, this effect was only pronounced in open sites opposed to closed canopy sites, where light limitation reduced the periphyton growth. This suggests that the effect of flow disturbances on macroinvertebrates was not direct, but an indirect effect via the reduction in periphyton cover. Since periphyton is less important as a community function in closed canopy sites, high flow disturbance did not affect the macroinvertebrates to the same extent in these sites (Death and Zimmermann, 2005).

Furthermore, the water temperature regime will also be affected by hydropeaking events. Production water from hydro reservoirs and dams is conventionally released from the hypolimnion, where the water temperature is normally approximate four degrees Celsius (Saltveit et al., 1994; Frutiger, 2004). Thus, hypolimnetic water will normally lead to decreased summer temperatures and increased winter temperatures in the regulated river, compared to natural conditions (Brittain, 1989). In rivers exposed to hydropeaking these temperature fluctuations will be abrupt, and occur on a daily basis in relation to the hydropeaking events (Carolli et al., 2011). This could cause challenges for stream biota. For instance, duration of egg incubation period and growth of nymphs are largely governed by water temperature(Brittain, 1989). Hence, hydro-regulation could have severe effects on the growth and life cycle of benthic macroinvertebrates. The benthic species growth pattern and type of life cycle could be decisive for the benthic species tolerance for altered thermal regime. Winter species hatching before the winter period, display some growth during winter and emerge during spring and early summer (Brittain, 1989; Söderström, 1991). Summer species, on the other hand, spend the winter period in the egg stage or as very small nymphs, grows rapidly and emerge during the summer (Brittain, 1989; Söderström, 1991). Because of increased winter temperatures downstream the outlet, species from the winter generation could accelerate their maturing stage and emerge as imagines when air temperature is too low. This could increase the mortality and reduce the reproductive success (Raddum, 1985). Different species also exhibit different life cycles. The life cycle of aquatic insects may be univoltine, with one generation per year, bivoltine, with two generations per year, mutivoltine, with more than two generations per year or semivoltine, which require more than one year to go from egg too adult (Engblom, 1996). Because of rapid egg development and short life cycle multivoltine species could have an advantage during unstable conditions by reappearing quickly after disturbance, and by being prevalent recolonizers to areas exposed to stress (Perry and Perry, 1986; Gillooly and Dodson, 2000; Raddum et al., 2006).

Altered temperature conditions may also affect Plecoptera and Ephemeroptera differently, and even species-specific responses could result from the alterations. For instance, Ephemeropteran species show a greater thermal demand and are more temperature dependent compared to Plecopteran species. During unfavorable conditions Plecopteran species have another advantage over Ephemeropteran species, by possessing the ability of nymphal diapause (Brittain, 1989). In a study from the regulated watercourse Aurlandvassdraget, Norway, alterations in growth and life cycle of Ephemropteran species were observed. As a consequence of increased temperatures, eggs hatched before the environment was favorable for the imagines. It also appeared that the growth pattern of the Plecoptera species *Laucta hippopus* and *Lauctra fusca* was altered (Raddum et al., 2005). On the contrary, Saltveit et al. (1994) claimed that the effect of temperature changes on diversity of the benthic fauna is less marked in North-Western-Europe compared to North-America, where most of the studies on thermal changes have been carried out (Saltveit et al., 1994). Due to a high degree of specialization and narrow niches of the diverse fauna in North-America, small environmental changes could have greater impact compared to the less diverse fauna in Western-Europe (Saltveit et al., 1987). If, on the other hand, the effects of change in water velocity is included, major changes in benthic fauna have been detected also in Western-Europe (Saltveit et al., 1994).

These abiotic and biotic changes brought upon a hydropeaked river show that frequent and fast flow fluctuations have more severe effects on the benthic fauna compared to traditional river regulation, with high flow maintained over longer periods of time.

1.2.2 Functional feeding groups

Maintenance of the river ecosystems is dependent upon several of the macroinvertebrate functions. The nutrient cycles, the primary production, decomposition and translocation of materials are all processes influenced by macroinvertebrates. But the interplay between the macroinvertebrates and their food source differ among species, and their functional role in the river is thereby different. In the heterogeneous environment of rivers, macroinvertebrate species have evolved different morphology and behaviour in order to acquire food. Due to these differences the macroinvertebrates have been divided into different functional feeding groups, which could occupy different niches and belong to different trophic layers. These are scrapers/grazers, shredders, gatherers, filterers and predators (Wallace and Webster, 1996). Scrapers/grazers are adapted to graze upon periphyton or alga attached to substrate surfaces. Shredders usually consume coarse particulate organic material (CPOM) covered by microorganisms. Predators feed on animal tissue by piercing cells and sucking out the cell content or by engulfing prey. Collectors primarily feed on fine particulate organic material (FPOM) and can be classified as collectors-gatherers which feed on organic matter deposited in the substrate, and collector-filterers with a variety of specialised mouthparts that can collect suspended particulate organic matter (Cummins and Klug, 1979; Wallace and Webster, 1996). As a consequence of different feeding behaviour and capability of movement some macroinvertebrates are more sensitive to fluctuations in discharge (Troelstrup and Hergenrader, 1990). Downstream of a hydropeaked hydropower station one might expect lower occurrence of scrapers and collector-gatherers since scrapers are easily exposed to high currents as their food thrive on top of stones, and collector-gatherers easily could be flushed along with their food source. Predators acquiring food by active foraging, opposed to sit-and-wait predators, could be exposed to sudden increase in flow (Englund and Malmqvist, 1996). Troelstrup and Hergenrader (1990) found lower numbers of collector-gatherers, collector-filterers and scrapers in the shallow part downstream of a dam with daily fluctuations in flow one year compared to a year without fluctuations.

1.3 Aims of the study

Increased knowledge on how rapid flow variation influence macroinvertebrates is important to get an idea of whether restrictions on the peaking operations are needed. The purpose of the present study have been to examine the effects of frequent and fast flow variations caused by hydropeaking on the diversity, species richness and density of the orders Ephemeroptera and Plecoptera. Density measures are applied to check whether the number of macroinvertebrates is reduced downstream the hydropower station. Furthermore, since species exhibit different tolerance to the alteration entailed by hydropeaking, species richness and diversity are measured.

We therefore compared density, diversity and species richness of the macroinvertebrate fauna upstream and downstream from the outlet of hydroelectric power stations in two hydropeaked rivers. More specifically we tested whether hydropeaking reduces density, species richness and diversity in the downstream section compared to the upstream section and whether this effect was more marked in the shallow areas, exposed to continual dewatering, compared to the deep, permanent water covered areas.

2 METHODS

2.1 Study site

The sampling was conducted in two rivers affected by hydropeaking, the Bævra River and the Lundesokna River. The hydropower stations in both rivers are high-head power stations, where water is stored in reservoirs and led through pressure shafts to the hydropower station. The Bævra River is situated in Surnadal and Rindal municipalites in North-Møre (63.04°N, 8.66°E), Norway (Fig. 1). The river has been regulated since 1963 by transferring 43 % of the catchment area of the tributaries Svorka and Lille Bævra, above the hydropower station, to Svorka hydropower station. This has resulted in strong reduction in discharge and partly drying out of the tributaries. Discharge in the Bævra River above the hydropower station is also reduced, but the variation in discharge is natural and is following the precipitation in the catchment area downstream the impoundment. Downstream from the Svorka hydropower station the total annual discharge remains unaltered, but the water discharge is changing frequent and fast in correlation with the operation of the hydropower station (Fig. 2 and Fig. 3) (Johnsen et al., 2011). The maximum discharge of Svorka hydropower station is 11 m^3/s. Svorka hydropower station has no requirement of minimum flow, and is not equipped with a bypass valve. Without a bypass valve the water level will become extremely low with a shutdown of the power station (Johnsen et al., 2011).

The shut-down from maximum production to cessation of production takes approximately three hours, while the run-up from minimum to maximum production takes approximately 5 to10 minutes. When the hydropower station is shut down approximately 6 to 8 meters of the riverbank will be exposed to drying at the sampling station of the current study. However, with a catchment area of 111.58 km^2 providing the river downstream the dam with water, the section downstream the hydropower station will rarely be dewatered (V. Fossøy, pers. comm. 22.05.2012). The distance from the Svorka hydropower station to the downstream sampling site is 150 m, and the distance to the upstream sampling site is 200 m.

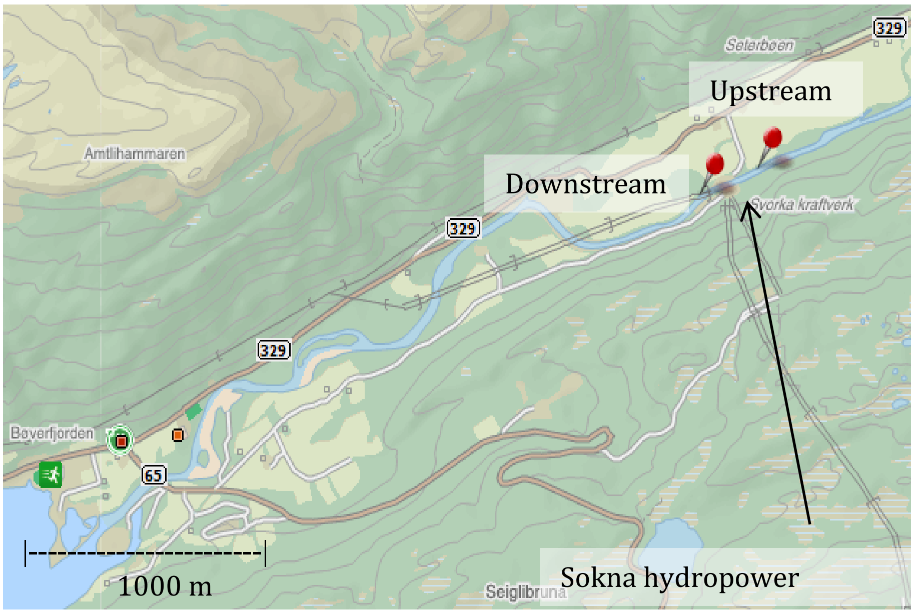

Figure 1. The Bævra River and Svorka hydropower station. The sampling sites upstream (reference site) and downstream (study site) of the hydropower station are marked. Map obtained from finn.no.

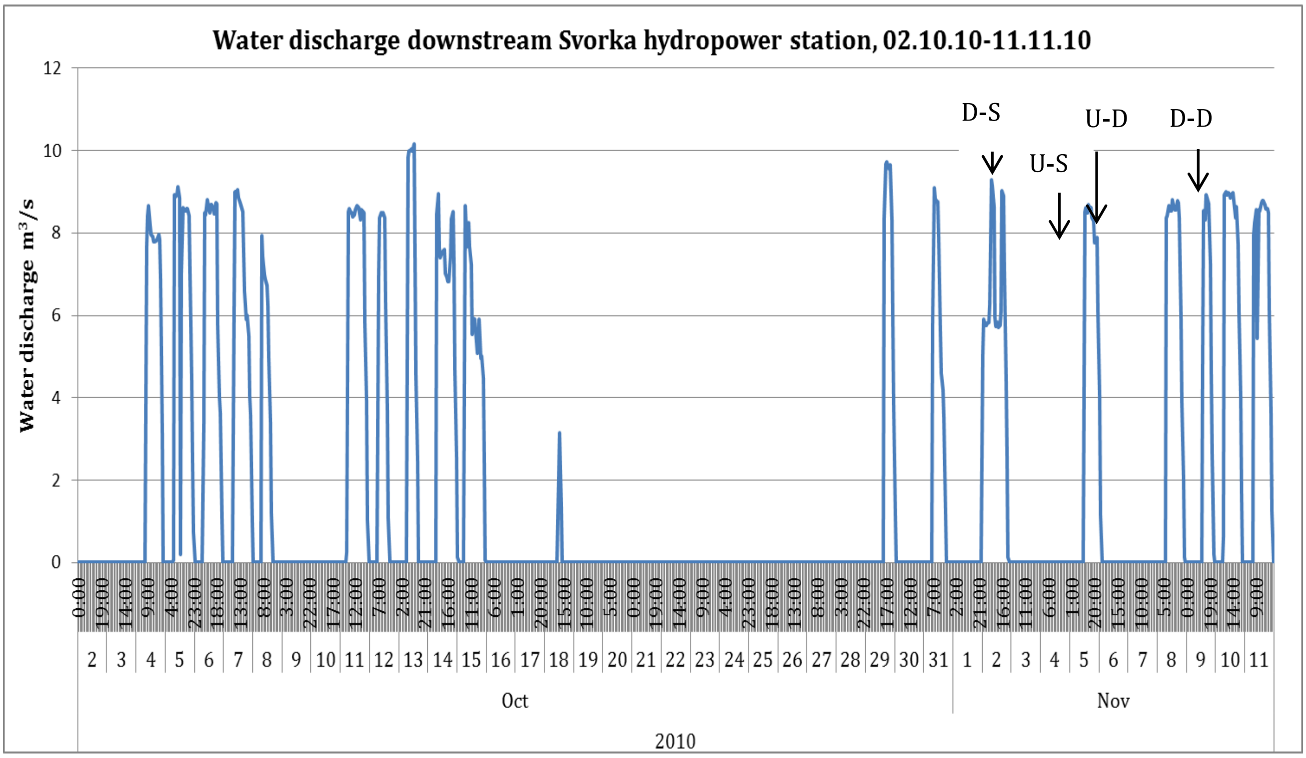

Figure 2. Overview of the water discharge downstream Svorka hydropower station in the period prior to the autumn sampling. The arrows are indicating when the sampling of the different zones was performed. D-S = Shallow zone downstream, D-D = Deep zone downstream, U-S = Shallow zone upstream and U-D = Deep zone upstream. Data was obtained from Statkraft AS.

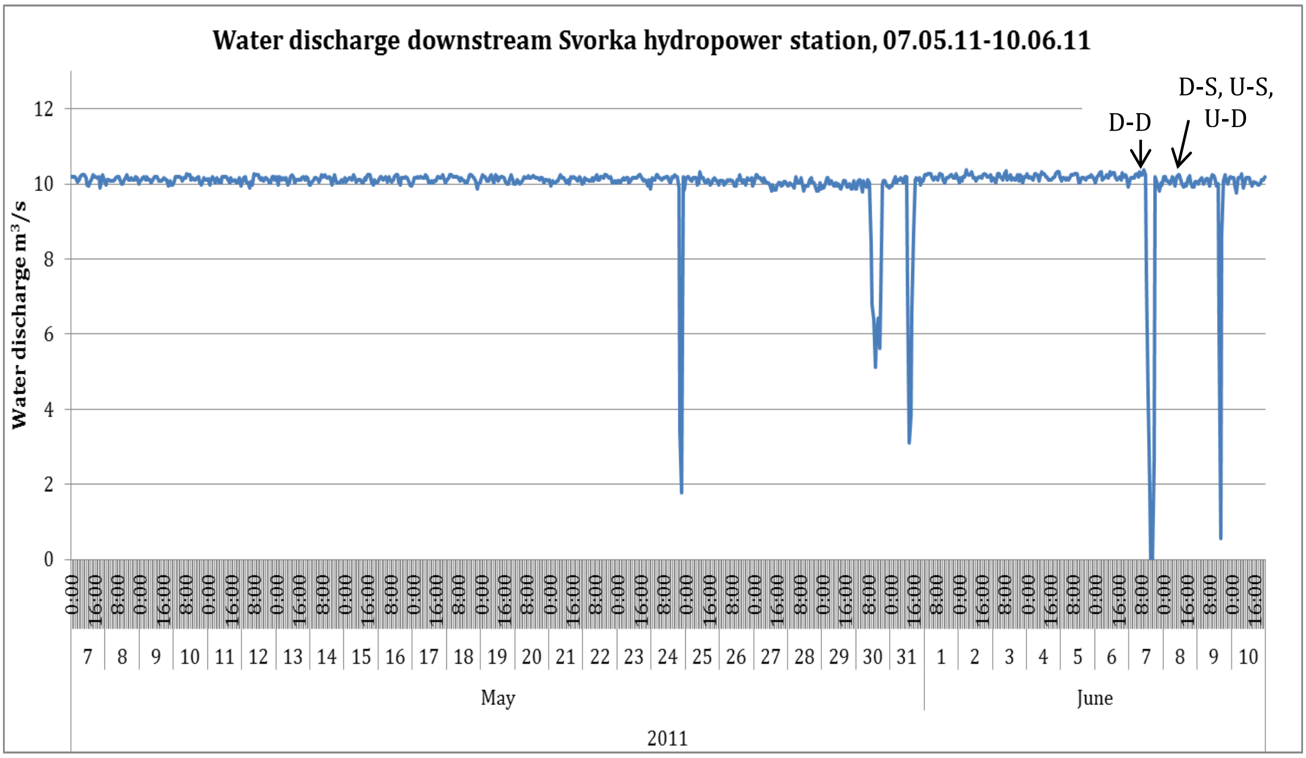

Figure 3. Overview of the water discharge downstream Svorka hydropower station in the period before the spring sampling. The arrows are indicating when the sampling of the different zones was performed. D-S = Shallow zone downstream, D-D = Deep zone downstream, U-S = Shallow zone upstream and U-D = Deep zone upstream. Data were obtained from Statkraft AS.

The Lundesokna River is a tributary of Gaula River and is regulated with three hydropower stations. The hydropower station of interest in this study is Sokna hydropower station, situated in Melhus municipality in South-Trøndelag, Norway (63.15°N, 10.32°E) (Fig. 4). The regulation of the Lundesokna River entails the transfer of water from the catchment area of two lakes (Holtsjøen Lake and Burusjøen Lake) and regulation of Samsjøen Lake and Håen Lake, the latter one is the impoundment for the Sokna hydropower station. Sokna hydropower station has been regulated since 1964, and has an absorption capacity of 20 m^3/s. There is a higher annual discharge in the Lundesokna River now compared to the situation before regulation. But similarly to the Bævra River, the discharge change is frequent and fast compared to natural conditions and is determined by maneuvering of the hydropower station (Fig. 5 and Fig. 6). Upstream the hydropower station discharge is also largely reduced. However, the variation in discharge is natural, following the precipitation of the reduced catchment area downstream Håen Lake. The Sokna hydropower station has no requirement of minimum flow, but has a requirement of letting 0.3 m^3/s pass the dam in the summer season (May – September) to supply a hatchery located upstream the hydropower station. Sokna hydropower station is not equipped with a bypass valve (V. Finset, pers. comm. 11.04 2012).

The shut-down from maximum production to cessation of production usually takes 5 to 15 minutes, but this is variable and a shutdown speed of 60 minutes can occur. The run-up from minimum to maximum production takes approximately 2 to3 minutes. When the hydropower station is shut down approximately 8 to20 meters of the riverbank will be exposed to drying at the sampling station of the current study. However, with a catchment area of 25.8 km^2 providing the river downstream the dam with water, the section downstream the hydropower station will rarely be dewatered (V. Finset, pers. comm. 11.04 2012). The distance from the Sokna hydropower station the downstream sampling site is 1900 m, and the distance to the upstream sampling site is 1600 m.

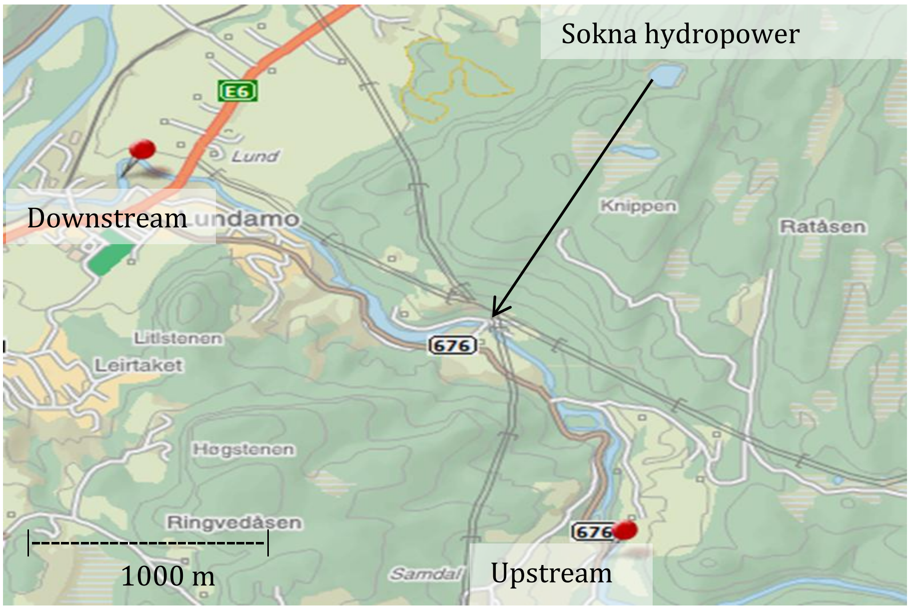

Figure 4. The Lundesokna River and Sokna hydropower station. The sampling sites upstream (reference site) and downstream (study site) of the hydropower station are marked. Map obtained from finn.no.

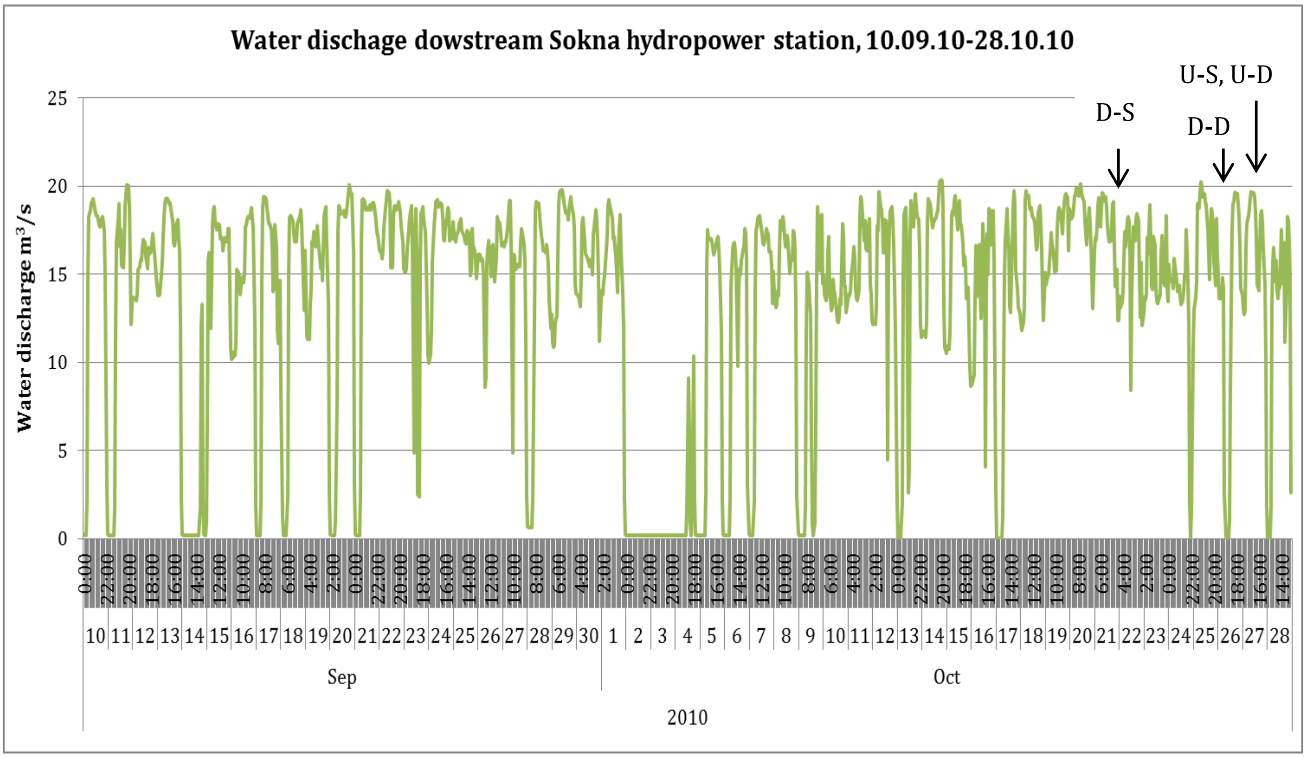

Figure 5. Overview of the water discharge downstream Sokna hydropower station in the period prior to the autumn sampling. The arrows are indicating when the sampling of the different zones was performed. D-S = Shallow zone downstream, D-D = Deep zone downstream, U-S = Shallow zone upstream and U-D = Deep zone upstream. Data were obtained from Norwegian University of Science and Technology.

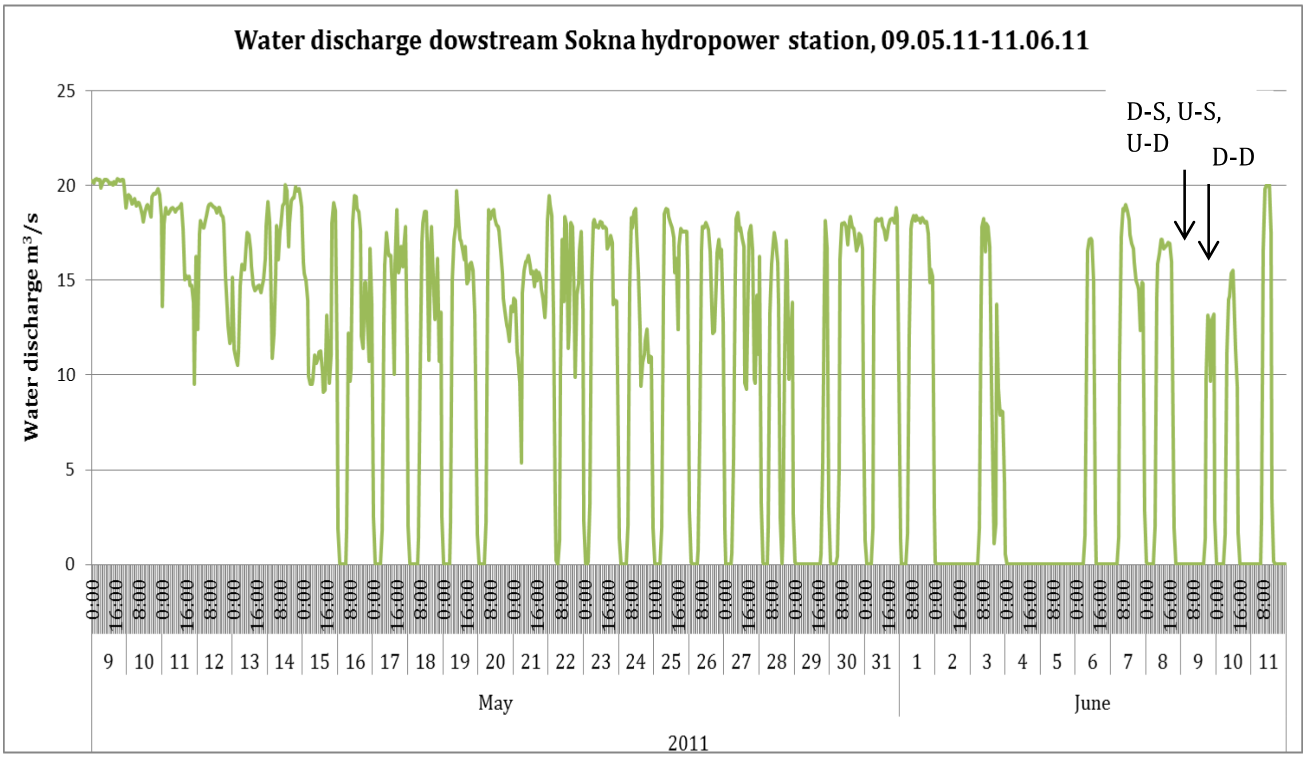

Figure 6. Overview of the water discharge downstream Sokna hydropower station in the period prior to the spring sampling. The arrows are indicating when the sampling of the different zones was performed. D-S = Shallow zone downstream, D-D = Deep zone downstream, U-S = Shallow zone upstream and U-D = Deep zone upstream. Data were obtained from Norwegian University of Science and Technology.

2.2 Experimental design

Macroinvertebrates are chosen as bioindicators because of their sensitivity to perturbation, short generation time and ability to disperse and recolonize disturbed areas (Hodkinson and Jackson, 2005). Furthermore, Plecoptera and Ephemeroptera are chosen because of their well-known taxonomic groups and because they are an important food source for fish (Raddum et al., 2005). To obtain representative samples of the benthic fauna, samples were collected during two field seasons, October/November 2010 representing autumn period and June 2011 representing summer period. The samples were obtained with a Surber sampler (Surber, 1937). Two sampling sections were established in each river, one upstream and one downstream of the hydropower station (Fig. 7). The upstream sections has a reduced discharge because of the reservoir further up in the river, but are not affected by fluctuating flow from the outlet of the hydropower station. These upstream sections are fed by water from the catchment area between the mountain impoundment and the hydropower station, and are therefore following natural and seasonal variations. Hence the upstream section (not hydropeked) will function as reference site for comparison with the downstream section (hydropeaked). Within the downstream and the upstream section, samples were obtained from deep and shallow zones. Both the shallow and the deep zone in the affected downstream section are subjected to frequent fluctuations in discharge and the subsequent alterations in abiotic and biotic factors. However, for the shallow zone these fluctuations also involve continual dewatering and inundation.

In the downstream and the upstream section seven samples were taken on a line in both the shallow zone and the deep zone (Fig. 7). The deep zone samples downstream the hydropower station were always taken when the hydropower station were shut down, and the shallow zone samples downstream the hydropower station were always taken when the hydropower station were turned on. The distance between two sample-units within zones was 2 to 3 meters, but exact position was also dependent upon the possibility to put down the Surber sampler. The distance between the shallow and the deep zone was approximately 3 to 4 meters. Painted stones were put down on each sampling spot, to be able to check whether the shallow zone downstream was dried up and whether the deep zone downstream was still water covered when the hydropower station was shut down. The sampling started furthest downstream in each zone to ensure that dislodged individuals did not colonize other sampling plots. In the field, samples were filtered through a sieve with 0.5 mm net mesh size and conserved separately on 70% ethanol for later sorting and identification in the laboratory. In the lab, five samples, randomly chosen, from each zone were analyzed.

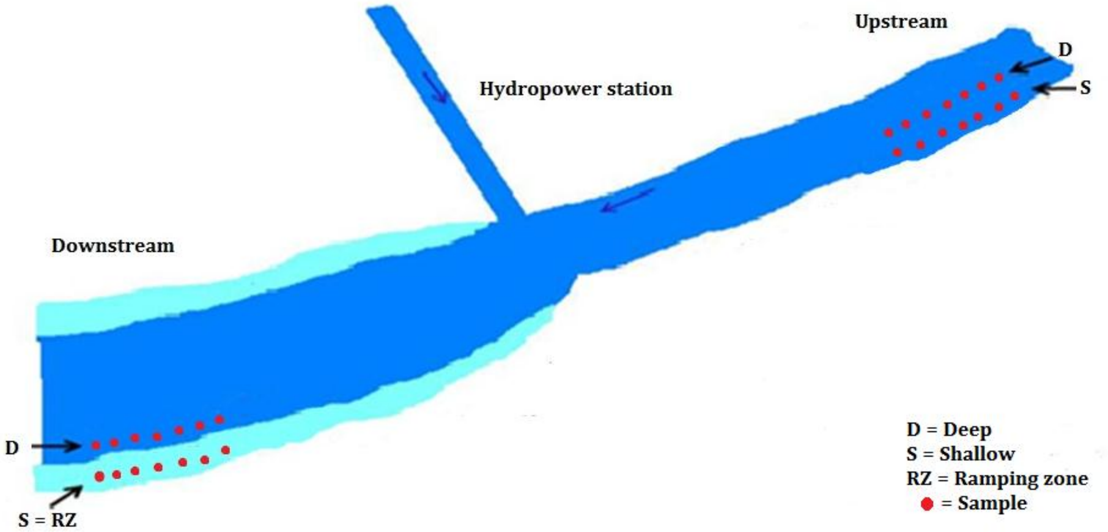

Figure 7. Illustration of the sampling design in the Bævra River and the Lundesokna River.

The Surber sampler has an area of 30×30 cm and a 0.5 mm net mesh size and consists of two quadrate shaped interlocked frames. One frame outlines the area of the river bed to be sampled while the other one is attached to a net. The substrate inside the frame on the river bed is stirred up and all the large stones are rubbed in such a way that macroinvertebrates and other materials are carried into the net by the current.

At each sampling point, depth, water velocity, substrate and vegetation measures were recorded to get measurements of the difference between the zones. Vegetation measures were only obtained for the June samples. Mini Air 2 flow meter (Schiltknecht Messtechnik AG, Sveits) was used to measure water velocity. Substrate was assessed according to the CASiMiR-model (Schneider et al., 2010). Dominant and sub-dominant substrate was recorded. Per cent coverage (0, 25, 50, 75 and 100 %) was used to assess the presence of bryophytes and alga.

In the laboratory, all organisms in the samples were classified into taxonomic groups and counted using a stereo-microscope. Furthermore, Ephemeroptera and Plecoptera were identified to the lowest possible taxonomic level by using taxonomic keys. The keys used for identification were Engblom (1996) and Lillehammer (1988).

All numeric counts were converted to density by dividing sample counts by the area covered by the Surber sampler (0.09 m^2). In addition to densities of Ephemeroptera and Plecoptera, total densities of all individuals in a sample were calculated. Two diversity metrics are used to assess the fauna of Ephemeroptera and Plecoptera: (1) Species richness which is assigned as the number of species in a sample and (2) diversity measures by Shannon-Weiner index, that in addition to species numbers takes species evenness into account (Magurran, 2004). Minimum value for the Shannon-Wiener index is zero, and occurs when only one species is present. Shannon-Wiener index is calculated from the equation:

$$H' = -\sum p_i \ln p_i$$

Where p_i is the proportion of individuals of a certain species in one sample obtained by the Surber sampler.

To easier provide an explanation for the possible dissimilar distribution of species in the shallow and the deep zone upstream and downstream of the hydropower station, all the species of Plecoptera and Ephemeroptera were categorized into functional feeding groups. To categorize the species into functional feeding groups supplementary material from Petrin (2011) were used. Relative proportions of different functional feeding groups were calculated for each zone upstream and downstream of the hydropower station. Several macroinvertebrates belong to several functional feeding groups during their life cycle, and some species will therefore be assigned to more than one functional feeding group and thereby be counted more than once (Appendix 3; Table 25). The total number of individuals in each zone was adjusted to this new number. Since species could belong to more than one functional feeding group this number was higher than the actual number of species in one zone. Lastly, the proportion of each functional group in the different zones was calculated.

2.3 Statistical analyses

The effects of hydropeaking on density, diversity and species richness were modeled separately for the two rivers. This is biologically justified because the rivers have different characteristics, and hydropeaking could consequently affect the rivers differently. For instance, the Lundesokna River is more or less thoroughly affected by regulation while the Bævra River could exhibit a more natural variation because of a larger catchment area and a larger influence by snow melting. The river Bævra is also situated in a coastal climate with a high annual precipitation (1500 - 4000 mm in 2011), while the Lundesokna River is exposed to an inland climate with lower annual precipitation (750 to 1500 mm, in 2011) (Meterologisk institutt, 2011). Moreover, the distance between the sampling stations and the hydropower station was longer in the Lundesokna River compared to the Bævra River. The downstream section in the Bævra River could therefore be exposed to a more abrupt change in discharge. Testing the rivers separately is supported by Doledec et al. (2007), which claim that since rivers have their own traits they could be affected differently, and should therefore be modeled separately in statistical tests. Even though the rivers are tested separately, the overall effects of hydropeaking are of interest.

In order to understand how hydropeaking affected the macroinvertebrate fauna, we first tested whether there was a significant interaction between the river section (upstream/downstream) and the zone (deep/shallow). Because of the dewatering of the shallow zone in the downstream section, a stronger difference was expected between the shallow and the deep zone in the downstream section compared to the upstream section. Analyses of variance (ANOVA) were performed where section (upstream/downstream), zone (shallow/deep) and season (autumn/summer) were entered as factors. When the three-way interaction was statistically significant ($p < 0.25$) (Underwood, 1997) the analysis was conducted separately for each season, in order to simplify the interpretation of the model. In these models, a section (upstream/downstream) effect on the difference between the deep and shallow zone was inferred from the interaction between section and zone. In most cases this interaction was significant. To further understand the cause of the interaction effect, the difference between the upstream and downstream section was analyzed separately for deep zones and for shallow zones. This comparison of the zones (deep/shallow) is in addition to the effect of dewatering in the shallow zone, testing the effect of altered abiotic and biotic factors in the affected site. For consistency, models without statistical significant interactions were also modeled separately for each season.

All statistical analyses were performed using the statistical software R, v. 2.14.1. (R Development Core Team., 2011). Statistical significance of specific terms was tested using likelihood ratio tests between models including and not including the term of interest. (Zuur et al., 2009). However, statistical significance should not be confounded with biological significance (Yoccoz, 1991), and we present the interaction effect between zone and section for each model in first part of the analyses.

To fulfill the assumption of normal distributed residuals total density, densities of Plecoptera and Ephemeroptera and species richness of Plecoptera and Ephemeroptera were log-transformed. Constancy of variance and normality of errors were checked by visual inspection of the data.

3 RESULTS

3.1 Total density

On average, shallow zones had a lower total density compared to the deep zones, but this effect was stronger in the downstream section than in the upstream section in both rivers (Table 1; Figure 8 and Figure 9). Furthermore, the magnitude of this effect was seasonal dependent in the Bævra River (interaction section × zone × season: $F_{2,32} = 3.19$, $p = 0.055$), but less in the Lundesokna River (interaction section × zone × season: $F_{2,32} = 1.28$, $p = 0.291$).

The greater difference in total density between the shallow and the deep zone downstream was generated by a considerably higher total density in the deep zone downstream compared to upstream and on average a lower total density in the shallow zone downstream compared to upstream (Table 2; Figure 8 and 9). The magnitude of the difference in total density between upstream and downstream deep zones depended on season in both the Bævra River (interaction section × zone: $F_{1,16} = 2.89$, $p = 0.109$) and the Lundesokna River (interaction section × zone: $F_{2,16} = 7.24$, $p = 0.016$). The direction of the effect was similar in both rivers, but the effect was greater in June in the Bævra River and in October in the Lundesokna River. Similarly, the magnitude of the difference in total density between the shallow zones upstream and downstream was season dependent in the Bævra River ($F_{2,16} = 3.57$, $p = 0.077$), but not in the Lundesokna River ($F_{2,16} = 0.99$, $p = 0.338$). In the Bævra River there was a larger total density in the shallow zone in the upstream section compared to the downstream section in June, but this effect was not apparent in November.

Table 1. Size of the effect ± SE of section (upstream/downstream) on the difference in average total density (in logarithmic scale) between the shallow and the deep zone in the Bævra River and the Lundesokna River in June and October/November. The size of the effect is given by: (shallow minus deep zone upstream) minus (shallow minus deep zone downstream).

	Estimate ± SE	t-value	p-value
Bævra			
June	-1.71 ± 0.44	-3.90	0.001
November	-0.11 ± 0.46	-0.25	0.806
Lundesokna			
June	-1.05 ± 0.45	-2.32	0.034
October	-2.22 ± 0.59	-3.78	0.002

Table 2. Comparison of average total density ± SE (in logarithmic scale) between the deep zones in the upstream and downstream section and between the shallow zones in the upstream and downstream section, the Bævra River and the Lundesokna River in June and October/November. The estimates are considered relative to the upstream section.

	Deep zones			**Shallow zones**		
	Estimate ± SE	t-value	p-value	Estimate ± SE	t-value	p-value
Bævra						
June	-0.93 ± 0.36	-2.57	0.033	0.79 ± 0.25	3.12	0.014
November	-0.12 ± 0.31	-0.40	0.70	-0.008 ± 0.34	-0.025	0.981
Lundesokna						
June	-0.13 ± 0.28	-0.48	0.647	0.91 ± 0.35	2.58	0.032
October	-1.74 ± 0.53	-3.29	0.012	0.48 ± 0.26	1.85	0.102

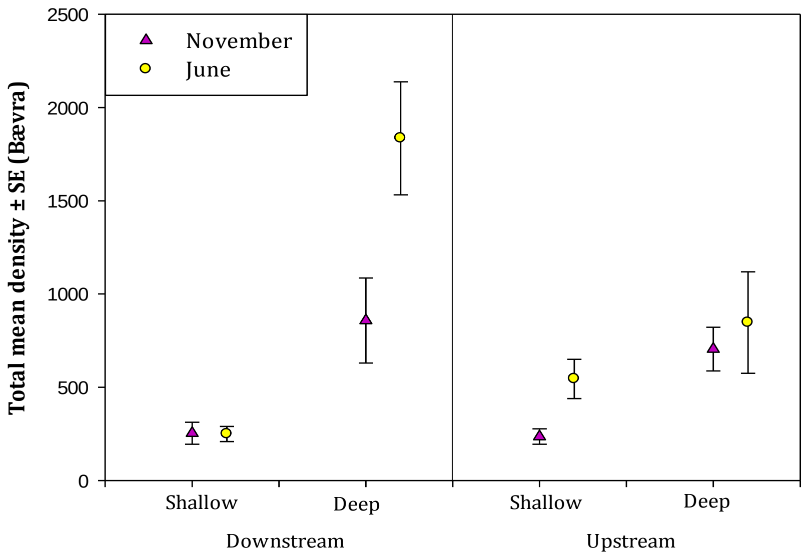

Figure 8. Total mean density (individuals/m^2) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Bævra River, in June and November.

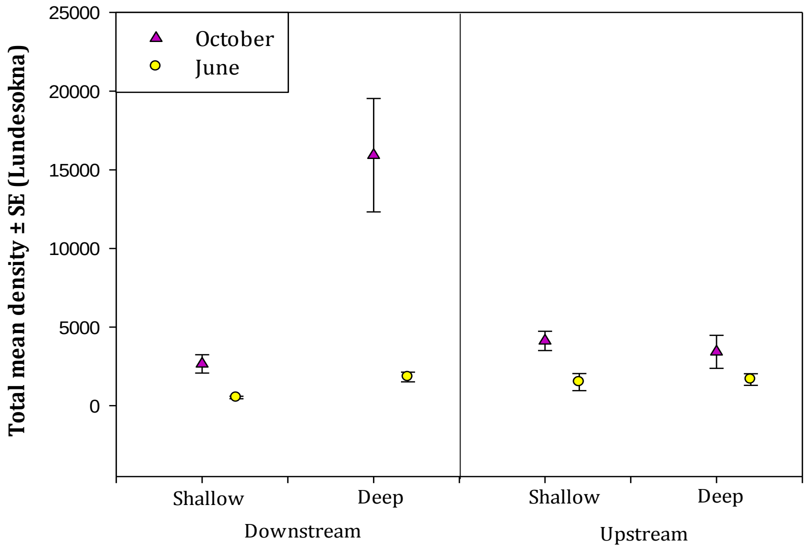

Figure 9. Total mean density (individuals/m[2]) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Lundesokna River, in June and October.

3.2 Density of Ephemeroptera and Plecoptera

Because the effects of hydropeaking on total density are not necessarily the same for different insect orders, the effects on Plecoptera and Ephemeroptera are considered in separate tests.

3.2.1 River Bævra

The results of the comparison of density between zones in the Bævra River do not exhibit marked differences between Ephemeroptera and Plecoptera. On average the density of both orders in the Bævra River was lower in the shallow zones than the deep zones, but this effect was stronger downstream than upstream (Table 3; Fig. 10 and Fig. 11). Furthermore, the magnitude of this effect differed between seasons for Ephemeroptera (interaction section × zone × season: $F_{2,32} = 7.65$, $p = 0.002$), the effect in November being stronger (Table 3; Fig. 10). For Plecoptera both the magnitude and direction of the effect was seasonal dependent (interaction section × zone × season: $F_{2,32} = 18.04$, $p < 0.001$) (Table 3; Fig. 11). The larger difference between the shallow and the deep zone in the downstream section was only apparent in November for the density of Plecoptera (Table 3; Fig. 11).

The greater difference in density between the shallow and deep zone downstream was generated by a considerable lower density in the shallow zone downstream compared to upstream for both orders, and in November a higher density in deep zone downstream compared to upstream for Ephemeroptera (Table 4; Figure 10 and Fig 11). In June the density in the deep zone upstream tended to be higher than the deep zone downstream for both Ephmeroptera and Plecoptera (Table 4; Figure 10 and Figure 11). Accordingly, the magnitude of the difference between the deep zones was seasonal dependent for both Ephemeroptera (interaction section × zone: $F_{1,16} = 15.58$, $p = 0.001$) and Plecoptera ($F_{1,16} = 11.45$, $p = 0.004$). The difference between shallow zones was not affected by the season, neither for Ephemeroptera (interaction section × zone: $F_{1,16} = 0.44$, $p = 0.52$) nor Plecoptera (interaction section × zone: $F_{1,16} = 1.05$, $p = 0.32$).

Table 3. In the Bævra River, size of the effect ± SE of section (upstream/downstream) on the difference in average density (in logarithmic scale) between the shallow and the deep zone. The size of the effect is given by: (shallow minus deep zone upstream) minus (shallow minus deep zone downstream).

	Estimate ± SE	**t-value**	**p-value**
Ephemeroptera			
June	-3.56 ± 0.78	-1.73	0.103
November	-2.35 ± 0.93	-2.52	0.023
Plecoptera			
June	0.41 ± 0.58	0.70	0.494
November	-2.11 ± 0.73	-2.90	0.010

Table 4. Comparison of the deep zones in the upstream and downstream section and of the shallow zones in the upstream and downstream section for Ephemeroptera and Plecoptera average density ± SE (in logarithmic scale) in the Bævra River. The estimates are considered relative to the upstream section.

	Deep zones			**Shallow zones**		
	Estimate ± SE	t-value	p-value	Estimate ± SE	t-value	p-value
Ephemeroptera						
June	0.60 ± 0.31	1.94	0.089	1.96 ± 0.72	2.72	0.026
November	-0.14 ± 0.31	-3.63	<0.001	1.21 ± 0.88	1.38	0.206
Plecoptera						
June	1.39 ± 0.40	3.44	0.009	0.98 ± 0.42	2.37	0.045
November	-0.32 ± 0.30	0.30	0.323	1.78 ± 0.70	2.71	0.027

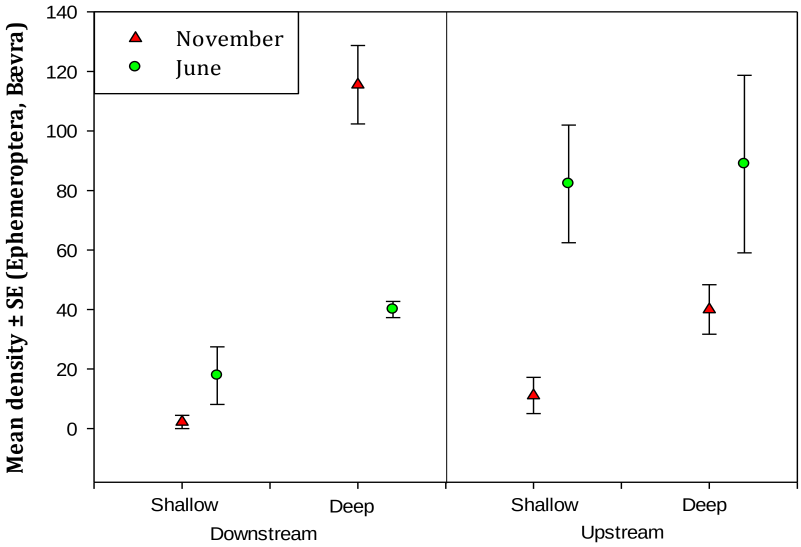

Figure 10. Ephemeroptera average density (individuals/m^2) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Bævra River.

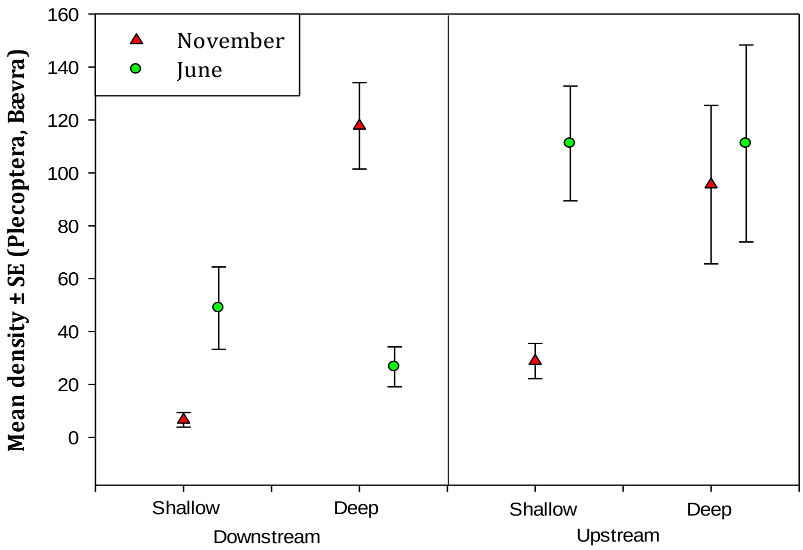

Figure 11. Plecoptera average density (individuals/m^2) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Bævra River.

3.2.2 River Lundesokna

The results of the comparison of density between zones in the Lundesokna River do not exhibit marked differences between Ephemeroptera and Plecoptera. In the Lundesokna River, the density for both orders was on average lower in the shallow zones than in the deep zones, this effect being stronger downstream than upstream (Table 5; Fig. 12 and Fig. 13). This effect was not affected by the season neither for Ephemeroptera (interaction section × zone × season: $F_{2,32} = 0.81$, p = 0.456) nor for Plecoptera (interaction section × zone × season: $F_{2,32} = 0.75$, p = 0.478).

The greater difference in density between the shallow and deep zone downstream was generated by a considerable lower density in the shallow zone downstream compared to upstream (Table 6; Fig. 12 and Fig. 13). The magnitude of the difference between the shallow zones was season dependent for Plecoptera (interaction section × zone: $F_{1,16}$ =11.48, p = 0.003), but not for Ephemeroptera (interaction section × zone: $F_{1,16} = 0.74$, p = 0.404). For Plecoptera in June the great difference between the shallow and deep zone downstream was also generated by a higher density in the deep zone downstream compared to upstream (Table 6; Fig. 13). For Ephemeroptera, on the other hand, there was a higher density in the deep zone upstream compared to downstream in both seasons (Table 6; Fig. 12). Accordingly, the direction and magnitude of the density difference between the deep zones was season dependent for Plecoptera (interaction section × zone: $F_{1,16} = 15.48$, p = 0.001), while the effect on Ephemeropteran density was similar in both seasons (interaction section × zone: $F_{1,16} = 0.021$, p = 0.89).

Table 5. In the Lundesokna River, size of the effect ± SE of section (upstream/downstream) on the difference in average density (in logarithmic scale) between the shallow and the deep zone. The size of the effect is given by: (shallow minus deep zone upstream) minus (shallow minus deep zone downstream).

	Estimate ± SE	**t-value**	**p-value**
Ephemeroptera			
June	-4.03 ± 0.43	-9.31	<0.001
October	-3.35 ± 0.76	-4.39	<0.001
Plecoptera			
June	-1.79 ± 0.34	-5.24	<0.001
October	-1.32 ± 0.42	-3.15	0.006

Table 6. Comparison of the deep zones in the upstream and downstream section and of the shallow zones in the upstream and downstream section for Ephemeroptera and Plecoptera average density ± SE (in logarithmic scale) in the Lundesokna River. The estimates are considered relative to the upstream section.

	Deep zones			**Shallow zones**		
	Estimate ± SE	t-value	p-value	Estimate ± SE	t-value	p-value
Ephemeroptera						
June	1.93 ± 0.29	6.64	<0.001	5.97 ± 0.32	18.64	<0.001
October	2.01 ± 0.45	4.76	0.001	5.35 ± 0.63	8.44	<0.001
Plecoptera						
June	-0.46 ± 0.25	-4.93	0.001	0.55 ± 0.23	2.38	0.045
October	0.40 ± 0.33	1.20	0.265	1.71 ± 0.25	6.72	<0.001

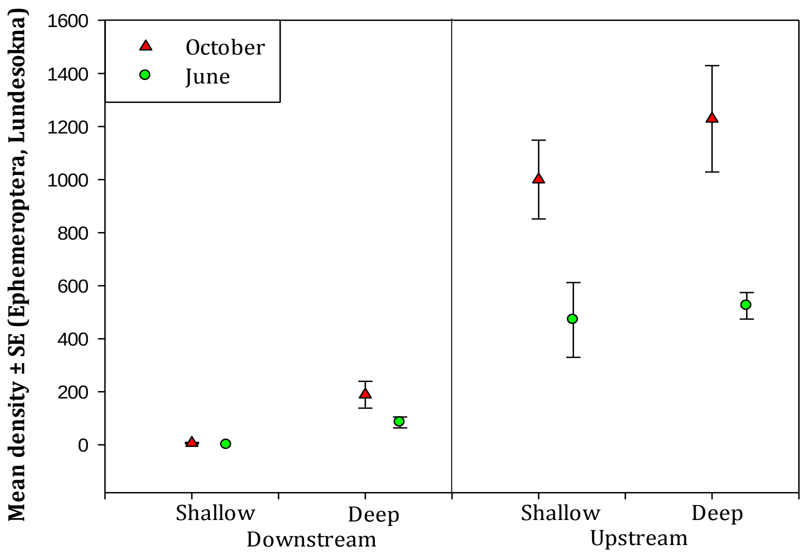

Figure 12. Ephemeroptera average density (individuals/m^2) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Lundesokna River. No individuals were sampled in shallow zone in the downstream section in June.

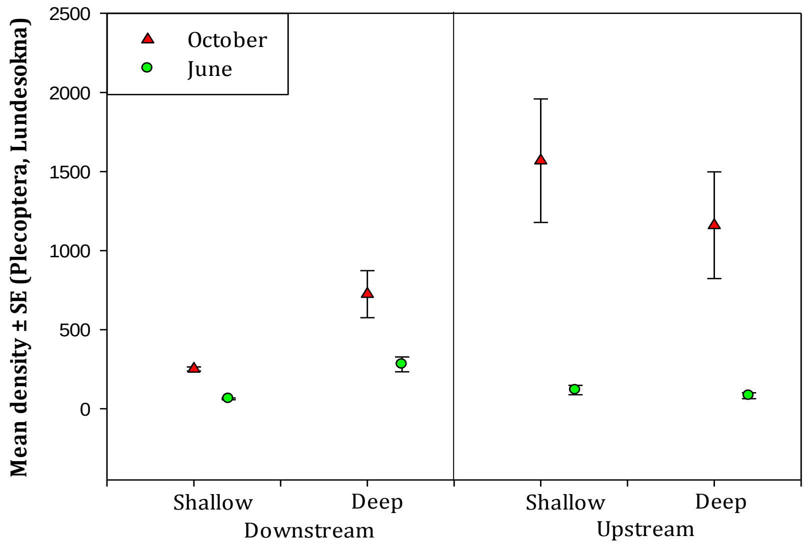

Figure 13. Plecoptera average density (individuals/m^2) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Lundesokna River.

3.3 Diversity of Ephemeroptera and Plecoptera

3.3.1 River Bævra

Overall, for both orders no effect of the section (upstream/downstream) on the difference in species diversity between the shallow and deep zone was found (Table 7; Fig. 14 and Fig. 15), but the variation in diversity among sections, zones and season differed between the two orders. For Ephemeroptera, the diversity tended to be lower in the shallow zones than in the deep zones in both seasons (interaction section × zone × season: $F_{2,32} = 0.08$, $p = 0.925$; Fig. 14), this effect being slightly stronger in the upstream section (Table 7; Fig. 14). This effect was caused by a slightly higher diversity in the deep zones upstream, but the magnitude of this effect was higher in June (interaction section × zone: $F_{1,16} = 1.18$, $p = 0.201$) (Table 8; Fig 14). However, in the comparison of the shallow zones in June, diversity of Ephemeroptera was lower in the downstream section (Table 8; Fig. 14). In November, no individuals of Ephemeroptera were sampled in the shallow zone in the downstream section.

For Plecoptera, the diversity in the shallow zones was much lower than in the deep zones for both sections in November (Fig. 15). However, In June, the diversity of Plecoptera was very similar in deep and shallow zones both upstream and downstream (Table 7; Fig. 15), and thereby generating a strong seasonal effect (interaction section ×

zone × season: $F_{2,32} = 5.8$, $p = 0.007$). The greater difference in Plecoptera diversity between the shallow and deep zone downstream compared to upstream in November was generated by a slightly higher diversity in the deep zone downstream compared to upstream, and a slightly lower diversity in the shallow zone downstream compared to upstream (Table 8; Fig. 15). For Plecoptera the magnitude of the differences between deep zones was not season dependent (interaction section × zone: $F_{1,16} = 0.47$, $p = 0.501$), neither was the difference between shallow zones (interaction section × zone: $F_{1,16} = 0.049$, $p = 0.827$).

Table 7. In the Bævra River, size of the effect ± SE of section (upstream/downstream) on the difference in average diversity (in logarithmic scale) between the shallow and the deep zone. The size of the effect is given by (shallow minus deep zone upstream) minus (shallow minus deep zone downstream).

	Estimate ± SE	**t-value**	**p-value**
Ephemeroptera			
June	0.056 ± 0.26	0.21	0.834
November	0.0026 ± 0.14	0.18	0.856
Plecoptera			
June	-0.20 ± 0.40	-0.50	0.627
November	-0.52 ± 0.27	-1.87	0.079

Table 8. Comparison of the deep zones in the upstream and downstream section and of the shallow zones in the upstream and downstream section for Ephemeroptera and Plecoptera average diversity ± SE (in logarithmic scale) in the Bævra River. The estimates are considered relative to the upstream section.

	Deep zones			**Shallow zones**		
	Estimate ± SE	t-value	p-value	Estimate ± SE	t-value	p-value
Ephemeroptera						
June	0.37 ± 0.22	1.704	0.127	0.32 ± 0.15	2.18	0.061
November	0.026 ± 0.14	0.18	0.858	*	*	*
Plecoptera						
June	-0.04 ± 0.28	-0.16	0.880	0.15 ± 0.28	0.54	0.602
November	-0.30 ± 0.24	-0.23	0.252	0.22 ± 0.14	1.63	0.141

* The estimate of the difference between shallow zones upstream and downstream is not obtained because zero diversity in all samples. Both upstream and downstream this is caused by only one or zero species present in the samples.

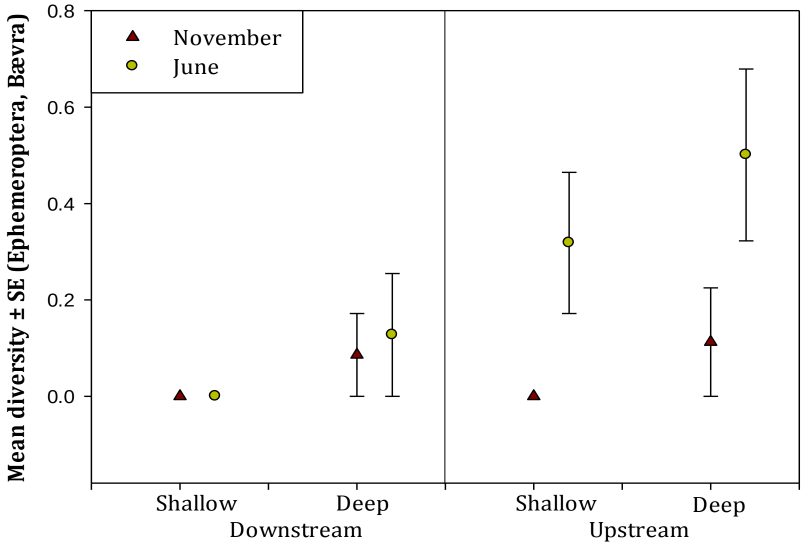

Figure 14. Ephemeroptera average diversity ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Bævra River. Only one species or no species were present in in the samples from the shallow zone in the downstream section in June and November and in the shallow zone in the upstream section in November, hence zero diversity.

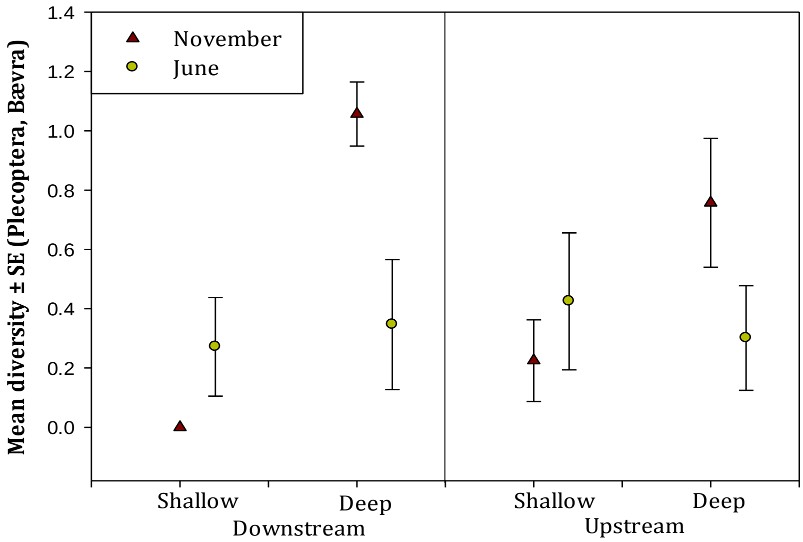

Figure 15. Plecoptera average diversity ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Bævra River. Only one species or zero species were present in the samples from the shallow zone in the downstream section in November, hence zero diversity.

3.3.2 River Lundesokna

On average, the diversity was lower in the shallow zones than in the deep zones for Ephemeroptera in both seasons and for Plecoptera in October, but this effect was stronger downstream than upstream (Table 9; Fig. 16 and Fig. 17). Furthermore, the magnitude of this effect differed between seasons for Ephemeroptera (interaction section × zone × season: $F_{2,32} = 4.24$, $p = 0.023$). For Plecoptera in June, shallow zones tended to have a higher diversity than the deep zones in both sections (Fig. 17). Furthermore, the section (upstream/downstream) effect on the difference in diversity between deep and shallow zones differed in magnitude between seasons for Plecoptera (interaction section × zone × season: $F_{2,32} = 6.94$, $p = 0.003$) (Table 9; Fig. 17).

For Ephemeroptera in both seasons and Plecoptera in October the greater difference between shallow and deep zone downstream was generated by a considerable lower diversity in the shallow zone downstream than upstream (Table 10; Fig. 16 and Fig. 17). For Plecoptera in June there was also a lower diversity in the shallow zone downstream compared to upstream. However, the magnitude of the difference between the shallow zones upstream and downstream was season dependent both for Plecoptera (interaction section × zone: $F_{1,16} = 7.59$, $p = 0.014$), and Ephemeroptera (interaction section × zone: $F_{1,16} = 17.52$, $p < 0.001$). The difference between the deep zones upstream and downstream was negligible for Ephemeroptera in both seasons and for Plecoptera in June (Table 10; Fig. 16 and Fig. 17). For Plecopteran in October, on the other hand, the diversity was higher in the deep zone upstream compared to downstream (Table 10; Fig. 16 and Fig. 17). Accordingly, the magnitude of this effect was season dependent for Plecoptera (interaction section × zone: $F_{1,16} = 2.08$, $p = 0.169$), but not for Ephemeroptera (interaction section × zone: $F_{1,16} = 0.23$, $p = 0.638$).

Table 9. In the Lundesokna River, size of the effect ± SE of section (upstream/downstream) on the difference in average diversity (in logarithmic scale) between the shallow and the deep zone. The size of the effect is given by: (shallow minus deep zone upstream) minus (shallow minus deep zone downstream).

	Estimate ± SE	**t-value**	**p-value**
Ephemeroptera			
June	-1.21 ± 0.25	-4.84	<0.001
October	-0.62 ± 0.16	-3.88	0.001
Plecoptera			
June	-0.29 ± 0.16	-1.74	0.100
October	-0.50 ± 0.16	-3.15	0.006

Table 10. Comparison of the deep zones in the upstream and downstream section and of the shallow zones in the upstream and downstream section for Ephemeroptera and Plecoptera average diversity ± SE (in logarithmic scale) in the Lundesokna River. The estimates are considered relative to the upstream section.

	Deep zones			**Shallow zones**		
	Estimate ± SE	t-value	p-value	Estimate ± SE	t-value	p-value
Ephemeroptera						
June	-0.20 ± 0.24	-0.80	0.443	1.02 ± 0.0069	15.5	<0.001
October	-0.006 ± 0.13	-0.49	0.637	0.55 ± 0.09	6.11	<0.001
Plecoptera						
June	0.10 ± 0.28	0.36	0.726	0.44 ± 0.18	2.50	0.037
October	0.52 ± 0.10	5.09	<0.001	1.03 ± 0.12	8.40	<0.001

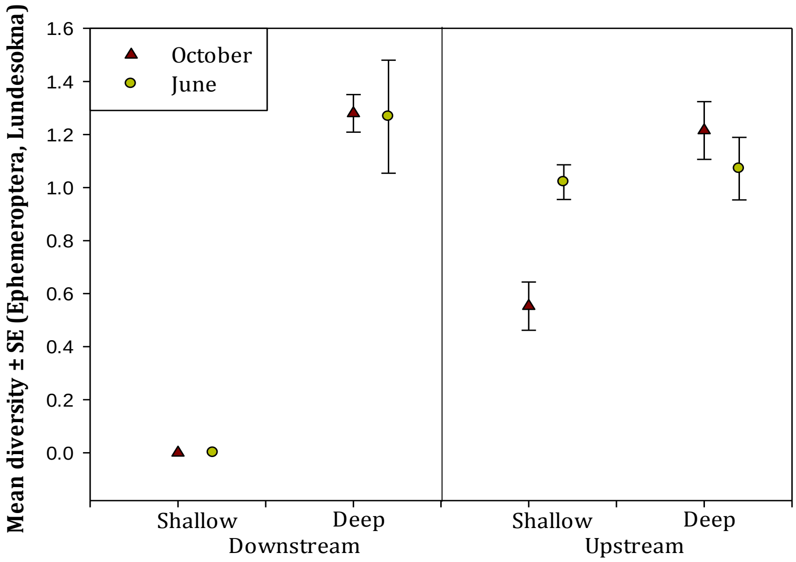

Figure 16. Ephemeroptera average diversity (individuals/m^2) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Lundesokna River. No individuals were sampled in shallow zone in the downstream section in June. In the shallow zone downstream in October, none of the samples had more than one species, hence zero diversity.

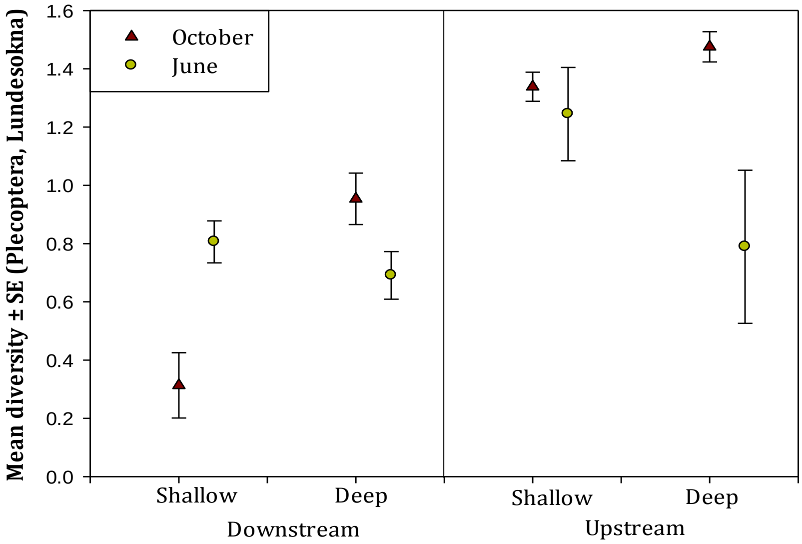

Figure 17. Plecoptera average diversity (individuals/m[2]) ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Lundesokna River.

3.4 Species richness of Ephemeroptera and Plecoptera

3.4.1 River Bævra

The results of the comparison of the species richness between zones in the Bævra River do not exhibit marked differences between Ephemeroptera and Plecoptera. Except for Plecoptera in June, species richness of both orders in the Bævra River was on average lower in the shallow zones than in the deep zones (Fig. 18 and Fig. 19). This effect, however, tended to be stronger downstream than upstream (Table 11; Fig. 18 and Fig. 19). The magnitude of this effect was stronger in November for both Ephemeroptera (interaction section × zone × season: $F_{2,32}$ = 1.76, p = 0.188) and for Plecoptera (interaction section × zone × season: $F_{2,32}$ = 9.39, p <0.001).

The greater difference in species richness between shallow and deep zone downstream tended to be generated by lower species richness in the shallow zone downstream compared to upstream for both Ephemeroptera and Plecoptera (Table 12; Fig. 18 and Fig. 19). The direction of this effect was the same for both seasons, but with a much higher magnitude for Plecoptera in November (interaction section × zone: $F_{1,16}$ = 2.12, p = 0.165), and for Ephemeroptera in June, though not season dependent (interaction section × zone: $F_{1,16}$ = 0.14, p =0.711). No marked differences in species richness were found between sections in the deep zone, except for Ephemeropteran species richness which were higher upstream in June (Table 12; Fig. 18 and Fig. 19). The effect of hydropeaking on the deep zones was thus season dependent for Ephemeroptera (interaction section × zone: $F_{1,16} = 3.57$, $p = 0.077$), but not for the Plecoptera (interaction section × zone: $F_{1,16} = 0.54$, $p = 0.473$).

Table 11. In the Bævra River, size of the effect ± SE of section (upstream/downstream) on the difference in average species richness (in logarithmic scale) between the shallow and deep the zone. The size of the effect is given by: (shallow minus deep zone upstream) minus (shallow minus deep zone downstream).

	Estimate ± SE	**t-value**	**p-value**
Ephemeroptera			
June	-0.02 ± 0.23	-0.92	0.919
November	-0.28 ± 0.25	-1.12	0.279
Plecoptera			
June	-0.0058 ± 0.22	-0.26	0.80
November	-0.61 ± 0.28	-2.23	0.040

Table 12. Comparison of the deep zones in the upstream and downstream section and of the shallow zones in the upstream and downstream section for Ephemeroptera and Plecoptera average species richness ± SE (in logarithmic scale) in the Bævra River. The estimates are considered relative to the upstream section.

	Deep zones			**Shallow zones**		
	Estimate ± SE	t-value	p-value	Estimate ± SE	t-value	p-value
Ephemeroptera						
June	0.36 ± 0.15	2.37	0.045	0.38 ± 0.17	2.24	0.056
November	1.05e-16 ± 0.11	0.00	1.00	0.28 ± 0.22	1.27	0.242
Plecoptera						
June	3.51e-17 ± 0.14	0.00	1.00	0.06 ± 0.17	0.33	0.748
November	-0.18 ± 0.19	-0.91	0.39	0.44 ± 0.20	2.23	0.056

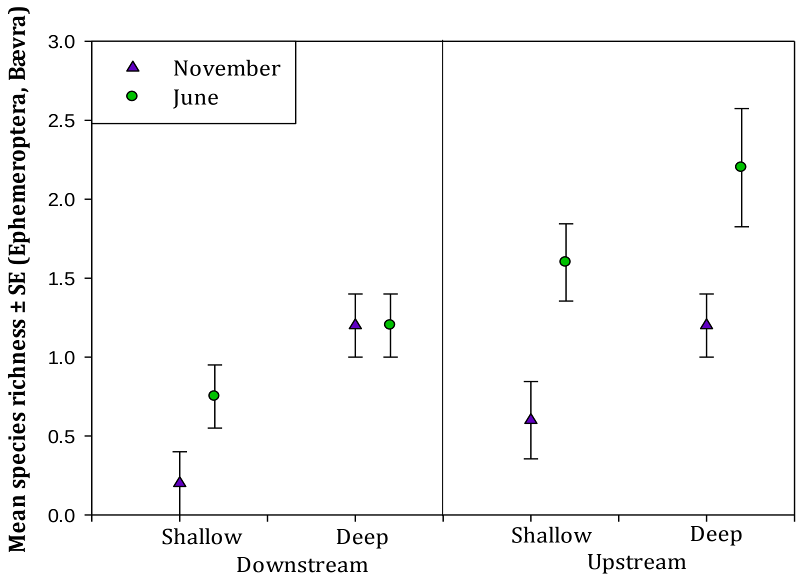

Figure 18. Ephemeroptera average species richness ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Bævra River.

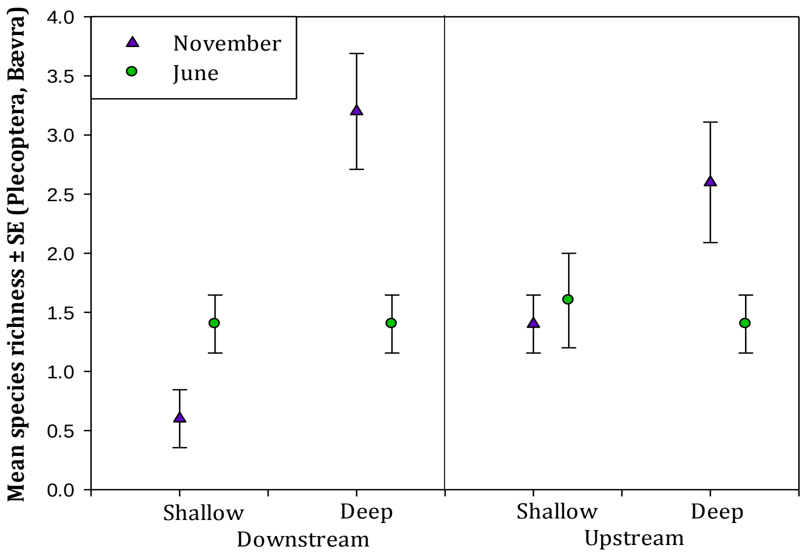

Figure 19. Plecoptera average species richness ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Bævra River.

3.4.2 River Lundesokna

The results of the comparison of the species richness between zones in the Lundesokna River do not exhibit marked differences between Ephemeroptera and Plecoptera. Species richness of both orders in the Lundesokna River was overall lower in the shallow than the deep zones in the downstream section, whereas in the upstream section this effect was not evident (Fig. 20 and Fig 21). Accordingly, the difference between the shallow and the deep zone was greater downstream than upstream for both Ephemeroptera and Plecoptera (Table 13; Fig. 20 and Fig. 21). The magnitude of this effect was, however, season dependent for Ephemeroptera (interaction section × zone × season: $F_{2,32}$ = 1.71, p = 0.196), but not for Plecoptera (interaction section × zone × season: $F_{2,32}$ = 0.55, p = 0.583).

The greater difference between shallow and deep zone downstream was generated by considerable lower species richness in the shallow zone downstream compared to upstream (Table 14; Fig. 20 and Fig. 21). The direction of this effect was the same for both seasons, but with a lower magnitude for Plecoptera in June. The magnitude of this effect was thus season dependent for Plecoptera (interaction section × zone: $F_{1,16}$ = 6.49, p = 0.022), but not for Ephemeroptera (interaction section × zone: $F_{1,16}$ = 0.85, p = 0.370). Considering the difference between the deep zones the species richness tended to be higher in the upstream section compared to the downstream section. The direction of this effect is in the same in both seasons, but with a much higher magnitude in October for both Ephemeroptera and Plecoptera. Accordingly, the difference between the deep zones was season dependent for both Ephemeroptera (interaction section × zone: $F_{1,16}$ =2.74, p = 0.117) and Plecoptera (interaction section × zone: $F_{1,16}$ = 10.05, p = 0.006).

Table 13. In the Lundesokna River, size of the effect ± SE of section (upstream/downstream) on the difference in average species richness (in logarithmic scale) between the shallow and the deep zone. The size of the effect is given by: (shallow minus deep zone upstream) minus (shallow minus deep zone downstream).

	Estimate ± SE	**t-value**	**p-value**
Ephemeroptera			
June	-1.67 ± 0.26	-6.51	<0.001
October	-1.00 ± 0.25	-4.02	<0.001
Plecoptera			
June	-0.92 ± 0.38	-2.42	0.028
October	-0.54 ± 0.30	-1.81	0.089

Table 14. In the Lundesokna River, average difference ± SE of the species richness (in logarithmic scale) between the deep zone in the upstream and downstream section, and between the shallow zone upstream and the shallow zone downstream. The estimates are considered relative to the upstream section.

	Deep zones			**Shallow zones**		
	Estimate ± SE	t-value	p-value	Estimate ± SE	t-value	p-value
Ephemeroptera						
June	0.07 ± 0.23	0.307	0.767	1.74 ± 0.12	16.2	<0.001
October	0.51 ± 0.13	3.94	0.004	1.52 ± 0.21	7.13	<0.001
Plecoptera						
June	0.06 ± 0.28	0.21	0.842	0.98 ± 0.26	3.77	0.005
October	1.23 ± 0.24	5.05	<0.001	1.78 ± 0.17	10.33	<0.001

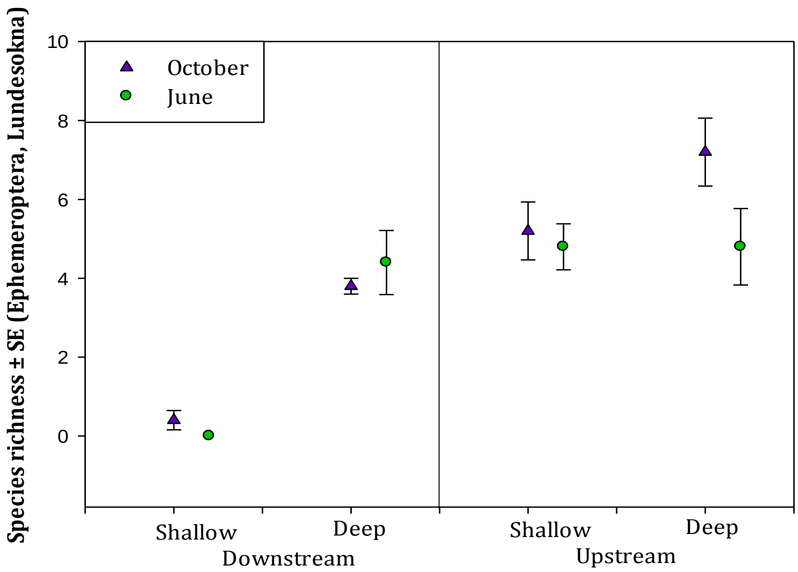

Figure 20. Ephemeroptera average species richness ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Lundesokna River. No individuals were sampled in shallow zone in the downstream section in June.

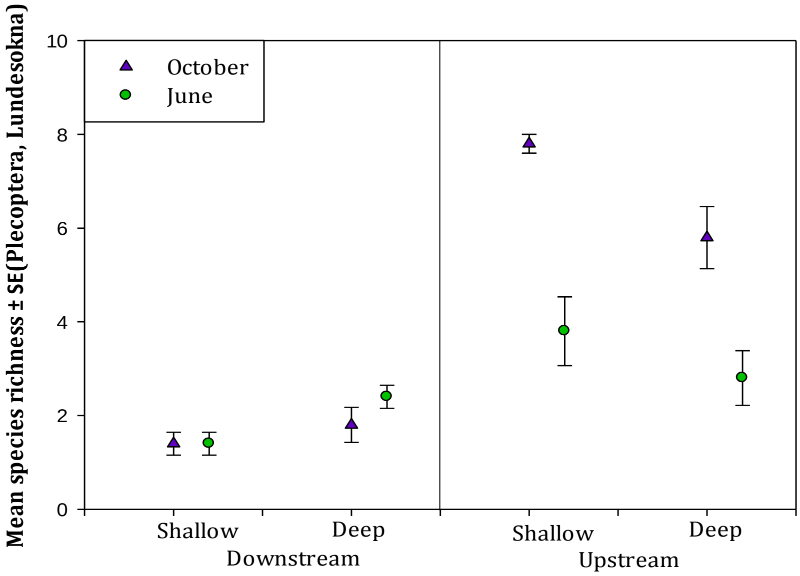

Figure 21. Plecoptera average species richness ± SE in shallow and deep zone, upstream and downstream of the hydropower station in the Lundesokna River.

3.5 Functional feeding groups

The proportional distribution of functional feeding groups of Plecopteran species in the Lundesokna River and the Bævra River are presented in Fig. 22 and Fig. 23. The distribution of functional feeding groups for Ephemeroptera is not included because almost all Ephemeropteran species sampled belong to the collector-gatherers/scrapers combination (Table 25; Appendix 3). Thus there was no variation across seasons and zones for Ephemeroptera. The functional feeding groups of Plecoptera, on the other hand, exhibit some variation across seasons and zones (Fig. 22 and Fig. 23).

The proportional distribution of functional feeding groups does not exhibit any clear difference between the Bævra River and the Lundesokna River (Fig. 22 and Fig. 23). Shredders seem to be present both in the deep zone and the shallow zone in the downstream section. The same is apparent for collector-gatherers in June (Fig. 22 and Fig. 23). Overall, scrapers and predators show some variation among the zones, but do not exhibit marked differences between upstream and downstream (Fig. 22 and Fig. 23).

Given that collector-filterers absent among Plecopteran species (Fig. 22 and Fig. 23), the occurrence of the collector-filterer Simulidae will represent this trait. In Lundesokna River, especially in October, there is low occurrence of Simulidae in the downstream section compared to the upstream section (Fig. 16; Appendix 1). However, in the Bævra River the differences are not that distinct (Fig. 15; Appendix 1).

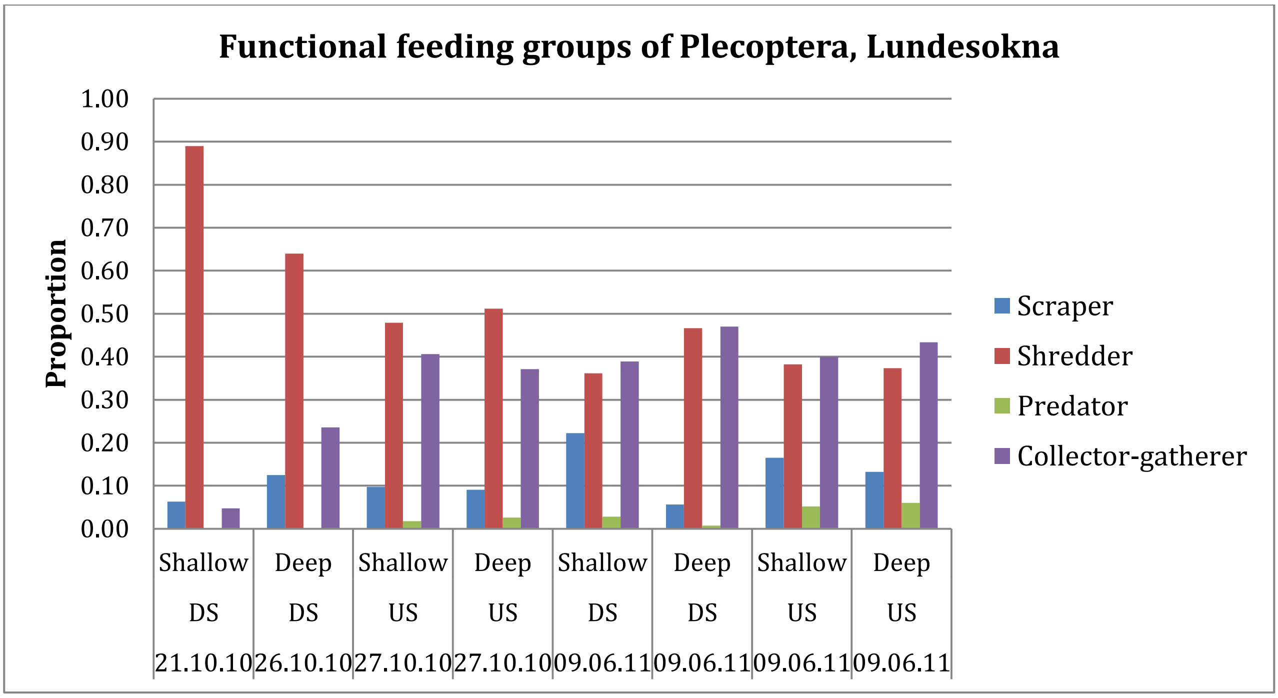

Figure 22. The proportional distribution of functional feeding groups of Plecoptera species in Lundesokna River in October 2010 and June 2011. DS = downstream, US = upstream.

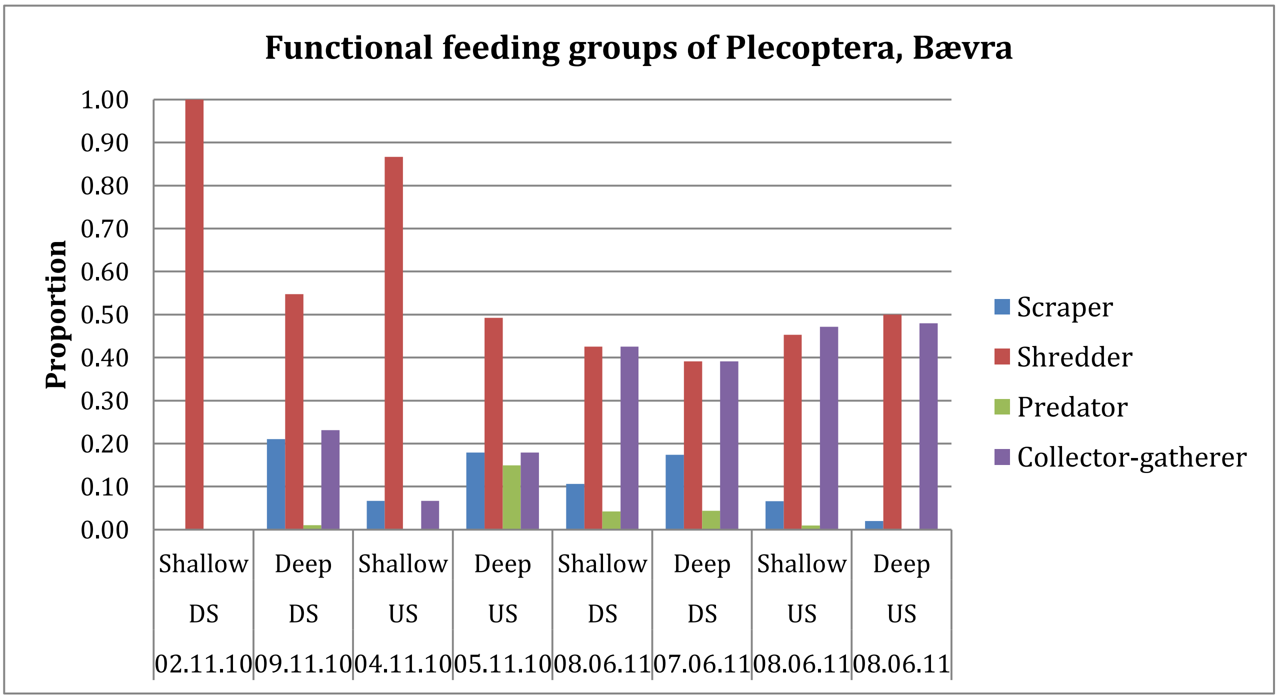

Figure 23. The proportional distribution of functional feeding groups of Plecoptera species in Bævra River in November 2010 and June 2011. DS = downstream, US = upstream.

4 DISCUSSION

The results of the current study denote that frequent and fast fluctuations due to hydropeaking events are negatively affecting the macroinvertebrate fauna. Overall, shallow zones, exposed to frequently dewatering, in the affected downstream section exhibit a reduction in total macroinvertebrate density and a reduction in density, diversity and species richness of Ephemeroptera and Plecoptera. This is demonstrated by an overall larger difference between shallow and the deep zone in the downstream section compared to the upstream section. Throughout the analyses this is due to lowered density, diversity and species richness in shallow zone in the downstream section compared to the shallow zone in the upstream section. By exposing the shallow zone in the downstream section to frequent drying, hydropeaking is the most likely cause of these findings.

In some of the analyses the great difference between the zones in the downstream section is further strengthened by a higher density, diversity and species richness in the permanently water covered zone downstream compared to upstream the outlet of the hydropower station. However, the comparisons of the deep zones upstream and downstream denote varying results. Only a small proportion of deep zones showed a reduction in density, diversity and species richness in the downstream section compared to the upstream section. Summing up, the results of the analyses suggest a marked negative effect of hydropeaking on makroinvertebrates in the frequently dewatered zone, whereas the macroinvertebrate fauna in the permanently water covered zone in the downstream section is less affected. The results are apparent for both the Lundesokna River and the Bævra River, and for total density and density, diversity and species richness of Plecoptera and Ephemeroptera

These effects, however, were in several of the analyses strongly dependent on the season. Indeed, the magnitude of the difference between zones differed in summer and autumn. Additionally, in some analyses the season effects differed between the Lundesokna River and the Bævra River. These findings could be an effect of life cycle induced differences in species composition between seasons (Table 15 and table 16; Appendix 1). Moreover, variations between rivers, like seasonal variations and difference in species composition, could affect the life cycle and thereby the timing of macroinvertebrate emergence. This demonstrates the importance of macroinvertebrate sampling throughout several seasons.

4.1 Evaluation of methods and design

In macroinvertebrate studies a Surber sampler, used in the current study, is often preferred. It represents a quantitative method and comparable replicates are easily obtained with this sampler. Compared to the kick-net-sampling the Surber sampler has shown to be beneficial by obtaining higher species richness and a higher number of low-occurrence taxa (Storey et al., 1991). Still it is important to keep in mind the limitations set by the Surber sampler. Species inhabiting the deepest and the shallowest part of the stream could be excluded because stream depth must be equal to or lower than the height of the sampler, simultaneously the depth must be deep enough for the water to flow through the sampler. Likewise, water velocity must neither be too high nor too low. However, in the current study it is not likely that the above mentioned weaknesses will affect the results. The substratum particle size is also a crucial factor when sampling location is chosen. The base of the sampler must be tightly fitted into the substrate, in order to avoid macroinvertebrates escaping through the space between the frame and the bottom. Course substrate in the upstream section in the Lundesokna River made the positioning of the sampler difficult, and this may cause underestimation of diversity, species richness and density. When using the Surber sampler, macroinvertebrates drifting from outside the sampling area could have been sampled. This could cause overestimation of diversity, species richness and density. Another possible source of error could be variation in the sampling effort due to differences between field workers.

The autumn samples in the current study were obtained in late October and early November. This timing was not optimal, especially for the Bævra River where ice formation had started in this period. This could potentially have influenced the result of the sampling, by underestimating density, diversity and species richness of the macroinvertebrates. Another possible source of error is the temporal and spatial variation in macroinvertebrate presence. The terrestrial and egg stage yields periods when some species are absent because of their synchronous life cycles, and not because of the hydropeaking. Likewise, the patchy distribution of the macroinvertebrates could make it difficult to get a representative samples of the macroinvertebrate fauna (Fjellheim, 1996).

4.2 The effect of hydropeaking on macroinvertebrates inhabiting the frequently dewatered zone in the downstream section

A number of studies have reported reduced density, variety and composition of benthic macroinvertebrates in the zone exposed to frequent dewatering and inundation (ramping zone) as an effect of pulse flows (Fisher and Lavoy, 1972; Humphries et al., 1996; McKinney et al., 1999). Troelstrup and Hergenrader (1990) showed a strong reduction in total density and number of taxa in the ramping zone compared to the permanently water covered zone in a stream exposed to fluctuating flow. However, in the absence of daily fluctuations they observed a sharp increase in total density and number of taxa in the ramping zone. Likewise, a study from Virginia, USA, documented lowered recolonization of the ramping zone when flows fluctuated daily (Perry and Perry, 1986). The current study confirms these previous results by revealing lowered density, diversity and species richness in the ramping zone compared to the permanently water covered deep zone in the downstream section, and compared to the shallow zone in the upstream section. This reduction is likely a result of the frequent change in discharge and the following dewatering of the ramping zone, which further could lead to stranding of invertebrates and degradation of the habitat (Cushman, 1985). Regarding the incidence of macroinvertebrate stranding, previous studies have reported variable results in rivers exposed to frequent fluctuations in flow. In a study by Patterson and Smokorowski (2011) stranding of invertebrates was visually observed during shutdown of the hydropower station in a hydropeaked river. On the other hand, in the Nidelva River, Norway, Arnekleiv et al. (1994) did not observe any increase in the rate of macroinvertebrate stranding in low flow periods. Low density and diversity of macroinvertebrates in the ramping zone, as a result of a degraded habitat, was suggested as an explanation for the absence of stranding. After several weeks of water cover, there were still no observations of increased macroinvertebrate density and diversity in the ramping zone. Accordingly, the zone was probably not preferred by the macroinvertebrates and thus a limited amount of stranding was observed.

Reduction in habitat suitability as a result of reduced occurrence of aquatic vegetation like alga, periphyton and macrophytes in the river-margin could hence explain the lowered diversity, species richness and density in the ramping zone in the current study (Johansen, 2000). The assessment of vegetation cover in the Lundesokna River and the Bævra River in June is based on a rather coarse scale, which makes it difficult to confirm a reduction of the aquatic vegetation in the ramping zone (Table 19-20 and table 23-24; Appendix 2). Nevertheless, reduction in the river-margin vegetation is a likely explanation for the lowered density, diversity and species richness in the ramping zone in the current study. Moreover, degradation of the ramping zone could also include clogging of the top layer of the channel sediments. Hypolimnentic water released from the dam will often transport fine sediments which will deposit in the interstitial space, and thereby impede the macroinvertebrates from using the hyporheic zone as refuge from dewatering and high flows. This could contribute to increased mortality in the ramping zone when the hydropower station is shut down (Bruno et al., 2009).

Furthermore, drift of macroinvertebrates from the river-margin during shutdown of the hydropower station could also contribute to the lowered macroinvertebrate density, diversity and species richness in the ramping zone. Arnekleiv et al. (1994) observed that macroinvertebrates, especially Ephemeroptera and Plecoptera, actively moved with the current when the hydropower station was shut down.

Both the Lundesokna River and the Bævra River exhibit lowered density, diversity and species richness in the shallow zone compared to deep zone downstream, but this relationship is more evident in the Lundesokna River. Naturally, the macroinvertebrate fauna in the Lundesokna River are more diverse and have a higher density compared to the Bævra River. This makes the results from the Bævra River more prone to chance effects. Furthermore, the results from the samples obtained in the Bævra River in November could have been influenced by bad sampling conditions. At the time of sampling ice formation had started, and this made the sampling difficult. Considering the results from the samples obtained in the Bævra River in June, it is important to keep in mind that water discharge was kept more or less at a constant high level in the month prior to sampling (Fig. 3). The ramping zone was hence less exposed to drying prior to sampling compared to the samplings in the Lundesokna River and the Bævra River in November. Since macroinvertebrates have a high colonization rate (Mackay, 1992), they could have started recolonization of the ramping zone during the time of high discharge prior to sampling.

Finally, alterations in abiotic and biotic factors in the downstream section and increased drift as an effect of increased discharge could contribute to differences in the macroinvertebrate fauna between the upstream and downstream section. See discussion below.

4.3 The effect of hydropeaking on macroinvertebrates inhabiting the downstream section

In the section above effects brought upon macroinvertebrates in the frequent dewatered zone are discussed. In the current chapter effects brought upon the permanent water covered area in the downstream section are also included, by discussing the effects of altered abiotic and biotic factors downstream the hydropower station. Because of these alterations macroinvertebrate density, diversity and species richness are predicted to display a reduction in the downstream section. This prediction is also based on previous studies, where negative effects on the macroinvertebrate fauna have been documented downstream of hydropeaked hydropower station (Cushman, 1985; Brittain and Saltveit, 1989; Cereghino and Lavandier, 1998b; Cereghino and Lavandier, 1998a; Cereghino et al., 2002).

However, these previous results are not fully supported by the results of the current study. In the comparison of the shallow zones upstream and downstream of the hydropower station there are clearly a higher density, diversity and species richness in the unaffected upstream section, but this is not the case in the comparison of the deep zones. The analyses of total density revealed either no difference between the deep zones upstream and downstream or higher total density in the downstream section. Regarding densities of Ephemeroptera and Plecoptera, approximately half of the analyses indicate a higher density in the deep zone upstream compared to the deep zone downstream. Moreover, less than half of the analyses demonstrate a higher diversity and species richness of Ephemeroptera and Plecoptera in the deep zone upstream compared to the deep zone downstream. Summing up, these results indicate that hydropeaking was not accompanied by a marked reduction in macroinvertebrate density, diversity and species richness in the permanently water covered zone downstream the hydropower station. Nevertheless, alterations in the macroinvertebrate fauna as an effect of altered abiotic and biotic factors downstream the hydropower stations cannot be excluded. However, based on these findings it is reasonable to assume that these factors have a minor effect on the macroinvertebrate fauna compared to the effect of dewatering of the ramping zone.

Other studies considering the permanently water covered zone downstream of the hydropower station in hydropeaked rivers, have made both similar and contradictory conclusions. A number of studies have documented negative effects on the macroinvertebrate fauna downstream of hydropeaked hydropower stations (Cushman, 1985; Brittain and Saltveit, 1989; Cereghino and Lavandier, 1998b; Cereghino and Lavandier, 1998a; Cereghino et al., 2002). These negative effects have been attributed to increased bed scour with subsequent increased drift of macroinvertebrates with the onset of the hydropower station (Bruno et al., 2010), altered temperature regime (Cereghino et al., 2002) and altered substrate conditions (Bruno et al., 2009). Yet, other studies have reported of no negative alterations of the macroinverterate fauna in the permanently water covered zone downstream of hydropeaked hydropower stations (Troelstrup and Hergenrader, 1990; Arnekleiv et al., 1994), which is concordant with the findings in this study. Fuller et al. (2011) even found higher macroinvertebrate densities downstream of a dam with frequent and severe flows compared to the downstream section of a run-of-river dam and an un-regulated river. Diversity, on the other hand, was highest downstream of the run-of-river dam and the un-regulated river. Several factors could possibly explain why the macroinvertebrate fauna in the deep zone appears to be little affected by frequent and fast flow fluctuations. Movement of macroinvertebrates from the less suitable ramping zone could contribute to higher densities of macroinvertebrates in the permanently water covered area downstream the hydropower station (Arnekleiv et al., 1994). Additionally, recolonization from upstream (drift), downstream (adult migration) and from the hyporheic zone could contribute to maintenance of densities in sites exposed to hydropeaking waves and subsequent catastrophic drift (Bruno et al., 2010).

Moreover, Cortes et al. (2002) suggested that habitat heterogeneity could act as a buffer against reduction in macroinvertebrate abundance and diversity in regulated streams, given that habitat heterogeneity is maintained. Habitat heterogeneity could also avert some of the unfortunate effects of high flows, by providing shelter (Matthaei et al., 2000). Additionally, the size of the substrate could be decisive for the preservation of density and variety of macroinvertebrates. The importance of grain size was demonstrated in a study from the Juma River, Beijing, where substrate composed of large particles had least change in taxa richness and macroinvertebrate composition over time (Duan et al., 2008). This indicates that substrate of big size are protective against disturbances. Several studies have also reported of increased species richness and density with increase in substrate size from sand to cobbles, and then decline in species richness and density when the substrate reach the size of boulder and bedrock (Minshall, 1984; Quinn and Hickey, 1990; Beisel et al., 1998). This relationship is suggested to be a result of increased stability of invertebrates and periphyton provided by large sized substrata (Quinn and Hickey, 1990). The assessment of the substrate in the current study is rather coarse, and it is therefore difficult to consider whether the habitat heterogeneity is preserved downstream of the hydropower stations. However, it is evident that the substrate in the permanently water covered zone downstream in both the Lundesokna River and the Bævra River is dominated by pebbles (2.0 – 6.0 cm), cobbles (6.0 – 12.0 cm) and stones (12.0 – 20.0 cm) (Appendix; Table 17-24). This course substrate could contribute to maintenance of macroinvertebrate density, diversity and species richness in the deep zone downstream of the hydropower station.

Regarding diversity and species richness, the results of the comparison of the deep zones upstream and downstream implies on average little difference between the zones. One possible explanation is that flow disturbance could be somewhat beneficial for diversity and species richness. McCabe and Gotelli (2000) tested the effects of disturbance on stream macroinvertebrate density and species richness. The highest average species richness was recorded at high-intensity and high-frequency disturbance, whereas the highest species density was recorded in undisturbed controls. This coincides with some scenarios from Hustons' dynamic-equilibrium model, which claims that different levels of disturbance could contribute in obtaining maximum diversity in a population. The level of disturbance that maximizes diversity is dependent upon the population growth and competitive displacement (McCabe and Gotelli, 2000). The diversity in populations with high growth rate and competition could benefit from high levels of disturbance. Most stream-living macroinvertebrates have a high growth rate (Mackay, 1992), and competition for food and space among macroinvertebrates has been demonstrated in a number of studies (McAuliffe, 1984; Dudley et al., 1990; Englund, 1991). Fluctuating flow caused by hydropeaking may reduce the dominance of competitive dominant species, and thereby contribute to higher diversity and species richness. The results in the current study do not exhibit an overall higher diversity or species richness in the deep zone downstream compared to upstream, but only a minority of the analyses indicate a reduction in the deep zone downstream compared to the deep zone upstream. Hence, possibly negative effects brought upon macroinvertebrate diversity and species richness in a river exposed by hydropeaking may be offset by the positive effects of disturbance.

Altered ice conditions in the winter season could possibly also affect macroinvertebrates in the downstream section of a hydropeaked hydropower station. The combination of fast and fluctuating flow together with frequent fluctuating temperature have shown to break up continuous ice cover along the shoreline and shorten the ice cover period, especially in areas near the outlet (Tjomsland and Bakken, 2012). Shorter period of ice cover and subsequent improved light conditions may accelerate the onset of the growing season for aquatic vegetation, and thereby improve habitat conditions for macroinvertebrates. This coincides with the findings of Koksvik and Reinertsen (2008). They demonstrated massive algal growth in an ice-free stretch in the Alta River, Norway, after regulation of the river. Simultaneously densities of the benthic fauna, especially of chironomids, increased. These observations were attributed to the improved light and nutrient condition following regulation, and the fact that alga function as food and shelter for macroinvertebrates.

4.4 The effect of hydropeaking on functional feeding groups

As an effect of different behavior and morphology, alterations in abiotic and biotic factors following hydropeaking could affect various functional feeding groups differently. In the current study functional feeding groups of Plecoptera is distributed differently between rivers, seasons and zones (Fig. 22 and Fig. 23). Since the sampled Ephemeropteran species almost exclusively consists of the scraper/collector-gatherer combination, it is impossible to connect their functional feeding group distribution to hydropeaking. They are therefore omitted from this discussion. Among the Plecopteran species, on the other hand, there is a broader representation of the functional feeding groups. It is apparent that shredders tolerate both the ramping zone and the permanently water covered zone in the downstream section in both rivers (Fig. 22 and Fig. 23). This finding is consistent with the finding of Englund and Malmqvist (1996), who found no effects on shredders inhabiting areas with high day-to-day variation in flow. One possible explanation is that shredders do not need to expose themselves to high flow in order to acquire food (Englund and Malmqvist, 1996). In addition, the downstream sites of both the Lundesokna River and the Bævra River are surrounded by trees providing supply of allochthonous material, which is an important food source for shredders. Considering the samples from June, also collector-gatherers seem to tolerate both zones in the downstream section (Fig. 22 and Fig. 23). In October/November, however, the ramping zone exhibits a low proportion of collector-gatherers in both rivers (Fig. 22 and Fig. 23). In a study by Troelstrup and Hergenrader (1990) it was suggested that collector-gatherers tolerated hydropeaking to some extent, but without fluctuation discharge collector-gatherers increased in the downstream section. The increase of collector-gatherers was attributed to the increased food availability when scouring of periphyton diminished. In the current study, it is difficult to explain the indication of low proportions of collector-gatherers in October/November in the ramping zone. In fact, it could simply be an effect of chance or a species-specific effect.

Furthermore, predators do not seem to exhibit any clear differences between zones and seasons (Fig. 22 and Fig. 23). This may indicate tolerance for all zones, but it may also be a result of chance, since only a small proportion of the sampled species is categorized as predators. Opposed to observations made by Troelstrup and Hergenrader (1990), the occurrence of scrapes seems to be more or less the same upstream and downstream of the hydropower station (Fig. 22 and Fig. 23). One possible explanation is that scrapers have morphological and behavioral adaptations that ensures stable position on surfaces exposed to high flow (Cummins and Klug, 1979). Moreover, two separate studies demonstrated that the scrapers *Baetis tricaudatus* and *Dicosmoecus gilvipes* were able to find food, even when periphyton where scarce and patchy distributed, by moving quickly in the search for patches of food (Hart, 1981; Kohler, 1984). This strong movement ability could contribute to their presence in the possibly periphyton scarce ramping zone. Since there were no collector-filterers among Ephemeroptera and Plecoptera, the distribution of Simulidae could represent this trait. In the Lundesokna River, Simulidae, exhibit low occurrence downstream the hydropower station (Table 16;

Appendix 1). Because collector-filterers often are exposed on top of stones and have fragile filtering devices, they could be negatively affected by frequently high flow (Englund and Malmqvist, 1996). However, in order to quantify the effect of collector-filterers, species of the collector-filterer rich order Trichoptera should have been considered.

Other differences between the functional feeding groups are observed, but these mostly look like seasonal effects and cannot be assigned to alterations in flow regime. Shredders have high occurrence in autumn compared to spring (Fig. 22 and Fig. 23). This could be an effect of leaf fall in autumn and thereby increased food availability for shredders (Hawkins and Sedell, 1981). Scarpers, on the other hand, is highly present in spring and summer (Fig. 22 and Fig. 23), probably as an effect of increased food availability of live plant tissue like alga. Even though no clear effect of hydropeaking were observed on any of the functional feeding groups, low densities of macroinvertebrates in the ramping zone could still reduce the functionality of this zone because of the overall reduction in functional feeding groups representation.

4.5 Species-specific effects

Even though there are minor differences in functional feeding groups between zones and the macroinvertebrate density, diversity and species richness show few differences between the deep zones upstream and downstream the hydropower station, there could be alterations in species composition. Table 15 and table 16 (Appendix 1) imply that species have different tolerance to the alterations generated by the peaking operations. These differences could be related to life history traits, functional feeding group characteristics or other species-specific traits.

Altered temperature regime could be one of the factors causing changes in species composition and occurrence downstream the hydropower station. In both the Lundesokna River and the Bævra River major variations in river temperature downstream the outlet is nicely matched up with hydropeaking events (Fig. 24-25 and Fig. 27-28; Appendix 4, must be viewed together with Fig. 2-3 and Fig. 5-6) In May/June the temperature downstream is increasing just as quickly as the hydropower station is shut down (Fig. 25 and Fig. 28; Appendix 4, must be viewed together with Fig. 3 and Fig.

6). In October we observe the opposite effect, the temperature is increasing when the hydropower station is turned on (Fig. 24 and Fig. 27; Appendix 4, must be viewed together with Fig. 2 and Fig. 5). This leads to quick and frequent changes in the temperature regime downstream of the hydropower station. An overall increase in winter temperature and reduction in summer temperature when water is released from hypolimnon is exactly as expected. Both the Lundesokna River and the Bævra River have hypolimnetic release, and exhibit low spring and early summer temperatures and high autumn and early winter temperature downstream compared to upstream the hydropower station (Fig. 26 and Fig. 29; Appendix 4). Mid-winter and mid-summer temperatures upstream and downstream are more or less the same (Fig. 26 and Fig. 29; Appendix 4).

4.5.1 Plecoptera

Diura nanseni are present in high densities in the upstream section compared to the downstream section in June, both in the Bævra River and the Lundesokna River (Table 15 and 16; Appendix 1). Since *D. nanseni* is highly temperature dependent (Raddum et al., 2005), this pattern could be explained by reduced temperature in spring and early summer downstream the outlet. In Aurlandvassdraget, Western Norway, eggs of *D. nanseni* hatched during July, and this will likely be similar in the Bævra River and in the Lundsokna River. If hatching is delayed, imiagines may not be able to finish their life cycle before the onset of winter (Stevens et al., 1997). However, low numbers of *D. nanseni* could also be a consequence of large sized larva (Raddum et al., 2005). Larva of large size is more prone to catastrophic drift with the onset of the hydropower station compared to larvae of small size (Bruno et al., 2010).

Capnia sp. and *Amphinemura borelis* seem to be unaffected by the alterations in temperature and discharge downstream the outlet (Table 15 and 16; Appendix 1). This is consistent with the findings in Aurlandvassdraget (Raddum et al., 2005). Furthermore, these species also appear to tolerate the harsh conditions in the ramping zone. Both *Capnia sp*. and *Amphinemura borelis* are small sized larvae, and could therefore likely use the hypoheric zone as a refuge when discharge is diminishing (Bruno et al., 2009).

4.5.2 Ephemeroptera

Ameletus inopinatus have low occurrence downstream the hydropower station in both rivers. This may be attributed to change in the natural flow regime. *A. inopinatus* prefer patches with slow flowing water, such as pools and margins of streams (Elliott and Humpesch, 2010). The sudden increase in flow at the downstream section may therefore restrict this species to the upstream section.

The densities of *Baetis rhodani* are lower downstream compared to upstream in the current study (Table 15 and 16; Appendix 1). This observation is consistent with the findings of a study from the hydropeaked watercourse Surna, Norway. Compared to the upstream section there was a major reduction in the number of *B. rhodani* in the downstream section, especially in the shallow area exposed to periodical dewatering. *B. rhodani* is characterized as a scraper and will therefore inhabit the substrate surface and thereby be exposed to sudden increase in discharge (Johnsen et al., 2010). On the other hand, *B. rhodani* appears to somewhat tolerate the harsh conditions downstream in the current study, by holding higher densities in the downstream section compared to most of the other species (Table 15 and 16; Appendix 1). This could possibly be explained by the flexible life cycle of *B. rhodani*, which enables adaption to a wide range of habitats and climates (Sand and Brittain, 2009). In a river 560 m. a.s.l. in western-Norway B. rhodani were found to be bivoltine (Baekken, 1981), whereas in the eastern part of Jotunheimen *B. rhodani* displayed a univoltine life cycle 1090 m a.s.l. and a semivoltine life cycle 1100-1300 m a.s.l. (Sand and Brittain, 2009). The altered temperature regime downstream in the hydropeaked rivers in the current study may therefore not be conclusive for the presence of *B. rhodani*. The fact that *B. rhodani* is characterised as a swimmer could additionally contribute to its recolonization of the ramping zone after a low flow period (Elliott et al., 1988; Mackay, 1992).

The reason for the presence and non-presence of species in the different zones in these the Lundesokna River and the Bævra River are only speculations, but the fact that the composition of macroinvertebrate species is altered upstream and downstream of the hydropower station is certain (Table 15 and 16; Appendix 1). Seen in a wider perspective, these alterations will not only affect the macroinvertebrate fauna, but could also have consequences further up in the food chain. The composition of macroinvertebrate species and their presence in particular periods of the year, are crucial for the food availability for fish. Density alone cannot be used as a measurement for food quality or quantity for fish. However, since some macroinvertebrate species are preferred over others, the species composition of macroinvertebrates is crucial for the food availability for fish. Furthermore, food availability in the shallow areas of the river is especially important for yearlings which inhabit these areas (Johnsen et al., 2010).

5 CONCLUDING REMARKS AND FUTURE IMPLICATIONS

The results of the current study show that frequent dewatering of the shallow areas in the river causes reduction in total macroinvertebrate density and density, diversity and species richness of the Ephemeroptera and Plecoptera. It is reasonable to assume that the frequent fluctuations caused by hydropeaking prevent establishment of normal benthic macroinvertebrate communities in the exposed shallow zone. The permanently water covered area in the downstream section, on the other hand, do neither display an overall reduction in total macroinvertebrate density, nor a reduction in density, diversity and species richness of the Ephemeroptera and Plecoptera. The minor alterations found in the permanently water covered zone may testify the importance of keeping a stable minimum flow downstream the hydropower station in rivers with a small catchment area. Even though there are no requirements of minimum flow in the Lundesokna River and in the Bævra River, both have large catchment areas providing the section downstream the hydropower station with water. However, although density, diversity and species richness showed minimal differences between the deep zones upstream and downstream of the hydropower station, some species display clear differences (Table 15 and 16; Appendix 1). In the long-term, an altered and diluted macroinvertebrate fauna could as stated earlier have consequences further up in the food chain (Johnsen et al., 2010).

For future surveys, a suggestion would be to examine whether restriction on the rate of flow change could mitigate the negative effects experienced by macroinvertebrates occupying the ramping zone. With a slower ramping rate aquatic organisms may have the time to respond to the change in flow by moving with the current and thereby prevent stranding. Halleraker et al. (2003) investigated this in relation to fish, and found a significant decrease in stranding of trout fry with a decrease in dewatered speed. However, for trout the magnitude of stranding was dependent on the water temperature. Likewise, it would have been interesting to examine whether the macroinvertebrate sensitivity to hydropeaking are dependent on season. In the current study the magnitude of the hydropeaking effect is in several analyses dependent on season, but it is not clear why this is observed. It would have been valuable to further examine whether season is decisive for the hydropeaking effect on macroinvertebrates, including both egg and nymphal stage.

Hydropower production by the use of hydropeaking is likely increasing in coming years. In order to provide environmental guidelines for the hydropower industry, it is therefore essential to increase the understanding of how changes brought upon hydropeaked rivers affect the aquatic ecosystem.

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7 APPENDIX

Appendix 1: Sampled taxonomic groups

Table 15. Density ± SD of Ephemeroptera and Plecoptera species in the shallow and deep zones, upstream and downstream of the hydropower station in the Bævra River in November and June.

Bævra	Date: 02.11.10	Date: 09.11.10	Date: 04.11.10	Date: 05.11.10	Date: 08.06.11	Date: 07.06.11	Date: 08.06.11	Date: 08.06.11
Taxonomic group	Downstream		Upstream		Downstream		Upstream	
	Shallow zone	Deep zone	Shallow zone	Deep zone	Shallow zone	Deep zone	Shallow zone	Deep zone
	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)
Plecoptera								
Diura nanseni		2.22 (4.97)		20 (24.09)	4.44 (9.94)			
Isoperla sp						2.22 (4.97)		
Brachyptera risi						4.44 (6.09)		
Siphonoperla burmeisteri				2.22 (4.97)			4.44 (6.09)	
Amphinemura sp.		22.22 (0)		4.44 (9.94)	4.44 (6.09)	4.44 (9.94)	8.89 (9.3)	4.44 (6.09)
Amphinemura borealis		6.67 (9.94)	2.22 (4.97)	17.78 (24.34)	37.78 (30.02)	15.56 (16.85)	95.56 (44.86)	102.22 (83.3)
Amphinemura sulcicollis					2.22 (4.97)		2.22 (4.97)	
Nemuridae indet.		20 (16.48)						
Nemoura sp.			2.22 (4.97)					
Capnia sp.	6.67 (6.09)	64.44 (33.7)	24.44 (9.3)	48.89 (31.03)				

Bævra Taxonomic group	Date: 02.11.10	Date: 09.11.10	Date: 04.11.10	Date: 05.11.10	Date: 08.06.11	Date: 07.06.11	Date: 08.06.11	Date: 08.06.11
	Downstream		**Upstream**		**Downstream**		**Upstream**	
	Shallow zone	**Deep zone**	**Shallow zone**	**Deep zone**	**Shallow zone**	**Deep zone**	**Shallow zone**	**Deep zone**
	Density (SD)	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**
Leuctra sp.				2.22 (4.97)				4.44 (6.09)
Leuctra fusca		2.22 (4.97)						
Total Plecoptera	6.67 (6.09)	117.78 (36.51)	28.89 (14.91)	95.56 (66.94)	48.89 (34.78)	26.67 (16.85)	111.11 (48.43)	111.11 (83.15)
Ephemeroptera								
Ameletus inopinatus		4.44 (9.94)	11.11 (13.61)	2.22 (4.97)				8.89 (9.3)
Baetis muticus					4.44 (6.09)	2.22 (4.97)	6.67 (14.91)	6.67 (6.09)
Baetis rhodani	2.22 (4.97)	111.11 (29.4)		37.78 (18.59)	13.33 (24.09)	37.78 (9.94)	71.11 (41.28)	73.33 (59.11)
Heptagenia dalecarlica							4.44 (6.09)	
Total Ephemeroptera	2.22 (4.97)	115.56 (29.48)	11.11 (13.61)	40 (18.59)	17.78 (21.66)	40 (6.09)	82.22 (44.17)	88.89 (66.67)
Other taxa groups								
Collembola			2.22 (4.97)					
Nematoda				2.22 (4.97)				
Oligochaeta	220 (113.15)	37.4 (497.93)	177.78 (93.95)	153.33 (87.63)	68.89 (55.78)	28.89 (21.66)	11.11 (11.11)	6.67 (6.09)
Hydrachnidae		6 (29.81)	2.78 (5.56)	6.67 (9.94)		2.22 (4.97)		2.22 (4.97)
Coleoptera				2.22 (4.97)				
Elmidae				8.89 (9.3)				
Hydraenidae								4.44 (9.94)

Bævra Taxonomic group	Date: 02.11.10	Date: 09.11.10	Date: 04.11.10	Date: 05.11.10	Date: 08.06.11	Date: 07.06.11	Date: 08.06.11	Date: 08.06.11
	Downstream		**Upstream**		**Downstream**		**Upstream**	
	Shallow zone	**Deep zone**	**Shallow zone**	**Deep zone**	**Shallow zone**	**Deep zone**	**Shallow zone**	**Deep zone**
	Density (SD)	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**
Trichoptera	6.67 (9.94)	1.67 (13.61)		62.22 (65.55)	2.22 (4.97)		4.44 (9.94)	4.44 (6.09)
Diptera	2.22 (4.97)	4 (33.88)	8.33 (5.56)	8.89 (9.3)			4.44 (9.94)	4.44 (6.09)
Simulidae		1 (4.97)	4.44 (9.94)		35.56 (21.37)	1646.67 (675.93)	113.33 (216.37)	377.78 (474.99)
Ceratopogonidae	13.33 (14.49)	15.8 (31.82)	2.22 (4.97)			2.22 (4.97)		4.44 (9.94)
Chironomidae			20 (38.81)	297.78 (249.74)	75.56 (44.03)	82.22 (51.88)	235.56 (43.32)	235.56 (84.4)
Tipulidae	2.22 (4.97)		5.56 (6.42)					
Heteroptera			11.11 (13.61)	37.78 (18.59)				
Magaloptera				2.22 (4.97)				
Total	253.33 (131.33)	857.78 (509.62)	235.56 (92.76)	704,44 (261,60)	248.89 (90.81)	1835.56 (677.75)	544.44 (235.44)	846.67 (607.99)

Table 16. Density ± SD of Ephemeroptera and Plecoptera species in the shallow and deep zones, upstream and downstream of the hydropower station in theLundesokna River in October and June.

Lundesokna **Taxonomic group**	**Date: 21.10.10**	**Date: 26.10.10**	**Date: 27.10.10**	**Date: 27.10.10**	**Date: 09.06.11**	**Date: 09.06.11**	**Date: 09.06.11**	**Date: 09.06.11**
	Downstream		**Upstream**		**Downstream**		**Upstream**	
	Shallow zone	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**
	Density (SD)	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**
Pelcoptera								
Diura nanensi			48.89 (49.44)	42.22 (27.67)		2.22 (4.97)	6.67 (9.94)	2.22 (4.97)
Isoperla sp.			2.22 (4.97)	2.22 (4.97)				4.44 (6.09)
Siphonoperla burmeisteri			4.44 (6.09)	11.11 (11.11)	4.44 (6.09)	2.22 (4.97)	6.67 (6.09)	4.44 (6.09)
Brachyptera risi		2.22 (4.97)	31.11 (9.3)	22.22 (22.22)			6.67 (6.09)	2.22 (4.97)
Taeniopteryx nebulosa	4.44 (6.09)	4.44 (9.94)	15.56 (16.85)	13.33 (18.26)				
Amphinemura sp.	4.44 (9.94)	126.67 (67.86)	191.11 (172.02)	102.22 (61.06)	31.11 (4.97)	31.11 (21.37)	22.22 (13.61)	15.56 (23.04)
Amphinemura borealis	4.44 (9.94)	124.44 (130.86)	922.22 (586.21)	486.67 (388.6)	26.67 (12.67)	211.11 (64.79)	40 (6.09)	40 (44.86)
Amphinemura standfussi							2.22 (4.97)	
Protonemura meyeri			2.22 (4.97)				2.22 (4.97)	
Nemouridae indet.	4.44 (9.94)	8.89 (4.97)						
Nemoura sp.	4.44 (6.09)	2.22 (4.97)	6.67 (9.94)					
Nemurella pictetii			2.22 (4.97)					

Lundesokna **Taxonomic group**	**Date: 21.10.10**	**Date: 26.10.10**	**Date: 27.10.10**	**Date: 27.10.10**	**Date: 09.06.11**	**Date: 09.06.11**	**Date: 09.06.11**	**Date: 09.06.11**
	Downstream		**Upstream**		**Downstream**		**Upstream**	
	Shallow zone	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**
	Density (SD)	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**
Capnia sp.	228.89 (23.04)	448.89 (138.91)	204.44 (178.92)	351.11 (279.06)				
Capnopsis schilleri		2.22 (4.97)	6.67 (6.09)	2.22 (4.97)				
Capnia pygmaea			11.11 (24.85)					
Leuctra sp.		4.44 (6.09)	106.67 (60.14)	115.56 (71.41)		33.33 (26.06)	31.11 (46.75)	13.33 (14.49)
Leutra nigra			13.33 (24.09)	11.11 (11.11)				
Total Plecoptera	251.11 (28.97)	724.44 (333.56)	1568.89 (872.71)	1160 (755.09)	62.22 (12.67)	280 (105.53)	117.78 (66.48)	82.22 (42.02)
Ephemeroptera								
Siphlonurus sp.							2.22 (4.97)	
Ameletus inopinatus	2.22 (4.97)	2.22 (4.97)	17.78 (12.67)	93.33 (36.51)		2.22 (4.97)	57.78 (116.9)	4.44 (6.09)
Baetidae indet.						2.22 (4.97)		2.22 (4.97)
Baetis sp.								8.89 (19.88)
Baetis fuscatus/scambus						11.11 (11.11)	2.22 (4.97)	6.67 (9.94)
Baetis muticus		2.22 (4.97)	115.56 (61.16)	95.56 (73.95)		6.67 (6.09)	251.11 (155.28)	228.89 (125.12)
Beatis niger				8.89 (9.3)				2.22 (4.97)
Baetis rhodani	2.22 (4.97)	75.56 (90.4)	784.44	824.44		17.78	122.22	215.56

Lundesokna Taxonomic group	Date: 21.10.10	Date: 26.10.10	Date: 27.10.10	Date: 27.10.10	Date: 09.06.11	Date: 09.06.11	Date: 09.06.11	Date: 09.06.11
	Downstream		**Upstream**		**Downstream**		**Upstream**	
	Shallow zone	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**
	Density (SD)	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**
			(374.46)	(368.3)		(16.85)	(110.27)	(111.28)
Heptagenia sp.		6.67 (14.91)	4.44 (9.94)	31.11 (29.81)		2.22 (4.97)	13.33 (14.49)	6.67 (9.94)
Heptagenia dalecarlica	2.22 (4.97)	20 (21.37)	13.33 (18.26)	66.67 (32.39)		26.67 (35.66)	13.33 (9.3)	35.56 (18.26)
Heptagenia joernensis						2.22 (4.97)	2.22 (4.97)	11.11 (15.71)
Ephemerella sp.		2.22 (4.97)						
Ephemerella aurivillii		28.89 (23.04)	55.56 (71.58)	60 (44.17)		6.67 (9.94)	4.44 (6.09)	
Ephemerella mucronata		51.11 (42.75)	6.67 (6.09)	15.56 (12.67)		4.44 (6.09)	2.22 (4.97)	
Leptophlebia sp.						2.22 (4.97)		2.22 (4.97)
Leptophlebiidae indet.			2.22 (4.97)	24.44 (19.88)				
Centroptilum luteolum				8.89 (14.49)				
Total Ephemeroptera	6.67 (6.09)	188.89 (112.87)	1000 (332.22)	1228.89 (448.08)		84.44 (46.21)	471.11 (315.41)	524.44 (111.78)
Other taxa groups								
Turbellaria			4.44 (6.09)					
Nematoda		6.67 (6.09)			2.22 (4.97)	2.22 (4.97)	2.22 (4.97)	8.89 (14.49)
Bivalvia	2.22 (4.97)	2.22 (4.97)						

Lundesokna Taxonomic group	Date: 21.10.10	Date: 26.10.10	Date: 27.10.10	Date: 27.10.10	Date: 09.06.11	Date: 09.06.11	Date: 09.06.11	Date: 09.06.11
	Downstream		**Upstream**		**Downstream**		**Upstream**	
	Shallow zone	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**	**Shallow zone**	**Deep Zone**
	Density (SD)	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**	**Density (SD)**
Sphaeriidae	2.22 (4.97)							
Gastropoda	66.67 (118.37)	20 (19.88)						
Lymnaeidae	6.67 (6.09)	2.22 (4.97)			2.22 (4.97)			
Planorbidae	4.44 (6.09)	64.44 (49.94)			2.22 (4.97)	4.44 (6.09)		2.22 (4.97)
Oligochaeta	2313.33 (1389.1)	2324.44 (1656.42)	248.89 (117.48)	148.89 (77.22)	293.33 (108.47)	211.11 (36)	151.11 (121.87)	166.67 (130.76)
Hydrachnidae		13.33 (29.81)	48.89 (35.66)	195.56 (144.36)	6.67 (9.94)	6.67 (9.94)	2.22 (4.97)	4.44 (9.94)
Coleoptera					22.22 (22.22)	122.22 (116.53)	40 (42.02)	51.11 (35.66)
Elmidae		55.56 (60.35)	28.89 (36.51)	93.33 (52.47)				
Hydrophilidae				2.22 (4.97)				
Hydraenidae			73.33 (44.86)	22.22 (32.39)				
Trichoptera	20 (19.88)	288.89 (134.26)	324.44 (250.6)	786.67 (452.8)	4.44 (6.09)	13.33 (14.49)	20 (24.09)	53.33 (33.7)
Diptera			24.44 (21.37)	22.22 (7.86)	17.78 (14.91)	31.11 (21.37)	8.89 (9.3)	15.56 (23.04)
Tipulidae		4.44 (9.94)						
Ceratopogonidae	8.89 (14.49)	4.44 (6.09)	8.89 (4.97)	8.89 (9.3)	4.44 (6.09)	2.22 (4.97)	6.67 (9.94)	

Lundesokna Taxonomic group	Date: 21.10.10	Date: 26.10.10	Date: 27.10.10	Date: 27.10.10	Date: 09.06.11	Date: 09.06.11	Date: 09.06.11	Date: 09.06.11
	Downstream		Upstream		Downstream		Upstream	
	Shallow zone	Deep Zone	Shallow zone	Deep Zone	Shallow zone	Deep Zone	Shallow zone	Deep Zone
	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)	Density (SD)
Chironomidae	57.78 (34.61)	12080 (6191.5)	455.56 (343.1)	575.56 (513.24)	88.89 (60.35)	1062.22 (549.56)	97.78 (47.4)	104.44 (45.54)
Empididae		146.67 (104.05)						
Limnoniidae		4.44 (9.94)						
Simuliidae		8.89 (4.97)	40 (20.18)	8.89 (9.3)	11.11 (11.11)	2.22 (4.97)	264.44 (297.77)	646.67 (705.68)
Psychodidae			291.11 (240.16)	33.33 (22.22)				
Total	2657.78 (1297.25)	15928.89 (8063.54)	4117.78 (1374.85)	3421.11 (2347.47)	517.78 (178.75)	1822.22 (686.38)	1498.22 (1204.69)	1662.22 (825.47)

Appendix 2: Environmental data

Table 17. Overview of measurements of dominant and sub-dominant substrate, velocity and depth in each sampling unit in the downstream the hydropower station in Bævra in November. Bryophyte and algae per cent coverage were not obtained for this sampling. Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 02.11.10					Date: 09.11.10				
	Downstream, Shallow zone					Downstream, Deep zone				
Sample	**1**	**2**	**3**	**6**	**7**	**1**	**2**	**4**	**5**	**6**
Substrate D.	Cobbles	Stones	Cobbles	Stones	Cobbles	Cobbles	Stones	Cobbles	Cobbles	Cobbles
Substrate SD.	Pebbles	Cobbles	Pebbles	Cobbles	Pebbles	Pebbles	Cobbles	Pebbles	Stones	Pebbles
Velocity (m^3/s)	0.26	0.33	0.13	0.47	0.28	0.20	0.14	0.08	0.10	0.27
Depth (cm)	20.00	15.00	14.00	21.00	15.00	28.00	20.00	27.00	29.00	32.00

Table 18. Overview of measurements of dominant and sub-dominant substrate, velocity and depth in each sampling unit upstream the hydropower station in Bævra in November. Bryophyte and algae per cent coverage were not obtained for this sampling Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 04.11.2010					Date: 05.11.2010				
	Upstream, Shallow zone					Upstream, Deep zone				
Sample	**2**	**4**	**5**	**6**	**7**	**1**	**2**	**4**	**5**	**6**
Substrate D.	Cobbles	Stones	Cobbles	Stones	Stones	Stones	Cobbles	Cobbles	Stones	Stones
Substrate SD.	Stones	Cobbles	Pebbles	Cobbles	Cobbles	Cobbles	Pebbles	Stones	Boulders	Boulders
Velocity (m^3/s)	0.61	0.68	0.70	0.47	0.67	0.56	0.45	0.34	0.06	0.64
Depth (cm)	31.00	34.00	30.00	30.00	36.00	33.00	35.00	37.00	46.00	38.00

Table 19. Overview of measurements of dominant and sub-dominant substrate, bryophyte and algae per cent coverage, velocity and depth in each sampling unit in the downstream section in Bævra in June. Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 08.06.11					**Date: 07.06.11**				
	Downstream, Shallow zone					**Downstream, Deep zone**				
Sample	**1**	**2**	**3**	**6**	**7**	**1**	**2**	**3**	**5**	**6**
Substrate D.	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones
Substrate SD.	Pebbles	Pebbles	Pebbles	Pebbles	Sand	Pebbles	Sand	Sand	Sand	Pebbles
Bryophytes (%)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Alga (%)	100	100	100	100	100	100	100	100	100	100
Velocity (m^3/s)	0.26	0.31	0.28	0.33	0.32	0.29	0.58	0.63	0.63	0.76
Depth (cm)	16.00	13.00	19.00	22.00	21.00	19.00	25.00	31.00	35.00	32.00

Table 20. Overview of measurements of dominant and sub-dominant substrate, bryophyte and algae per cent coverage, velocity and depth in each sampling unit upstream the hydropower station in Bævra in June. Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 07.06.11					**Date: 07.06.11**				
	Upstream, Shallow zone					**Upstream, Deep zone**				
Sample	**1**	**3**	**4**	**6**	**7**	**2**	**4**	**5**	**6**	**7**
Substrate D.	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones
Substrate SD.	Pebbles	Pebbles	Pebbles	Pebbles	Sand	Sand	Pebbles	Pebbles	Pebbles	Pebbles
Bryophytes (%)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Alga (%)	100	100	100	100	100	100	100	100	100	100
Velocity (m^3/s)	0.42	0.15	0.45	0.21	0.57	0.84	0.47	0.28	0.63	0.53
Depth (cm)	19.00	19.00	18.00	19.00	25.00	30.00	34.00	29.00	30.00	40.00

Table 21. Overview of measurements of dominant and sub-dominant substrate, velocity and depth in each sampling unit downstream the hydropower station in the Lundesokna River in October. Bryophyte and algae per cent coverage were not obtained for this sampling Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 21.10.10					**Date: 26.10.10**				
	Downstream, Shallow zone					**Downstream, Deep zone**				
Sample	**1**	**2**	**3**	**4**	**5**	**1**	**3**	**4**	**5**	**6**
Substrate D.	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones
Substrate SD.	Cobbles	Cobbles	Cobbles	Cobbles	Cobbles	Cobbles	Cobbles	Cobbles	Cobbles	Cobbles
Velocity (m^3/s)	0.58	0.65	0.75	0.60	0.65	0.39	0.13	0.25	0.29	0.30
Depth (cm)	25.00	27.00	25.00	28.00	26.00	25.00	28.00	30.00	39.00	29.00

Table 22. Overview of measurements of dominant and sub-dominant substrate, velocity and depth in each sampling unit in the upstream the hydropower station in the Lundesokna River in October. Bryophyte and algae per cent coverage were not obtained for this sampling. Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 27.10.2010					**Date: 27.10.2010**				
	Upstream, Shallow zone					**Upstream, Deep zone**				
Sample	**2**	**3**	**4**	**6**	**7**	**1**	**2**	**3**	**4**	**7**
Substrate D.	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones	Stones
Substrate SD.	Boulders	Boulders	Boulders	Boulders	Boulders	Gravel	Gravel	Gravel	Gravel	Gravel
Velocity (m^3/s)	0.64	0.49	0.78	0.36	0.57	0.31	0.37	0.45	0.37	0.35
Depth (cm)	13.00	13.00	16.00	14.00	14.00	41.00	39.00	38.00	29.00	31.00

Table 23. Overview of measurements of dominant and sub-dominant substrate, bryophyte and algae per cent coverage, velocity and depth in each sampling unit downstream the hydropower station in the Lundesokna River in June. Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 09.06.11					**Date: 09.06.11**				
	Downstream, Shallow zone					**Downstream, Deep zone**				
Sample	**2**	**3**	**4**	**6**	**7**	**1**	**2**	**3**	**4**	**6**
Substrate D.	Stones	Stones	Stones	Fine gravel	Fine gravel	Stones	Stones	Stones	Pebbles	Stones
Substrate SD.	Fine gravel	Fine gravel	Fine gravel	Stones	Stones	Pebbles	Fine gravel	Pebbles	Stones	Pebbles
Bryophytes (%)	< 25	< 25	< 25	< 25	< 25	25-50	25-50	25-50	25-50	50-75
Alga (%)	25-50	25-50	25-50	25-50	25-50	< 25	< 25	< 25	< 25	< 25
Velocity (m^3/s)	0.69	0.97	0.81	0.85	1.14	0.13	0.19	0.19	0.13	0.13
Depth (cm)	27.00	28.00	30.00	29.00	30.00	15.00	10.00	15.00	17.00	13.00

Table 24. Overview of measurements of dominant and sub-dominant substrate, bryophyte and algae per cent coverage, velocity and depth in each sampling unit upstream the hydropower station in the Lundesokna River in June. Substrate D. = Dominant substrate, Substrate SD. = Sub-dominant substrate.

	Date: 09.06.11					**Date: 09.06.11**				
	Upstream, Shallow zone					**Upstream, Deep zone**				
Sample	**1**	**2**	**5**	**6**	**7**	**3**	**4**	**5**	**6**	**7**
Substrate D.	Pebbles	Stones	Stones	Pebbles	Stones	Stones	Stones	Stones	Stones	Stones
Substrate SD.	Stones	Pebbles	Pebbles	Stones	Pebbles	Pebbles	Pebbles	Pebbles	Pebbles	Pebbles
Bryophytes (%)	< 25	< 25	0.00	0.00	0.00	0.00	< 25	< 25	0.00	0.00
Alga (%)	< 25	< 25	< 25	0.00	0.00	< 25	< 25	< 25	< 25	< 25
Velocity (m^3/s)	0.40	0.41	0.45	0.16	0.32	0.52	0.38	0.47	0.33	0.33
Depth (cm)	16.00	13.00	14.00	11.00	12.00	23.00	17.00	26.00	20.00	20.00

Appendix 3: Functional feeding groups

Table 25. Functional feeding groups of Ephemeroptera and Plecoptera species. Sc = scraper, P= Predator, CG = Collector-gatherer, Sh = Shredder.

Pelcoptera	**Functional group**
Diura nanensi	Sc/P
Isoperla sp.	CG/P
Siphonoperla burmeisteri	CG/Sc/P
Brachyptera risi	Sc
Siphonoperla burmeisteri	CG/Sc/P
Taeniopteryx nebulosa	CG/Sc/Sh
Amphinemura sp.	CG/Sc/Sh
Amphinemura borealis	CG/Sh
Amphinemura standfussi	CG/Sh
Amphinemura sulcicollis	CG/Sc/Sh
Protonemura meyeri	Sh
Nemouridae indet.	CG/Sc/Sh
Nemoura sp.	Sc/Sh
Nemurella pictetii	Sc/Sh
Capnia sp.	Sh
Capnopsis schilleri	Sh
Capnia pygmaea	Sh
Leuctra sp.	CG/Sh
Leuctra fusca	CG/Sh
Leutra nigra	CG/Sh
Ephemeroptera	
Siphlonurus sp.	CG/Sc/Sh/P
Ameletus inopinatus	CG/Sc
Baetidae indet.	CG/Sc
Baetis sp.	CG/Sc
Baetis fuscatus/scambus	CG/Sc
Baetis muticus	CG/Sc
Beatis niger	CG/Sc
Baetis rhodani	CG/Sc
Heptagenia sp.	CG/Sc
Heptagenia dalecarlica	CG/Sc
Heptagenia joernensis	CG/Sc
Ephemerella sp.	CG/Sc
Ephemerella aurivillii	CG/Sc
Ephemerella mucronata	CG/Sc
Leptophlebia sp.	CG/Sc/Sh
Leptophlebiidae indet.	CG/Sc/Sh
Centroptilum luteolum	CG/Sc

Appendix 4: Temperatures upstream and downstream of the hydropower stations

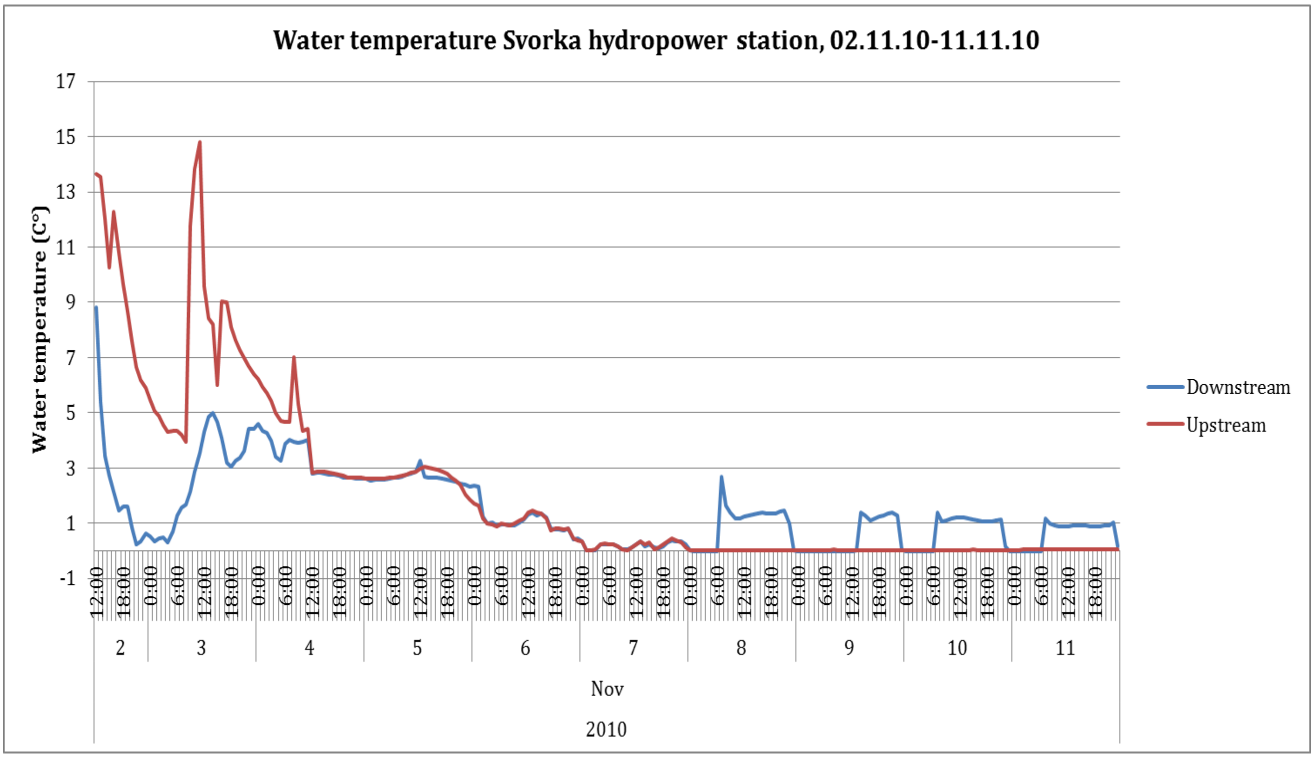

Figure 24. Overview of the water temperature downstream and upstream of Svorka hydropower station in the autumn sampling period. Temperature data prior to the sampling period are missing. Data were obtained from Norwegian institute for nature research (NINA) and The Freshwater Ecology & Inland Fisheries Laboratory (LFI), Trondheim.

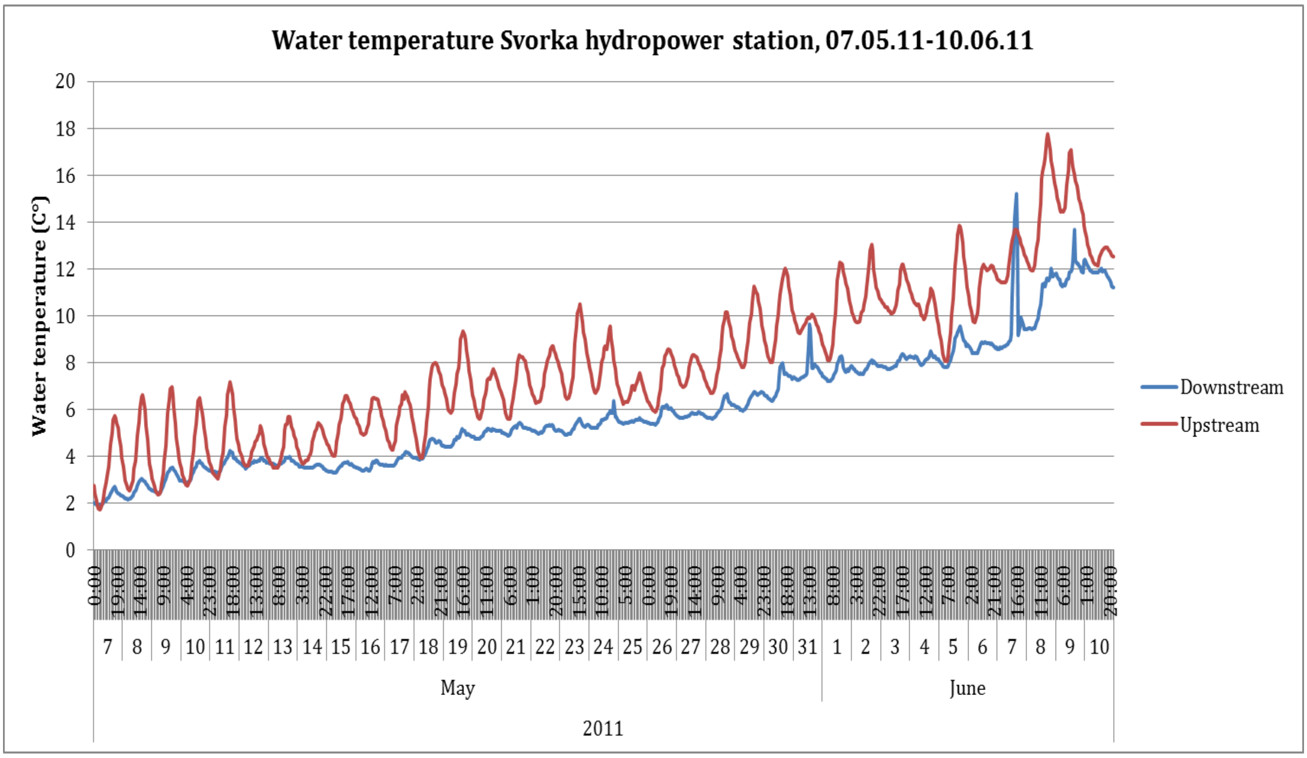

Figure 25. Overview of the water temperature downstream and upstream of Svorka hydropower station prior to the spring sampling period. Data were obtained from Norwegian institute for nature research (NINA) and The Freshwater Ecology & Inland Fisheries Laboratory (LFI), Trondheim.

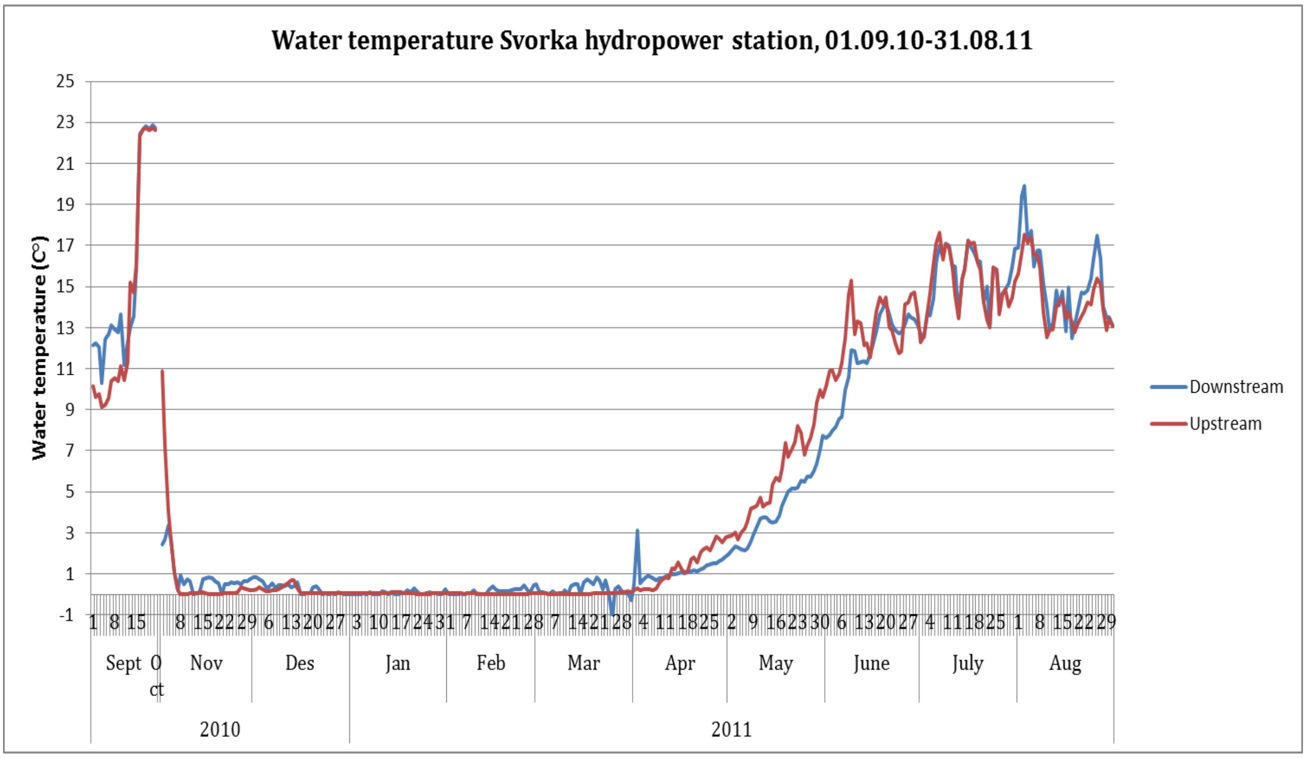

Figure 26. Overview of the yearly variation in water temperature upstream and downstream of Svorka hydropower station, starting prior to the autumn sampling and ending after the spring sampling. Temperature data from October is missing. Data were obtained from Norwegian institute for nature research (NINA) and The Freshwater Ecology & Inland Fisheries Laboratory (LFI), Trondheim.

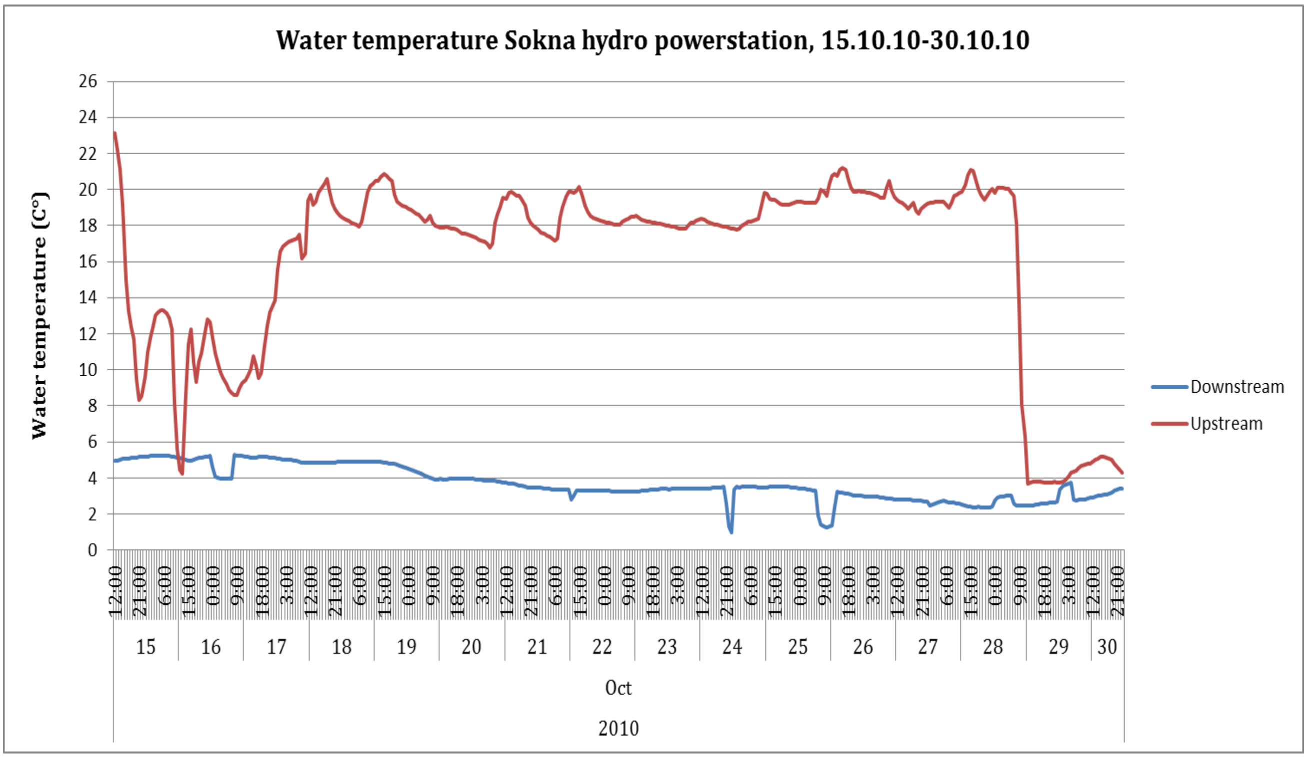

Figure 27. Overview of the water temperature downstream and upstream of Sokna hydropower station prior to the autumn sampling period. Temperature data prior to 15. October is missing. Data were obtained from Norwegian University of Science and Technology.

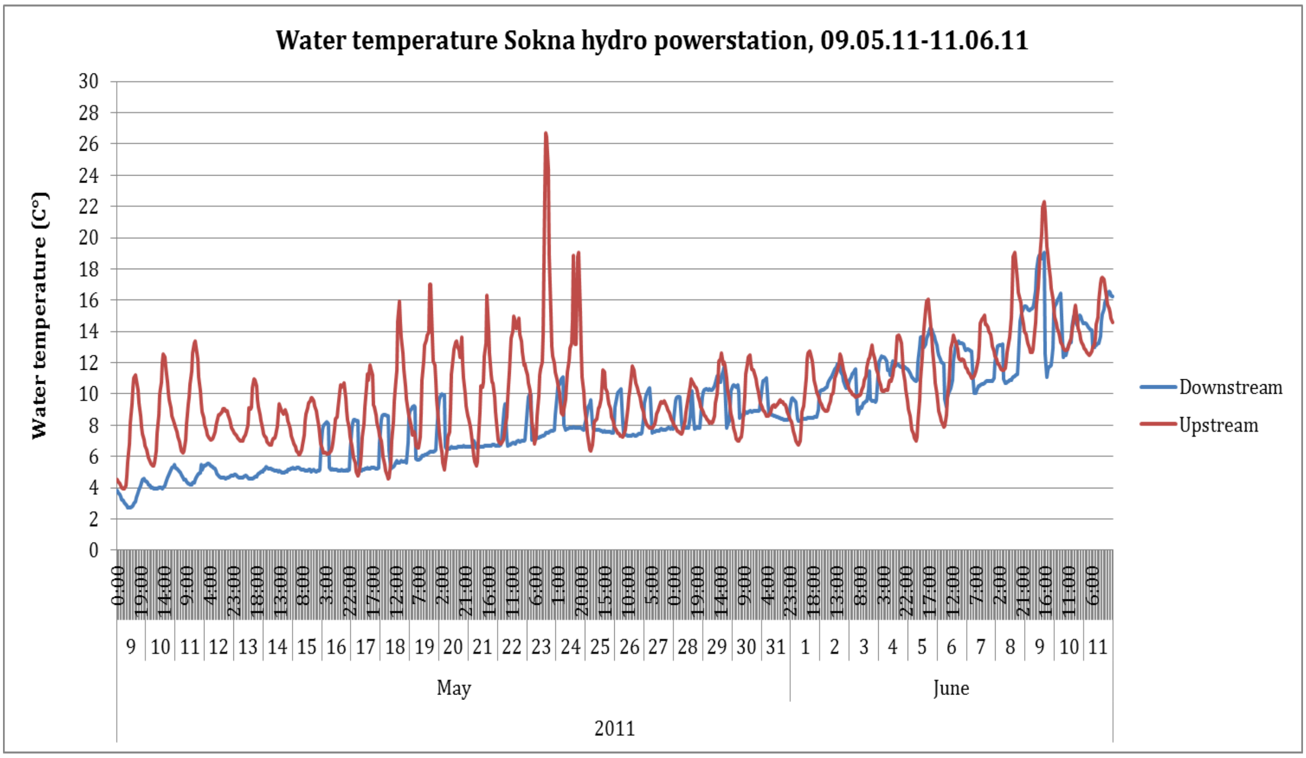

Figure 28. Overview of the water temperature downstream and upstream of Sokna hydropower station prior to the the spring sampling period. Data were obtained from Norwegian University of Science and Technology.

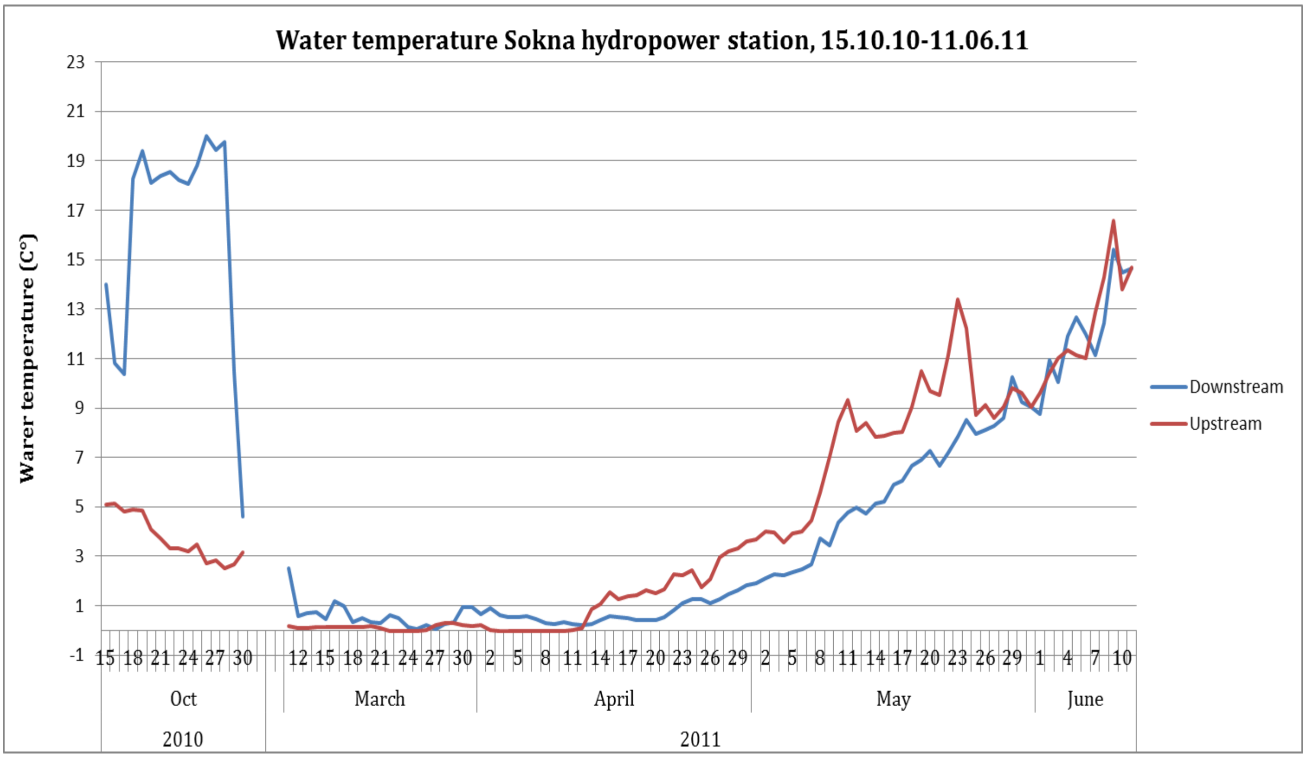

Figure 29. Overview of the yearly variation in water temperature upstream and downstream of Sokna hydropower station, starting prior to the autumn sampling and ending after the spring sampling. Temperature data from November to 11. March and from July to August is missing. Data were obtained from Norwegian University of Science and Technology.