

Hydropeaking Effects on Riverine Benthic Invertebrate Fauna Composition and Drift

Vegard Pedersen Sollien

Biology Submission date: May 2015 Supervisor: Jo Vegar Arnekleiv, IBI Co-supervisor: Ole Kristian Berg, IBI

Norwegian University of Science and Technology Department of Biology

Preface

This study was carried out at the NTNU University Museum (NTNU VM) as a part of the requirements for a Master of Science degree in the field of Biology at the Norwegian University of Science and Technology (NTNU). The study was connected to the Environmental Impacts of Hydropeaking (EnviPEAK) project for the Centre for Environmental Design of Renewable Energy (CEDREN). I would like to thank my two supervisors, Jo Vegar Arnekleiv at NTNU VM and Ole Kristian Berg at NTNU, for all the knowledge they have sheared with me within these years, for their supervision, and for their patience with me.

Thank you so much Ari Husko and Teppo Vehanen for all the work you have done to make this study possible, and to Michael Puffer here in Trondheim for advices and discussions on the setup. Thanks to Gaute Kjærstad at NTNU VM for shearing your knowledge with me in the lab and teaching me invertebrate taxonomy, and to Per Harald Olsen, NTNU, for helping me with the fieldworks.

Jan Davidsen, Lars Rønning and Aslak D. Sjursen at NTNU VM, for giving me fieldwork experience, motivation and some rather good fishing tips (most wanted and appreciated). A great thank you and hugs to all my good friends, fellow students and colleagues. There are a lot of you and you know who you are, but I'm not sure if you all know how much you've meant to me. Don't be strangers. And a special thank you to KnutA, Torgeir and Øystein. Last, but not the least, my family. Thank you, Åge. For support, understanding, and for taking care of whatever needed when I didn't have the time. For conversations and for kick ass heavy metal concerts (more of them to come). Mom. For having raised me in a very good way, and for those good genes. My brain always came from you. Dad. I owe it all to you. Taking me fishing since pre-kindergarten and giving me my great interest for nature and wildlife. For never giving me up when I in an age of 12 was covered in sand, looking for nymphs and caddis larvae while we were supposed to catch graylings. Wish we could go fishing one more time.

Abstract

In earlier studies, changes have been detected in the composition of the lotic benthic macroinvertebrate fauna as a consequence of hydropeaking. Rapid fluctuations in discharge lead to sudden dewatering of river bed area when discharge drops. Stranding of organisms is a well-known consequence of dewatering. But also in the water column, hydropeaking leads to frequent changes in the habitats. In rivers, where stranding in greater or lesser extent always occurs with rapid discharge fluctuations, it may be difficult to distinguish whether the observed changes in invertebrate fauna is caused by the stranding, or if other factors play a role as well. An experiment was therefore performed with rapid discharge fluctuations in a setup with semi-natural stream channels in Paltamo, Finland, where dewatering of the river bed was eliminated. The stream channels were kept under two different discharge regimes in both a winter and a summer experimental period. Abiotic factors and total water flow throughout the experimental periods was identical for each of the stream channels. Hence, we could test if rapid discharge fluctuations without dewatering changed the benthic macroinvertebrate density, diversity and drift.

The study revealed no significant changes in the total density of benthic macroinvertebrates or for the density within the taxonomic groups. Small indications of changes within individual groups could be observed, though. Drift samples show the same indication of changes in some lower taxonomic levels, but mostly no changes were detectable. This is consistent with earlier studies in which it have been shown that drift densities of macroinvertebrates are higher immediate after a peaking operation. The results from this study imply along with the earlier findings that the major challenges for the lotic fauna under a hydropeaking discharge regime are dewatering and stranding.

Sammendrag

I tidligere studier har det blitt påvist forandringer i sammensetningen av bunndyrfaunaen i lotiske økosystemer som en konsekvens av effektkjøring. Raske vannstandsendringer fører til plutselig tørrlegging av elvebunn når vannføringen minker. Stranding av organismer er en velkjent konsekvens av tørrlegging. Men også i de frie vannmassene fører effektkjøring til hyppige forandringer i habitatene. I elver, der stranding i større eller mindre grad alltid inntreffer ved slike vannstandsvariasjoner, kan det være vanskelig å stadfeste om de observerte forandringene i invertebratfaunaen skyldes stranding, eller om også andre årsaker spiller inn. Et forsøk ble derfor gjennomført med vannstandsendringer i et oppsett med seminaturlige renner i Paltamo, Finland, der tørrlegging ble eliminert. Rennene ble holdt under to ulike vannføringsregimer for både en vinter- og en sommereksperimentsperiode. Abiotiske faktorer og totalvannføring gjennom rennene i forsøksperiodene var identiske for alle rennene. Slik kunne vi teste om raske vannstandsvariasjoner uten tørrlegging endret tetthet, artsmangfold og drift av bunndyr.

Det ble ikke påvist signifikante endringer på den totale tettheten av bentiske makroinvertebrater eller på tettheten av individer innen de ulike taksonomiske gruppene. Små indikasjoner på forandringer innenfor enkelte grupper kunne antydes. Drivprøvene viste hovedsakelig de samme små indikasjonene på forandring på enkelte lavere taksonomiske nivåer som Surberprøvene, men ingen forandringer kunne påvises.. Dette samsvarer med tidligere studier, der det er vist at tettheten av invertebrater i driv er høyest umiddelbart etter en rask vannstandsøkning som en følge av utvasking for så senere å avta. Resultatene fra denne studien impliserer sammen med tidligere funn at de største utfordringene for den lotiske faunaen ved effektkjøring er tørrlegging og stranding.

Table of Contents

Preface	i
Abstract	iii
Sammendrag	V
1. Introduction	1
2. Materials and methods	5
2.1 Study area	5
2.2 Study design	6
2.3 Sampling and classification of benthic macroinvertebrates	7
2.4 Statistical analyses	8
3. Results	9
3.1 Benthic macroinvertebrate fauna composition	9
3.1.1 Winter macroinvertebrate fauna	9
3.1.2 Summer macroinvertebrate fauna	
3.2 Drift of benthic macroinvertebrates	11
3.2.2 Winter drift	11
3.2.2 Summer drift	13
4. Discussion	17
4.1 Effects on benthic macroinvertebrate fauna composition	17
4.2 Effects on drift of benthic macroinvertebrates	
4.3 Study design	
4.4 Future perspectives	21
References	23
Appendix	27
Appendix 1: Total flow in stream channels	
Appendix 2: Flow through drift nets	27
Appendix 3: Depth and water current velocity data in stream channels	
Appendix 4: Winter Surber samples	
Appendix 5: Summer Surber samples	
Appendix 6: Winter daytime drift	
Appendix 7: Winter nighttime drift	
Appendix 8: Summer daytime drift	41
Appendix 9: Summer nighttime drift	43

1. Introduction

Benthic macroinvertebrates are a highly diverse group, reflected in a huge variation in morphology, adaptions and habitat use. Because of this diversity, invertebrates are expected to respond to environmental stress and changes in environmental conditions in different ways, which makes benthic macroinvertebrates suitable study organisms to use when investigating effects of different ecological variables (Dolédec et al., 1999). Benthic macroinvertebrates contribute to the nutrient cycling in freshwater systems by decomposition of organic matter in different ways. Feeding, by piercing, scraping, shredding or collecting by filtering or gathering, makes nutrients from dead organic matter or from primary producers available to other organisms. Other groups of macroinvertebrates are predators and regulate the abundance of their prey. Invertebrates are also themselves an important food resource for other organisms. Hence, benthic macroinvertebrates play an important role in many ecological processes (Covich et al., 1999).

Benthic macroinvertebrates exhibit adaptions to moderate and seasonally predictable variations in river discharge both in morphological and life history traits. Still, macroinvertebrate faunas may be strongly affected or even eliminated by large and unpredictable floods. Hence, recolonization from surviving assemblages or from other sites in the river system is required (Gibert et al., 1994, 2008; Jones & Mulholland, 2000). Duration of egg incubation and growth of larvae and nymphs are largely governed by water temperature, and vary both between and within taxa. Winter species gain some growth wintertime, and emerge in spring and early summer. Summer species grows rapidly and emerge in summertime, after spending the winter in the egg stage or as small nymphs (Brittain, 1989; Söderström, 1991). The life-cycle history of macroinvertebrates ranges from semi- to multivoltine species (Engblom, 1996) and with their short generation time, multivoltine species may have an advantage in recolonization of stress-exposed areas (Perry & Perry, 1986; Gillooly & Dodson, 2000; Raddum et al., 2006). Benthic macroinvertebrates actively drift with the flow to colonize available sites. Just as invertebrate density and diversity vary throughout the year, so do the drift of benthic macroinvertebrates and invertebrate species found in drift (Brittain & Eikeland, 1988). Benthic macroinvertebrate drift usually reach a minimum wintertime (Clifford, 1972). Summertime studies have shown that invertebrate drift is a result of several factors, but that the level of activity of the macroinvertebrates is crucial (Elliot, 1967, 1968). Variations in drift throughout the day are

1

also recorded, and studies have shown that the drift increases at dusk and at nighttime. This variation is to a great extent related to size and behavior (Bergan & Nystad, 2003).

River flow varies on timescales from minutes to years (Poff et al., 1997). Discharge is mainly determined by precipitation and groundwater influx. As a result of the temperate climate, discharge in northern natural flowing rivers follows a distinct four-seasonal change. Winter flows are low when precipitation is in the form of snow. Snow-melting in springtime leads to a peak flood, decreasing to lower discharges in summer with drier periods. Autumn, with rainy periods, can give smaller or larger floods (Valentin et al., 1996; Jensen & Johnsen, 1999). The discharge of a water system affects water velocity, fouling, composition of the river bed substrate and the amount of river bed area covered with water at a given time (Saltveit, 2006). Hydropower production affects these natural variations, and although climate friendly when it comes to climate gas emissions, the use of hydropower might thus lead to environmental challenges as changes in the habitats for freshwater fauna, and hence the lotic ecosystem (Harby et al., 2004; Jackson et al., 2007). Regional and local factors, such as the geography of the area and the design of the specific hydropower dam, imply that the consequences of river stream regulations might vary (Jackson et al., 2007), but indications for certain patterns in ecological change as a result of rapid and frequent discharge fluctuations from hydropower production are observed (Brittain & Saltveit, 1989; Harby et al., 2004).

Worldwide, renewable energy today accounts for about 20% of the total energy production, mainly based on hydropower (75%), wind power (10%) and solar power (<5%) (The Shift Project, 2014). Due to environmental considerations, there has been an increased focus on producing a larger proportion of the electric energy from renewable sources in recent years, implying an increased use of solar and wind power. While the demands for electricity changes throughout the day as well as between weekdays and weekends (Saltveit, 2006), solar- and wind based power production varies due to natural factors. Thermal power plants have lags in their production and therefore lack the ability to be regulated quickly. Hydropower has the benefit that its energy resource can be stored in reservoirs. In periods where power production from other renewable sources by their natural variation is low, dam storage makes it possible to use hydropower as a buffer (Borsanyi, 2005). Utilizing this flexibility will on the other hand give more rapid and frequent discharge fluctuations than under natural hydrological conditions or conventional use of hydropower, but with significant lower max water flow than

for instance naturally yearly floods. This full flex usage of hydropower reservoirs is known as hydropeaking (Saltveit, 2006; Charmasson & Zinke, 2011).

Benthic macroinvertebrate diversity and density may decrease as a result of hydropeaking (e.g. Gersich & Brusven, 1981; Cushman, 1985; Moog, 1993). Some mayfly species are sensitive to a changing discharge regime, but there are also examples of invertebrate groups, e.g. oligochaeta, that are more tolerant to such changes and can achieve increased densities under hydropeaking conditions. Thus, although the species composition and densities may be altered or reduced, the total invertebrate biomass may increase (Jackson et al., 2007).

The taxonomic composition of the benthic macroinvertebrate fauna has been used to assess the environmental state of river systems in a great number of studies. Such an assessment may not be sufficient to distinguish between influences from distinct variations within spatial gradients, geology, geography or hydrology under natural conditions (Dolédec et al., 2011). Effects of damming and hydropeaking may differ in different downstream areas of the river. In periods with low hydropower production, thus a low downstream water discharge, river bed will be exposed to dewatering to a greater or lesser extent. Cross section sampling from river Nidelva, Trondheim, Norway, showed that the macroinvertebrate fauna in the areas most exposed to dewatering. In dewatered areas, the densities of macroinvertebrates were about 90 % lower than in areas not exposed to dewatering, and the study documented a negative correlation between the number of dewatering episodes and density and diversity of benthic macroinvertebrates (Arnekleiv et al., 1994).

Most studies on consequences of damming and hydropeaking have been done in rivers, where dewatering occurs (Poff & Zimmerman, 2010). During dewatering events, stranding of organisms is a well-known consequence, and it can affect survival of both invertebrates and fish (e.g. Harby et al., 2004; Nagrodski et al., 2012). A reduced density of aquatic invertebrates may potentially affect the composition, density and life history variables of fish in the river system (e.g. Mortensen et al., 1988; Ensign et al., 1990). While rapid drops in discharge leads to dewatering and stranding, peaking operations may on the other hand affect benthic macroinvertebrate drift. With more rapid increases in water levels than under natural hydrological conditions or conventional hydropower operations, invertebrate fauna is at risk of being washed out of the system (Charmasson & Zinke, 2011). If hydropeaking leads to an

increase in water velocity, it might also be that food is drifting too fast for fish to capture (e.g. Hill & Grossman, 1993; Braaten et al., 1997; Piccolo, Hughes & Bryant, 2008).

The main objectives of this thesis are to investigate the consequences on the composition and drift of the benthic macroinvertebrate fauna, as a result of a shift in the water discharge regime with sudden and rapid fluctuations, in an experiment where the risk of stranding is eliminated. Are the earlier observed changes in benthic macroinvertebrate fauna under hydropeaking conditions mainly an effect of stranding, or might it be that hydropeaking also changes the lotic habitats in a way so that other invertebrate taxa than those found under natural discharge regimes will dominate, even without stranding events? And even if the daily total discharge in a river system is identical, will a changed discharge regime with hydropeaking lead to a higher total catastrophic drift of macroinvertebrates? If the composition of the benthic macroinvertebrate fauna is changed even when stranding events are eliminated and if catastrophic drift will differ under a hydropeaking regime will be tested in this study.

2. Materials and methods

2.1 Study area

The study was conducted in 2011 at the Finnish Game and Fisheries Research Institute's Kainuu fisheries research station in Paltamo, Central Finland (64°30' N; 27°10' E).

Six parallel, semi-natural outdoor stream channels (each 25.5m long \times 1.5m wide) were used in the experiment. A 10-15 cm layer of coarse pebble gravel (20-35 mm in diameter) made up the river bed in the channels. The substrate was arranged with nine gravel deflectors in each channel. These deflectors protruded the water surface, creating a meandering flow pattern in the channels with varying streams and varying water velocity. Using the seminatural stream channels made it possible to eliminate the effects of stranding as a result of sudden discharge drop. The stream channels were given numbers from 1 to 6, number 1 being far left and number 6 far right seen upstream (Figure 1).

Channels were provided with water from a nearby lake. The water source was shared by all six channels, hence giving them the same temperature regime. The region has a continental climate, and the landscape is largely dominated by boreal forests.



Figure 1: Overview of the six semi-natural stream channels in Paltamo, Finland. (Photo: Vegard P. Sollien)

2.2 Study design

Experiments were conducted throughout two separate periods. The winter experiment started on the 10th of January 2011 and lasted until the 22th of March, while the summer experiment was conducted in the period from 16th of May until 31st of July. Hydropeaking was done on a diurnal basis throughout the experimental periods, while the stream channels were held under a constant discharge regime (equivalent to control discharge) between the experimental periods.

Experiments were carried out as a 3×3 replicate. During the experimental periods, three of the channels were kept under stable discharge conditions (stabile discharge 35 L s⁻¹) as a control. The other three channels were hydropeaked, with a high discharge (65 L s⁻¹) for 9 hours (07:00 - 16:00; UTC +2) and a low discharge (18 L s⁻¹) for 15 hours (16:00 - 07:00; UTC +2). The total discharge during 24 hours was the same for both the control and the hydropeaked channels (3060 m³). Under the different treatments, the water-covered area were



Figure 2: Stream channel with meandering water flow. (Photo: Vegard P. Sollien)

nearly constant, being 35 m^2 in control stream channels and 35 m^2 during low discharge and 36 m^2 during high discharge conditions in hydropeaked (dewatered area under low discharge treatment <3%). The water temperature was recorded by temperature loggers (Hobo H8; www.onsetcomp.com and 83 Tinytags TG4100; www.geminidataloggers.com) every second hour. In the winter experimental period, a mean of 2.3°C (range: 1.7°C - 2.7°C) was recorded, while summer period had a mean of 14.8°C (range: 8.3°C - 19.5°C). Water column velocity and water dept were recorded in 25 cross-sectional transects (1 meter apart), with four points at each transect (100 measurements in each stream channel). At a discharge corresponding to the flow in the control

channels during the experiments, mean dept in all six channels were compared, varying between 9.8 cm and 11.9 cm with a mean water velocity between 29.9 cm s⁻¹ and 35.6 cm s⁻¹. In the hydropeaked channels, mean dept at low discharge varied between 6.4 cm and 7.6 cm and at high discharge between 13.7 cm and 15.5 cm. Water velocity in these channels varied

between a mean of 22.3 and 24 cm s⁻¹ at low discharge and a mean between 37 and 38.9 cm s^{-1} at high discharge. The substrate in the stream channels was arranged in a manner so that to give a peered water column where the substrate protruded the water surface, and with strait upward concrete walls in the rest of the channel (Figure 2).

At a given discharge, abiotic factors were thus the same for all six channels. Hence, it was possible to test for the effects of the rapid changes in water discharge and a changing river stream velocity, and the consecutive consequences of clogging of the river bed or substrate or fauna being washed out of the system, while stranding was eliminated from the study.

2.3 Sampling and classification of benthic macroinvertebrates

For all of the stream channels, input of benthic invertebrates came from the natural surroundings with drift from the common water intake or from the air.

Sampling of benthic invertebrates was done in two different experimental periods.

Benthic samples were collected using a Surber sampler (0.04 m^2 frame, 0.30mm mesh) in week 11 (16th, 17th and 21st of March) and week 23 (8th and 9th of June). Each channel was divided into 72 cells (1m x 0.5m size) and a random number generator was used to pick six cells from which samples were taken. If randomization outcome resulted in an implied sampling in areas where substrate was protruding the water surface in a stream channel, a new randomization was done for this sample and hence excluding the dry areas from the study. Thus, 36 benthic samples were taken during each sampling period.

Drift sampling was done about 1.5 m distance upstream from the lower end of the stream channels, using three sample nets side by side in each channel. As for the surber samples, sampling was done in week 11 (16th and 17th of March), and week 23 (8th and 9th of June). Drift samples used in this study was done in intervals lasting over three hours, with two samplings per 24 hour (01:00 UTC +2 and 13:00 UTC +2). In the two center stream channels (channel 3 and 4), sampling was repeated for two consecutive days (48 hours) in both periods. Drift samples were done with 10cm opening (0.250mm mesh size) drift nets (10cm diameter opening). In total, 48 drift samples were taken during each sampling period, 24 samples nighttime (corresponding to low water discharge in hydropeaked stream channels) and 24 daytime (corresponding to high water discharge).

Samples were preserved in ethanol (70%). All macroinvertebrates were classified to the lowest possible taxonomic level with main focus on mayflies (Ephemeroptera) according to classification literature (Nilsson, A.N. (ed): Aquatic insects of North Europe - A taxonomic handbook, 1996; Arnekleiv, J.V.: Bestemmelsesnøkkel til norske døgnfluelarver (Ephemeroptera larvae), 1994; Størset, L.: Smådyr i ferskvann, 1995) and with use of a stereomicroscope in the laboratory. Individuals of benthic macroinvertebrates in a non-aquatic stage of their life cycle were classified as terrestrial, and excluded from the study along with terrestrial taxa and planktonic cladoceras or copepods.

2.4 Statistical analyses

Numbers of individuals found in Surber samples were adjusted to give mean individuals (n) per square meter (m²) in each stream channel. For the statistical analyzes, a two-way Mann-Whitney U test was used for each of the distinguished taxa. Wilcoxon test for paired samples was used for the channels as a total. The three lowermost Surber samples for the summer experiment from two of the stream channels were incorrectly labeled at the study site, and it was not possible to distinguish from what channel they were sampled. To maintain a balanced study, the same samples were excluded from all of the channels. The numbers of collected individuals from drift samples were adjusted for different discharges and expressed as number of collected individuals (n) per m³. For analyzes of drift samples, two-way Mann-Whitney U test was used for each taxon. Drift densities were calculated separately for the samples collected daytime and nighttime and for winter and summer experiments due to differences in flow through the drift nets. Mean drift densities per channel was calculated. The samples from the two different days in stream channel 3 and 4 were assumed independent, also giving more power to the drift densities analyzes. For some taxa, species were grouped due to low findings in drift. Genera Baetis (B. muticus and B. rhodani identified), Heptagenia (H. dalecarlica and H. sulphurea identified) and Ephemerella (E. mucronata and E. ignita identified) were tested on their respective genera basis, the same were genus Caenis. Statistical analyzes were performed in R, version 2.14.1 (R Project, 2011). All tests were performed at a probability level of 5 % for type I errors.

3. Results

In total twenty-eight different macro invertebrate taxa were distinguished. Of these were nine mayfly (Ephemeroptera) species.

3.1 Benthic macroinvertebrate fauna composition

3.1.1 Winter macroinvertebrate fauna

Winter macroinvertebrate fauna was dominated by Chironomidae (54%), Plecoptera (14%) and Ephemeroptera (13%). Genera Heptagenia (60%) and Baetis (28%) dominated the benthic Ephemeroptera winter fauna. It was not possible to distinguish a change in the winter macroinvertebrate fauna composition as a total (p=0.4777) as a result of the changed discharge regime. The results slightly indicate (table 1) for an increased density under hydropeaking conditions for Turbellaria (p=0.077) and Chironomidae (p=0.100), though.

	Winter benthic macroinvertebrate densities (n × m ⁻²)			
Taxon	Control (mean ± SD)	Hydropeaked (mean \pm SD)	<i>p</i> value	
Ephemeroptera	422.22 (263.40)	470.83 (270.16)	1.000	
Leptophlebia marginata	13.89 (12.03)	16.67 (1.02)	0.643	
_eptophlebia vespertina	13.89 (9.62)	18.06 (12.72)	1.000	
Ephemerella sp.	2.78 (4.81)	8.33 (7.21)	0.369	
Baetis sp.	130.56 (73.40)	122.22 (92.45)	1.000	
Caenis sp.	0.00 (-)	0.00 (-)	-	
Heptagenia sp.	247.22 (191.41)	291.67 (188.24)	1.000	
Plecoptera	429.17 (68.59)	512.50 (412.33)	1.000	
Trichoptera	120.83 (116.89)	80.56 (62.68)	1.000	
Simuliidae	238.89 (136.44)	158.33 (183.48)	0.400	
Ceratopogonidae	1.39 (2.41)	1.39 (2.41)	1.000	
Chironomidae	1537.50 (342.88)	2030.56 (100.03)	0.100	
Elmidae	9.72 (8.67)	2.78 (4.81)	0.354	
Turbellaria	11.11 (9.62)	41.67 (23.20)	0.077	
Oligochaeta	11.11 (12.73)	6.95 (6.36)	1.000	
Lymnaeidae	36.11 (8.67)	18.06 (13.39)	0.268	
Asellus aquaticus	247.22 (190.22)	247.22 (56.72)	0.700	
Odonata	0.00 (0)	1.39 (2.41)	0.505	

Table 1: Mean benthic macroinvertebrate densities in winter, and corresponding p-values for observed changes.

3.1.2 Summer macroinvertebrate fauna

Summertime, the invertebrate fauna was dominated by Chironomidae (35%), Simuliidae (28%) and *Asellus aquaticus* (17%). Ephemeroptera (5%) drift was again dominated by genus Caenis (58%). In contrast to the results for the winter experiments, indications for Chironomidae was a decreased density (p=0.100) under hydropeaking conditions (table 2). These indications were clear for Trichoptera (p=0.077), while indications for Oligochaeta were an increased density under hydropeaking conditions (p=0.064). No changes could be distinguished within other taxa, but the total density of benthic macroinvertebrates was slightly indicated (p=0.102) to decrease.

Taxon	Control (mean ± SD)	Hydropeaked (mean ± SD)	<i>p</i> value
Ephemeroptera	225.00 (158.99)	88.89 (37.57)	0.700
Leptophlebia marginata	0.00 (-)	2.78 (4.81)	0.505
Ephemerella sp.	30.56 (17.34)	0.00 (-)	0.064
Baetis sp.	50.00 (46.40)	5.56 (9.62)	0.354
Caenis sp.	119.44 (104.86)	61.11 (26.79)	0.700
Heptagenia sp	22.22 (19.24)	16.67 (16.67)	0.814
Plecoptera	25.00 (8.33)	19.44 (20.97)	0.825
Trichoptera	400.00 (101.04)	125.00 (87.79)	0.077
Simuliidae	1422.22 (2243.36)	191.67 (248.88)	1.000
Ceratopogonidae	8.33 (14.43)	5.56 (4.81)	1.000
Chironomidae	1366.67 (142.16)	658.33 (435.01)	0.100
Elmidae	88.89 (54.22)	91.67 (50.69)	1.000
Turbellaria	5.56 (4.81)	19.44 (26.78)	0.814
Nematoda	2.78 (4.81)	2.78 (4.81)	1.000
Lymnaeidae	5.56 (9.62)	5.56 (4.81)	1.000
Oligochaeta	0.00 (-)	30.56 (12.73)	0.064
Asellus Aquaticus	302.78 (87.53)	661.11 (441.46)	0.400
Hydrachnidae	0.00 (-)	2.78 (4.81)	0.505

Table 2: Summer mean benthic macroinvertebrate densities, and corresponding p-values for observed changes.

3.2 Drift of benthic macroinvertebrates

In total, twenty-five different taxa were distinguished in drift, eight of these different species of Ephemeroptera. Taxa dominating in drift were all found in benthic samples, except for winter drift dominating Chaoboridae. All taxa found in winter drift were present in summer drift as well, except for the two Ephemeroptera species *Leptophlebia marginata* and *Heptagenia sulphurea*.

3.2.2 Winter drift

In total, seventeen taxa were found in winter drift, seven of these different species of Ephemeroptera. The drift was dominated by Chironomidae (36%), Chaoboridae (29%) and Ephemeroptera (20%). The Ephemeroptera drift mainly consisted of the two species *Leptophlebia vespertina* (45%) and *Leptophlebia marginata* (32%). The results suggest no changes in daytime drift densities (table 3).

Table 3: Winter mean benthic macroinvertebrate drift densities daytime, and corresponding p-values
for observed changes.

Winter daytime drift densities (n × m ⁻³)			
Taxon	Control (mean ±SD)	Hydropeaked (mean ±SD)	<i>p</i> value
Ephemeroptera	0.035 (0.010)	0.061 (0.030)	0.343
Leptophlebia marginata	0.004 (0.005)	0.013 (0.008)	0.307
Leptophlebia vespertina	0.022 (0.015)	0.045 (0.031)	0.349
Baetis sp.	0.006 (0.007)	0.003 (0.006)	0.620
Heptagenia sp.	0.002 (0.003)	0.000 (-)	0.453
Caenis sp.	0.002 (0.004)	0.000 (-)	0.453
Plecoptera	0.011 (0.013)	0.016 (0.010)	0.663
Trichoptera	0.002 (0.004)	0.002 (0.003)	1.000
Simuliidae	0.015 (0.018)	0.003 (0.003)	0.645
Chironomidae	0.108 (0.068)	0.212 (0.153)	0.486
Chaoboridae	0.011 (0.014)	0.024 (0.019)	0.309
Elmidae	0.000 (-)	0.000 (-)	-
Turbellaria	0.000 (-)	0.000 (-)	-
Asellus aquaticus	0.004 (0.004)	0.012 (0.008)	0.191
Collembola	0.000 (-)	0.000 (-)	-
Hydrachnidae	0.000 (-)	0.000 (-)	-

Nighttime, *L. marginata* had a significant (p=0.029) higher drift density under hydropeaked conditions. Results for Simuliidae slightly indicated the opposite (p=0.104). For the rest of the taxa, it was not possible to distinguish any changes (table 4).

Winter nighttime drift densities (n \times m ⁻³)			
Taxon	Control (mean ±SD)	Hydropeaked (mean ±SD)	<i>p</i> value
Ephemeroptera	0.062 (0.031)	0.135 (0.059)	0.343
Leptophlebia marginata	0.015 (0.014)	0.063 (0.010)	0.029
Leptophlebia vespertina	0.032 (0.019)	0.034 (0.038)	0.886
Baetis sp.	0.011 (0.008)	0.031 (0.038)	0.772
Caenis sp.	0.000 (-)	0.000 (-)	-
Heptagenia sp.	0.003 (0.004)	0.007 (0.015)	0.869
Plecoptera	0.016 (0.001)	0.024 (0.031)	1.000
Trichoptera	0.004 (0.065)	0.000 (-)	0.453
Simuliidae	0.040 (0.030)	0.007 (0.015)	0.104
Chironomidae	0.091 (0.065)	0.110 (0.099)	0.886
Chaoboridae	0.179 (0.201)	0.201 (0.125)	0.886
Elmidae	0.002 (0.004)	0.000 (-)	0.453
Turbellaria	0.004 (0.005)	0.010 (0.014)	0.642
Asellus aquaticus	0.017 (0.016)	0.010 (0.012)	0.460
Collembola	0.000 (-)	0.004 (0.007)	0.453
Hydracnidae	0.002 (0.004)	0.000 (-)	0.453

Table 4: Mean benthic macroinvertebrate drift densities in winter nighttime, and corresponding p-values for observed changes.

Comparing the two datasets from the winter study for the drift dominating taxa, both Chaoboridae (p=0.018) and *L. marginata* (p=0.031) had a significant higher drift density during nighttime compared to daytime (table 5). For the other taxa, no differences between day and nighttime drift were affirmed.

Time of day differences in winter drift densities (n × m ⁻³)			
Taxon	Day (mean ±SD)	Night (mean ±SD)	<i>p</i> value
Ephemeroptera	0.048 (0.025)	0.099 (0.059)	0.074
L. marginata	0.008 (0.008)	0.039 (0.028)	0.031
L. vespertina	0.033 (0.026)	0.033 (0.028)	0.879
Plecoptera	0.013 (0.011)	0.020 (0.020)	0.561
Trichoptera	0.002 (0.003)	0.002 (0.006)	0.700
Simuliidae	0.009 (0.013)	0.023 (0.028)	0.351
Chironomidae	0.160 (0.113)	0.101 (0.078)	0.328
Chaoboridae	0.018 (0.017)	0.190 (0.156)	0.018
Asellus aquaticus	0.008 (0.008)	0.013 (0.014)	0.488

Table 5: Mean drift densities daytime and nighttime in winter, and corresponding p-values for observed differences.

3.2.2 Summer drift

In total twenty-three taxa were distinguished in summer drift, six of these different species of Ephemeroptera. Most prevalent taxa were Chironomidae (47%), Simuliidae (26%), Ephemeroptera (7%), *Asellus aquaticus* (5%) and Trichoptera (5%). Genus Caenis dominated to a great extend among the Ephemeroptera.

As a result of hydropeaking, Trichoptera clearly indicated (p=0.059) a higher drift density. For Elmidae, the indices for a changed drift rate were nearly as clear (p=0.069), but the drift density was low with no individuals found in the control at all. The trend was present for genera Baetis (*B. muticus* and *B. rhodani* identified) as well (p=0.122), but it was not possible to distinguish any change for any of the other taxa (table 6) in daytime summer drift.

Summer daytime drift densities (n × m ⁻³)			
Taxon	Control (mean ±SD)	Hydropeaked (mean ±SD)	<i>p</i> value
Enhomorontoro			0.000
Ephemeroptera	0.030 (0.017)	0.093 (0.145)	0.886
Ephemerella ignita	0.015 (0.020)	0.001 (0.001)	0.124
Leptophlebia vespertina	0.002 (0.005)	0.004 (0.008)	1.000
Baetis sp.	0.007 (0.005)	0.001 (0.003)	0.122
Caenis sp.	0.003 (0.007)	0.082 (0.150)	0.180
Heptagenia sp.	0.000 (-)	0.002 (0.004)	0.453
Plecoptera	0.005 (0.007)	0.012 (0.006)	0.465
Trichoptera	0.014 (0.022)	0.067 (0.037)	0.059
Simuliidae	0.350 (0.354)	0.135 (0.127)	0.486
Ceratopogonidae	0.018 (0.031)	0.028 (0.056)	0.869
Chironomidae	0.504 (0.135)	0.552 (0.042)	1.000
Chaoboridae	0.000 (-)	0.000 (-)	-
Argulus	0.002 (0.005)	0.000 (-)	0.454
Asellus aquaticus	0.056 (0.067)	0.093 (0.083)	0.468
Collembola	0.000 (-)	0.000 (-)	-
Corixidae	0.000 (-)	0.002 (0.004)	0.454
Hydrophilidae	0.000 (-)	0.002 (0.003)	0.453
Haliplidae	0.000 (-)	0.000 (-)	-
Elmidae	0.000 (-)	0.030 (0.024)	0.069
Turbellaria	0.023 (0.016)	0.022 (0.034)	0.772
Nematoda	0.005 (0.006)	0.007 (0.011)	1.000
Oligochaeta	0.019 (0.022)	0.016 (0.032)	0.869
Hydrachnidae	0.003 (0.006)	0.001(0.002)	1.000

Table 6: Mean summer daytime benthic macroinvertebrate drift densities, and corresponding p-values for observed changes.

At summer nighttime, Plecoptera had a significant increase in (p=0.027) drift density as a result of hydropeaking. At the same time, indications were that the drift density for Asellus aquaticus (p=0.069) decreased. It was not possible to distinguish any changes for other taxa (table 7).

Summer nighttime drift densities (n × m^{-3})			
Taxon	Control (mean ±SD)	Hydropeaked (mean ±SD)	<i>p</i> value
F ull success to as			0.000
Ephemeroptera	0.023 (0.017)	0.118 (0.201)	0.686
Ephemerella ignita	0.002 (0.004)	0.009 (0.017)	1.000
Leptophlebia vespertina	0.000 (-)	0.000 (-)	-
Baetis sp.	0.007 (0.009)	0.005 (0.010)	0.878
Caenis sp.	0.014 (0.012)	0.013 (0.026)	0.069
Heptagenia sp.	0.000 (-)	0.008 (0.016)	0.453
Plecoptera	0.002 (0.004)	0.114 (0.103)	0.027
Trichoptera	0.062 (0.026)	0.043 (0.040)	0.686
Simuliidae	0.318 (0.300)	0.190 (0.121)	0.686
Ceratopogonidae	0.002 (0.004)	0.000 (-)	0.453
Chironomidae	0.332 (0.111)	0.395 (0.117)	0.686
Chaoboridae	0.000 (-)	0.010 (0.201)	0.453
Argulus	0.000 (-)	0.000 (-)	-
Asellus aquaticus	0.037 (0.040)	0.000 (-)	0.069
Collembola	0.000 (-)	0.013 (0.027)	0.453
Corixidae	0.002 (0.005)	0.008 (0.016)	1.000
Hydrophilidae	0.000 (-)	0.004 (0.009)	0.453
Haliplidae	0.002 (0.005)	0.007 (0.014)	1.000
Elmidae	0.007 (0.013)	0.000 (-)	0.453
Turbellaria	0.015 (0.024)	0.009 (0.011)	1.000
Nematoda	0.000 (-)	0.000 (-)	-
Oligochaeta	0.003 (0.006)	0.005 (0.010)	1.000
Hydrachnidae	0.004 (0.005)	0.005 (0.010)	0.868

Table 7: Mean summer nighttime benthic macroinvertebrate drift densities in summer, and corresponding p-values for observed changes.

Chironomidae had a significant (p=0.010) higher drift density at daytime compared to nighttime. The same was slightly indicated for *A. aquaticus* (p=0.070). Ephemeroptera species in drift was generally found in very low drift densities, except for individuals of Caenis. All drifting individuals of *L. vespertina* were found daytime. It was not possible to distinguish any differences between daytime and nighttime drift for any other of the Ephemeroptera species, or for other taxa (table 8).

Time of day differences in summer drift densities (n × m ⁻³)				
Taxon	Day (mean ±SD)	Night (mean ±SD)	<i>p</i> value	
Ephemeroptera	0.062 (0.101)	0.070 (0.142)	0.721	
Leptophlebia vespertina	0.003 (0.006)	0.000 (-)	0.171	
Ephemerella sp.	0.008 (0.015)	0.005 (0.012)	0.365	
Baetis sp.	0.004 (0.005)	0.006 (0.009)	1.000	
Caenis sp.	0.042 (0.105)	0.013 (0.019)	0.956	
Heptagenia sp.	0.001 (0.002)	0.004 (0.011)	1.000	
Plecoptera	0.009 (0.007)	0.058 (0.090)	0.455	
Trichoptera	0.040 (0.040)	0.052 (0.033)	0.494	
Simuliidae	0.243 (0.271)	0.254 (0.221)	0.798	
Chironomidae	0.523 (0.096)	0.363 (0.111)	0.010	
Asellus aquaticus	0.074 (0.072)	0.019 (0.033)	0.070	
Elmidae	0.015 (0.022)	0.003 (0.009)	0.270	

Table 8: Mean drift densities in summer daytime and nighttime, and corresponding p-values for observed differences.

4. Discussion

The results of the hydropeaking discharge regime generally suggest minor changes on the benthic macroinvertebrate fauna when dewatering is eliminated. For the composition of the invertebrate fauna, no changes in the densities could be affirmed neither for any of the single taxa or for the benthic macroinvertebrate fauna as a total. Some slight indications could be observed, though. The results did not affirm any changes in the macroinvertebrate drift densities as a total, either.

4.1 Effects on benthic macroinvertebrate fauna composition

No significant changes in the benthic macroinvertebrate fauna were detected, though indications were present for some taxa. Trichoptera slightly indicated a reduced density under hydropeaking conditions, though not significant. More diverse taxa are constituted by several genera and species and intra taxonomic changes may have occurred, even though no changes were confirmed for the density of the different Ephemeroptera species. Some of the characterized by apparently patchy distributed assemblies observations are of macroinvertebrate. Surber samplers used in this study had a sampling area of only 0.04 m², which may have contributed to these recordings. It might also be that the habitats within the stream channels varied, corresponding to the downstream decreasing stream velocity gradient. Both catastrophic drift in the upper parts of the channels, as well as too harsh conditions and a subsequent behavioral drift to more suitable habitats for the invertebrates may have occurred (e.g. Mackay, 1992; Robinson et al., 2004c; Zbinden et al., 2008). For the summer surber samples, it would have been desirable to include more samples from each channel and hence maybe reduce the effects of the patchiness in the results, but looking briefly on the excluded samples they were likely as variable in findings as the ones included. The channels were also initially colonized by drifting invertebrates, and it is not possible to say anything about the compensative effect of the continuous colonization. Reflecting the diversity in life history traits, benthic macroinvertebrate fauna was dominated by Chironomidae, Plecoptera and Ephemeroptera in winter. Summer, Chironomidae, Simuliidae and A. aquaticus dominated. Benthic Ephemeroptera fauna was dominated by Heptagenia and Baetis in winter and by Caenis in summer.

4.2 Effects on drift of benthic macroinvertebrates

Few statistically significant effects were found in the drift experiments. The low number of individuals actually found in drift and the high variation in findings contribute to these results. Indications for changes were observed, though. Indications for a higher drift of Ephemeroptera at night were seen. It is worth noting that while Heptagenia and Baetis dominated in winter benthic fauna, the two Leptophlebia species L. marginata and L. vespertina dominated the Ephemeroptera drift. The observed increase in drift density was only present for L. marginata and only in nighttime where no washouts as a result of hydropeaking occurred. As for the drift dominating taxa Chaoboridae, L. marginata and L. vespertina mainly inhabit lenthic systems. Hence, the findings indicate that the drifting fauna in the stream channels was influenced by the fauna of the upstream lake to some degree. Chaoboridae had a significant higher drift density at night, which can be explained by their performance of horizontal movements throughout the day and usually being situated at deeper areas daytime. When moving higher up in the water column of the intake water at nighttime, they may easily be carried away by surface currents. It was not possible to distinguish any changes in the drift density for Chaoboridae under hydropeaking conditions, nor for the dominating Chironomidae. Simuliidae on the other hand, slightly indicated a reduced drift density nighttime. The results for A. aquaticus suggest no effect of hydropeaking. For all other taxa found in winter drift, including Plecoptera and Trichoptera, drift densities were very low. The same trends in observations were done in the summer. While drift rates indicated an increased drift for the taxa Trichoptera and Elmidae daytime, genus Baetis indicated the opposite. Genus Caenis were found to have higher drift densities, but as the standard deviations indicate, the findings were very patchy. The only change indicated for Chironomidae was the observation of higher drift densities daytime than nighttime. Based on these results it seems like other factors, as time of the day or the taxon itself influences the results just as much as the hydropeaking. The findings in the drift studies indicate that drift rate for lotic species not increase as a result of the higher discharge.

Daytime drift samples for the study were collected in the time period from 10:00 - 13:00, while peaking operation occurred at 07:00. It has been shown that macroinvertebrate drift strongly increase during the initial peaking operation (Bruno, 2014). Drift rates might thus have been higher earlier in the morning as a consequence of washout events during the sudden peak in discharge. An earlier collecting of drift samples might on the other hand have

overestimated the daytime drift of benthic macroinvertebrates radically in this study, while a later collection could have underestimated the drift density. As an estimation of drift density, the chosen time period was thus believed to be a good compromise. Juvenile Salmo salar inhabited the stream channels during the experimental periods. The fish showed a tremendous growth (Puffer, 2014), and drifting invertebrates are important for fish nutrition (e.g. Watz, 2013). It has been shown in artificial environment studies that fish might not be able to feed immediate after the start of hydropeaking events because of a to high water velocity (Frankiewicz et al., 1993; Wootton, 1998). As a result of higher drift rates during and immediately after peaking events, the Salmonides mainly fed within 2-4 hours (Lagarrigue et al., 2002). Hence, this slightly overlaps with the time period for daytime collection in the drift experiments as well and it is likely that the daytime drift densities thus are underestimated in the hydropeaked channels. For the night samples, with a rapid decrease in discharge in the hydropeaked stream channels, no initial differences in drift densities as a result of a changed discharge should be expected, but studies imply that drift densities increase at dusk and in nighttime because of an increased activity (e.g. Bergan & Nystad, 2003). The nighttime samples (collected in the time period from 22:00 - 01:00) in this study might thus have overestimated the drift density for the low discharge period of day. The presence of the fish might have had influences on the composition of the benthic macroinvertebrate fauna, but as for the results of this study on the invertebrates, the fish growth study of Puffer (2014) only showed minor changes under a hydropeaking regime. Hence, it is not believed to have an impact on the result of this study.

4.3 Study design

The stream channels were a controllable approach to hydropeaked rivers where dewatering of the river bed under a hydropeaking discharge regime could be eliminated. In addition, they provided the benefits of including a control directly comparable with the experimental group. The water source was placed just upstream the channels, and the findings of lenthic fauna in the drift samples indicated that fauna from the intake water affected the findings in the study. Even if this apparently might indicate a source to errors, the water intake could be comparable to parts of a river system with less current (e.g. hydropower dams) and its associated invertebrate fauna. In addition to the elimination of dewatering and stranding from the experiments, the shared water source eliminated the factor of a changed temperature regime from the system. Water temperature determines the combustion, and hence the growth of poikilothermic organisms. When water is stored in reservoirs with deep release, thermal changes are pronounced in the downstream river. Water released from the hypolimnion will in general lead to a decreased river water temperature in summer, and increased temperatures wintertime (Saltveit, 1994). A change in growth would otherwise be expected under a changed temperature regime (Raddum, 1985; Fjellheim et al., 1996). Lasting over several months and with daily peaking operations, the conditions for the study assembled conditions found in regulated rivers in other aspects. Between the two experimental periods, there was a gap in hydropeaking operations. Taken into account that the samples for the summer experimental period were collected just three weeks after the startup of hydropeaking operations, it might have influenced the fauna composition results by a recolonization of more vulnerable invertebrate taxa from behavioral drift to some extent. For the drift density studies, it is notable that even though daytime discharge was increased to 65 L s⁻¹ in the hydropeaked stream channels compared with a control discharge of 35 L s⁻¹, maximum water velocities in the hydropeaked stream channels under high discharge not differ very much from the water velocity in the control. Hence, this may contribute to the findings of small differences in invertebrate drift densities.

What really was tested in this study was if the density of macroinvertebrates in drift differed between hydropeaked stream channels and a control at two given times of the day. Driving factor for an eventual difference was predicted to be the increased or decreased water velocity as a result of a changed discharge regime. Changes were observed for some taxa and indicated for others, while most of the taxa seem to remain unaffected. Due to the low numbers of invertebrates found in drift in this study, and hence the statistical uncertainty, it is not possible to exclude the chance that some changes did occur. The findings reflect the diversity in benthic macroinvertebrate behavior and morphology, and are in accordance with previous studies where densities in drift have been found to be highest as a result of washout under the initial peaking event. The habitats in fresh water stream systems are changing with the discharge. Sites providing a suitable habitat for some species at one discharge may be suitable for other species at a changed discharge. Meanwhile, characters may have changed at other sites and become suitable for the former, given that they reach there in time and not get carried away by oncoming increased water currents. The ramping rate might thus be the most important factor for maintenance of biodiversity.

20

4.4 Future perspectives

The results in this study support earlier findings, where consequences of hydropeaking in particular affect areas of the river exposed to dewatering (e.g. Arnekleiv, 1994; Harby, 2004). In regulated rivers, it is harder to avoid dewatering than under experimental conditions, and an approach to river channelization would lead to other changes in natural habitats (Borsanyi, 2005) and thus still have impacts on the lotic ecosystems. Nevertheless, it has been shown that stranding of fish to a great extent can be reduced by reducing the ramping rate (Harby, 2004), and it might be predicted that this reduce the consequences for benthic macroinvertebrates as well.

The demand for renewable energy is expected to increase in future years. Hence, the pressure upon countries beneficiary of such resources to contribute to an international goal of reducing climate gas emissions will increase as well. Even if the consequences of hydropower production are reduced to a species specific level, less abundant species still may possess crucial features for ecosystem functioning. Functional groups are in modern time often used as an assessment for maintenance of the environment (Dolédec et al., 1999; 2011). Today, extinction rates found in freshwater ecosystems worldwide are comparable to those found in the rainforests (Gibert, 2008). In this context, it is important to remember not only to maintain the functioning of ecosystems and ecosystem services for the future, but also the biodiversity and its intrinsic value.

References

- Arnekleiv, J. V. (1994). Bestemmelsesnøkkel til Norske Døgnfluelarver (Ephemeroptera Larvae). Norway, Trondheim: Trondheim University Museum.
- Arnekleiv, J. V., Koksvik, J. I., Hvidsten, N. A. & Jensen, A. J. (1994). Virkninger av Bratsbergreguleringen (Bratsberg kraftverk) på bunndyr og fisk i Nidelva, Trondheim (1982-1986). Norwegian University of Science and Technology University Museum Zoologic Series Report 1994-7, 1-56.
- Bergan, M. A. & Nystad, B. E. (2003). Drivfauna, bunndyr og ernæring hos laks (Salmo salar) om vinteren i Stjørdalselva, Nord-Trøndelag. MSc thesis, Norwegian University of Science and Technology.
- Borsanyi, P. (2005). A classification method for scaling river biotopes for assessing hydropower regulation impacts. Ph.D. thesis, Norwegian University of Science and Technology.
- Braaten, P. J., Dey, P. D. & Annear, T. C. (1997). Development and evaluation of bioenergetic-based habitat suitability criteria for trout. *Regulated Rivers: Research & Management* 13, 345-356.
- Brittain, J. E. (1989). Life history strategies in *Ephemeroptera* and *Plecoptera*. In I. C.Campbell (ed.), *Mayflies and Stoneflies; Life Histories and Biology* (pp. 1-12).Netherlands, Dordrecht: Kluwer Academic Publishers.
- Brittain, J. E. & Eikeland, T. J. (1988). Invertebrate drift a review. *Hydrobiologica* **166**, 77-93.
- Brittain, J. E. & Saltveit, S. J. (1989). A review of the effect of river regulations on mayflies (*Ephemeroptera*). *Regulated Rivers: Research & Management* **3**, 191-204.
- Bruno, M. C., Biffi, S., Cashman, M. J. & Maiolini, B. (2014) Effects of repeated hydropeaking waves on benthic invertebrates: a flume study. In *10th International Symposium on Ecohydraulics*, Trondheim, Norway, 23-27 June 2014.
- Charmasson, J. & Zinke, P. (2011). Mitigation measures against hydropeaking effects. SINTEF Energy Research Report **TRA7192**, 1-51.
- Clifford, H. F. (1972). A year's study of the drifting organisms in a brown-water stream of Alberta, Canada. *Canadian Journal of Zoology* **50**, 975-983.
- Covich, A. P., Palmer, M. A., & Crowl, T. A. (1999). The role of benthic invertebrate species in freshwater ecosystems - zoobenthic species influence energy flows and nutrient cycling. *Bioscience* 49, 119-127.
- Cushman, R. M. (1985). Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management* **5**, 330-339.
- Dolédec, S., Statzner, B., & Bournard, M. (1999). Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology* 42, 737-758.

- Dolédec, S., Phillips, N., & Townsend, C. (2011). Invertebrate community responses to land use at a broad spatial scale: trait and taxonomic measures compared in New Zealand rivers. *Freshwater Biology* 56, 1670-1688.
- Ensign, W. E., Strange, R. J. & Moore, S. E. (1990). Summer food limitation reduces brook and rainbow-trout biomass in a southern Appalachian stream. *Transactions of the American Fisheries Society* **119**, 894-901.
- Elliott, J. M. (1967). Invertebrate drift in a Dartmoor stream. *Archive für Hydrobiologie* **63**, 202-237.
- Elliott, J. M. (1968). The daily activity patterns of mayfly nymph (*Ephemeroptera*). Journal of Zoology **155**, 201-221.
- Engblom, E. (1996). *Ephemeroptera*, mayflies. In A. N. Nilsson (ed.), *Aquatic Insects of North Europe - A Taxonomic Handbook* (pp. 13-54). Denmark, Stenstrup: Apollo Books.
- Fjellheim, A. (1996). Distribution of benthic invertebrates in relation to stream flow characteristics in a Norwegian river. *Regulated Rivers: Research & Management* 12, 263-271.
- Frankiewicz, P., Zalewski, M. & Thorpe, J. E. (1993). Feeding pattern of brown trout (Salmo trutta L.) from the river Earn (Scotland), in relation to invertebrate drift. Polish Archives of Hydrobiology 40, 15-29.
- Gersich, F. M. & Brusven, M. A. (1981). Insect colonization rates in near-shore regions subjected to hydroelectric power peaking flows. *Journal of Freshwater Ecology* 1, 231-236.
- Gibert, J., Culver, D. C., Danielopol, D. L., Griebler, C. Gunatilaka, A., Notenboom, J. & Sket, B. (2008). Groundwater ecosystems: human impacts and future management. In N. Polunin (ed.), *Aquatic Ecosystems* (pp. 30-44). UK, Cambridge: Cambridge University Press.
- Gibert, J., Danielpool, D. L. & Stanford, J.A. (1994). *Groundwater Ecology* (p. 571). USA, San Diego: Academic Press.
- Gillooly, J. F. & Dodson, S. I. (2000). The relationship of egg size and incubation temperature to embryonic development time in univoltine and multivoltine aquatic insects. *Freshwater Biology* 44, 595-604.
- Harby, A., Alfredsen, K., Arnekleiv, J. V., Foodmark, L. E. W., Halleraker, J. H., Johansen, S. & Saltveit, S. J. (2004). Raske vannstandsendringer i elver virkninger på fisk, bunndyr og begroing. *SINTEF Energy Research Technical report* TRA5932, 1-39.
- Hill, J. & Grossman, G. D. (1993). An energetic model of microhabitat use for rainbow-trout and rosyside dace. *Ecology* **74**, 685-698.
- Jackson, H. M., Gibbins, C. N. & Soulsby, C. (2007). Role of discharge and temperature variation in determining invertebrate community structure in a regulated river. *River Research and Applications* 23, 651-669.
- Jensen, A. J. & Johnsen, B. O. (1999). The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology* 13, 778-785.
- Jones, J. B. & Mulholland, P. J. (2000). *Streams and Ground Waters* (p. 425). USA, San Diego: Academic Press.

- Lagarrigue, T., Cereghino, P., Lim, P., Reyes-Marchant, P., Chappaz, R., Lavandier, P. & Belaud, A. (2002). Diel and seasonal variations in brown trout (*Salmo trutta*) feeding patterns and relationships with invertebrate drift under natural and hydropeaking conditions in a mountain stream. *Aquatic Living Resources* 15, 129-137.
- Mackay, R. J. (1992). Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 617-628.
- Moog, O. (1993). Quantification of daily peak hydropower effects on aquatic fauna and management to minimize environmental impacts. *Regulated Rivers: Research & Management* 8, 5-14.
- Mortensen, E., Geertz-Hansen, P. & Marcus, E. (1988). The significance of temperature and food as factors affecting the growth of brown trout (*Salmo trutta* L.) in four Danish streams. *Polish Archives of Hydrobiology* **35**, 533-544.
- Nagrodski, A., Raby, G. D., Hasler, C. T., Taylor, M. K. & Cooke, S. J. (2012). Fish stranding in freshwater systems – sources, consequences, and mitigation. *Journal of Environmental Management* 103, 133-141.
- Perry, S. A. & Perry, W. B. (1986). Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. *Hydrobiologia* 134, 171-182.
- Piccolo, J. J., Hughes, N. F. & Bryant, M. D. (2008). Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*). *Canadian Journal of Fisheries and Aquatic Sciences* 65, 266-275.
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E. & Stromberg, J. C. (1997). The natural flow regime: a paradigm for river conservation and restoration. *Bioscience* 47, 769-784.
- Poff, N. L. & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55, 194-205.
- Puffer, M. (2014). *Effects of rapidly fluctuating water levels on juvenile Atlantic salmon* (*Salmo salar* L.). Ph.D. thesis, Norwegian University of Science and Technology.
- Raddum, G. G. (1985). Effects of winter warm reservoir release on benthic stream invertebrates. *Hydrobiologia* **122**, 105-111.
- Raddum, G. G., Arnekleiv, J. V., Halvorsen, G. A., Saltveit, S. J. & Fjellheim, A. (2006).
 Bunndyr. In Saltveit, S. J. (ed.), Økologiske Forhold i Vassdag Konsekvenser av Vannføringsendringer (pp. 65-79). Norway, Oslo: Norwegian Water Resources and Energy Directorate.
- Robinson, C. T., Tockner K., & Burgher, P. (2004). Drift benthos relationships in the seasonal colonization dynamics of alpine streams. *Archives für Hydrobiologie* 160, 447-470.
- Saltveit, S. J. (2006). Økologiske prosesser i rennende vann. In S. J. Saltveit (ed.),
 Økologiske Forhold i Vassdrag Konsekvenser av Vannføringsendringer (pp. 7-16).
 Norway, Oslo: Norwegian Water Resources and Energy Directorate.

- Saltveit, S. J., Bremnes, T. & Brittain, J. E. (1994). Effect of a changed temperature regime on the benthos of a Norwegian regulated river. *Regulated rivers: Research & Management* 9, 93-102.
- Söderström, O. (1991). Life cycle and nymphal growth of twelve coexisting mayfly species in a boreal river. In J. Alba-Trecedor & A. Sanchez-Ortega (eds.), Overview and Strategies of Ephemeroptera and Plecoptera (pp. 503-514). USA, Gainesville: Sandhill Crane Press.

Størset, L. (1995). Smådyr i Ferskvann (pp. 1-103). Norway, Trondheim: Tapir Forlag.

- Valentin, S., Lauters, F., Sabaton, C., Breil, P. & Souchon, Y. (1996). Modelling temporal variations of physical habitat for brown trout (*Salmo trutta*) in hydropeaking conditions. *Regulated Rivers: Research & Management* 12, 317-330.
- Watz, J. (2013). Winter behaviour of stream salmonids: effects of temperature, light, and ice *cover*. Licentiate thesis, Karlstad University.
- Wootton, R. J. (1998). *Ecology of Teleost Fishes*. 2nd edition. Dordrecht: Kuwer Academic Publishers.
- Zbinden, M., Hieber, M., Robinson, C. T. & Uehlinger, U. (2008). Short-term colonization patterns of macroinvertebrates in alpine streams. *Archives für Hydrobiologie* 171, 75-86.

ELECTRONICAL REFERENCES

The Shift Project, (2014). Url: http://www.tsp-data-portal.org

Appendix

Appendix 1: Total flow in stream channels

Total flow i	n stream channels*
Control	126,9
Hydropeaked, low	65,5
Hydropeaked, high	232,6
	*all flows are m ³ /hour

Appendix 2: Flow through drift nets

	Week 11	(15-17 March 2011	1)	
Stream Channel	Discharge	Flow, net 1	Flow, net 2	Flow, net 3
1	Control	6,97	9,98	12,91
2	High	9,89	18,56	18,75
2	Low	7,17	12,86	11,99
3	Control	12,9	14,98	17,62
4	High	16,01	17,52	19,5
4	Low	3,32	3,77	4,51
5	Control	6,41	13,09	9,13
6	High	6,78	15,64	19,5
6	Low	1,77	4,92	7,59
		*	all flows are m3/hou	ır

	Week	23 (7-9 June 2011)		
Stream Channel	Discharge	Flow, net 1	Flow, net 2	Flow, net 3
1	Control	8,76	14,04	12,81
2	High	11,49	19,59	16,67
2	Low	5,36	10,38	6,26
3	Control	8,1	11,49	13,09
4	High	12,05	14,32	17,14
4	Low	3,46	5,78	6,23
5	Control	6,97	14,13	9,7
6	High	12,52	24,68	13,75
6	Low	3,33	6,01	6,51
		*	all flows are m3/hou	ur

Channel 1			Dep	th [c	m]	١	Wate	er vel	ocity	[cm/s]	Channel 3		[Dept	h [cn	n]	Wate	er vel	ocity	[cm/s]	Channel	5	[Dept	h [cr	n]	Wate	er vel	ocity	[cm/s]
Discharge	meter	30	60	90	120)	30	60	90	120	Discharge	meter	30	60	90	120	30	60	90	120	Discharg	e meter	30	60	90	120	30	60	90	120
Control	1	7	8	4	8		51	60	40	34	Control	1	8	10	9	5	58	46	29	8	Control	1	10	10	8	8	51	54	57	26
Control	2	13	11	5	0		73	88	0		Control	2	9	10	8	5	42	75	11	2	Control	2	10	12	10	4	65	66	3	1
Control	3	4	13	13	9		0	75	30	2	Control	3	3	9	12	8	6	65	56	31	Control	3	2	8	13	10	24	67	60	8
Control	4	0	5	12	8			0	87	49	Control	4	0	0	10	12			69	76	Control	4	4	8	13	13	1	9	77	58
Control	5	8	10	13	7		1	40	89	46	Control	5	11	15	15	14	0	2	38	73	Control	5	10	17	18	11	4	31	62	24
Control	6	12	13	6	0		23	66	0		Control	6	12	12	6	0	22	45	59		Control	6	16	15	12	0	38	63	18	
Control	7	14	12	12	5		47	67	2	0	Control	7	13	17	15	13	39	41	3	1	Control	7	13	12	17	16	42	60	18	1
Control	8	8	11	13	9	:	31	67	33	8	Control	8	8	10	14	11	23	52	40	9	Control	8	7	10	11	10	30	51	44	12
Control	9	7	10	14	11		2	50	55	28	Control	9	3	7	15	13	4	30	57	27	Control	9	5	11	11	12	0	43	62	44
Control	10	11	14	12	0		21	58	40		Control	10	11	14	8	0	18	42	48		Control	10	11	11	4	0	25	63	0	
Control	11	11	11	9	9		48	70	16	1	Control	11	7	10	10	8	50	64	36	1	Control	11	8	10	12	12	55	73	11	1
Control	12	12	13	13	10		32	51	18	4	Control	12	8	9	12	11	9	46	56	17	Control	12	9	12	12	11	13	53	32	2
Control	13	0	11	13	12			3	57	35	Control	13	0	6	14	17		3	53	53	Control	13	0	10	13	13		3	62	46
Control	14	13	20	13	16		2	7	57	43	Control	14	12	18	18	15	1	4	47	39	Control	14	15	15	16	10	1	21	63	22
Control	15	19	17	11	0		6	46	51		Control	15	16	13	6	0	31	63	2		Control	15	15	13	8	7	37	69	1	1
Control	16	10	14	12	7		43	61	18	0	Control	16	17	18	16	17	34	23	2	2	Control	16	10	15	19	12	38	55	15	1
Control	17	0	10	11	8			61	59	27	Control	17	3	7	14	13	14	37	46	17	Control	17	2	10	18	15		44	48	21
Control	18	10	16	13	12		2	45	66	29	Control	18	13	15	18	14	2	26	48	10	Control	18	10	12	10	6	29	42	51	21
Control	19	17	18	8	0		15	52	3		Control	19	14	14	7	0	28	57	7		Control	19	12	10	13	6	47	69	2	1
Control	20	11	16	17	15		11	36	34	3	Control	20	9	16	16	14	26	39	7	2	Control	20	12	16	13	12	39	55	17	1
Control	21	0	6	15	17			0	60	18	Control	21	0	0	10	14			67	53	Control	21	0	0	11	13			71	41
Control	22	13	18	15	12		1	14	51	33	Control	22	11	12	17	14	2	1	11	59	Control	22	8	11	10	11	1	10	47	47
Control	23	15	16	8	0		23	52	44		Control	23	17	12	11	0	10	27	28		Control	23	14	12	6	0	23	45	51	
Control	24	11	11	12	7		47	56	7	1	Control	24	13	15	11	5	46	49	1	1	Control	24	15	16	12	10	45	28	2	2
Control	25	10	15	18	17		44	55	17	1	Control	25	13	14	19	17	42	31	16	1	Control	25	12	13	16	16	38	53	10	0

Channel 2			Dept	h [cı	m]	Wa	ter v	velo	city [cm/s]	Channel 2		I	Dept	n [cn	n]	Wate	er vel	ocity	[cm/s]	Channel 2		1	Dept	h [cr	n]	Wat	er vel	ocity	[cm/s]
Discharge	meter	30	60	90	120	30	6	0	90	120	Discharge	meter	30	60	90	120	30	60	90	120	Discharge	meter	30	60	90	120	30	60	90	120
Control	1	7	7	8	6	64	7	9	59	31	Low	1	4	4	4	3	52	49	31	17	High	1	10	10	10	8	55	52	52	40
Control	2	9	11	2	0	92	9	1	2		Low	2	7	4	2	1	14	63	23		High	2	11	12	8	0	80	89	2	
Control	3	8	13	15	11	57	7	2	25	1	Low	3	2	7	8	5	3	56	23	9	High	3	11	17	18	15	52	78	27	1
Control	4	10	11	12	13	1	1	3	83	53	Low	4	2	6	7	7	6	31	52	39	High	4	5	11	16	15	2	3	89	52
Control	5	14	18	17	14	0	1	5	71	44	Low	5	8	10	10	7	8	26	44	11	High	5	16	18	20	15	2	13	73	53
Control	6	12	14	13	0	46	5	7	5		Low	6	5	7	7	0	32	47	2		High	6	13	18	12	1	34	60	12	0
Control	7	14	15	16	16	50	6	5	3	1	Low	7	8	11	12	9	29	45	4	1	High	7	16	19	22	20	60	50	4	1
Control	8	10	14	14	12	31	5	3	40	10	Low	8	5	6	10	7	15	39	32	18	High	8	15	14	17	12	38	56	32	3
Control	9	10	11	18	16	2	6	0	58	35	Low	9	5	7	10	11	6	28	28	27	High	9	10	14	19	18	3	67	59	26
Control	10	15	16	10	0	21	6	1	2		Low	10	9	11	8	0	9	31	1		High	10	18	18	12	0	23	63	3	
Control	11	8	15	14	11	44	6	1	20	3	Low	11	6	7	9	6	24	45	16	2	High	11	10	16	17	11	63	76	22	6
Control	12	15	14	14	9	33	5	3	50	22	Low	12	8	9	9	4	8	36	34	14	High	12	15	14	16	11	48	51	43	12
Control	13	0	12	16	8		3	3	76	60	Low	13	0	6	10	6		2	64	16	High	13	0	13	18	10		2	73	64
Control	14	19	18	17	15	1	1	9	62	35	Low	14	11	10	12	6	2	10	55	2	High	14	18	18	21	19	1	12	65	55
Control	15	14	15	12	0	38	6	9	7		Low	15	9	9	6	0	23	51	10		High	15	14	15	14	3	38	68	42	0
Control	16	14	17	18	15	41	6	3	10	3	Low	16	9	14	15	12	14	43	7	1	High	16	17	22	18	17	42	70	13	1
Control	17	2	10	16	16	1	5	5	50	8	Low	17	0	4	10	11		36	34	8	High	17	2	14	18	16	7	62	52	11
Control	18	11	12	12	14	20	5	2	48	13	Low	18	6	6	6	6	24	43	36	13	High	18	15	13	13	13	27	60	48	20
Control	19	13	13	6	0	50	6	0	0		Low	19	8	8	3	0	49	45	0		High	19	14	14	9	0	51	72	1	
Control	20	15	17	17	17	46	5	3	4	1	Low	20	9	15	14	10	41	31	1	2	High	20	11	18	19	18	51	59	5	1
Control	21	0	6	11	15		6	0	47	33	Low	21	0	4	9	8		45	45	7	High	21	0	11	15	17		65	64	30
Control	22	11	12	16	11	1	1	1	57	50	Low	22	9	10	11	9	1	2	44	31	High	22	12	17	18	16	1	8	79	44
Control	23	18	13	13	0	36	5	1	57		Low	23	10	9	6	0	15	35	42		High	23	16	16	14	1	27	58	46	6
Control	24	10	12	11	6	57	4	2	1	0	Low	24	11	10	7	6	35	34	1	0	High	24	15	15	11	8	73	78	14	2
Control	25	17	20	20	18	33	5	2	6	4	Low	25	10	13	17	17	23	28	3	2	High	25	18	18	21	19	60	43	9	3

Channel 4			Dept	th [c	m]	w	ate	r velo	ocity	[cm/s]	Channel 4			Dept	h [cr	n]	Wat	er vel	ocity	[cm/s]	Channel	L I	[Dept	h [cr	n]	Wate	er vel	ocity	[cm/s]
Discharge	meter	30	60	90	120	30	0	60	90	120	Discharge	meter	30	60	90	120	30	60	90	120	Discharg	e meter	30	60	90	120	30	60	90	120
Control	1	5	7	7	6	83	3	68	54	32	Low	1	3	4	4	3	48	50	51	8	High	1	9	10	13	13	63	66	74	41
Control	2	10	8	9	6	49	9	65	2	2	Low	2	7	7	6	4	9	43	12	5	High	2	14	17	14	9	72	84	2	1
Control	3	6	10	11	8	36	6	61	53	10	Low	3	5	6	4	4	6	39	41	22	High	3	11	17	16	14	50	66	42	7
Control	4	0	10	10	8			1	77	48	Low	4	0	4	6	7		11	52	42	High	4	3	13	18	15	0	1	85	45
Control	5	15	14	16	10	3	3	22	67	39	Low	5	8	8	8	5	2	24	40	2	High	5	18	18	19	14	2	17	84	51
Control	6	14	11	12	0	3	1	59	1		Low	6	9	8	4	0	19	45	2		High	6	18	21	17	3	34	77	5	0
Control	7	11	14	15	9	44	4	55	11	4	Low	7	8	8	10	3	19	37	8	1	High	7	15	19	18	15	55	60	9	6
Control	8	5	10	13	11	2'	1	41	47	15	Low	8	3	8	8	7	8	25	26	14	High	8	10	18	15	16	28	60	48	8
Control	9	0	10	13	11			34	56	37	Low	9	0	6	9	7		17	45	30	High	9	6	11	18	17	3	19	70	46
Control	10	11	11	12	0	32	2	54	55		Low	10	6	7	7	0	20	46	17		High	10	15	17	16	0	34	67	54	
Control	11	11	13	15	10	39	9	66	5	2	Low	11	8	10	9	6	22	39	2	0	High	11	18	21	18	15	52	70	2	4
Control	12	9	13	13	14	18	8	51	29	2	Low	12	6	9	10	9	2	28	19	5	High	12	15	19	20	18	40	61	24	1
Control	13	3	7	11	10	0)	6	57	44	Low	13	0	6	7	5		12	49	31	High	13	2	11	18	17	0	1	75	44
Control	14	12	13	12	10	3	3	24	51	37	Low	14	8	10	10	6	2	23	44	2	High	14	17	18	16	17	1	19	72	40
Control	15	13	11	11	2	44	4	67	8	0	Low	15	7	10	6	0	34	47	1		High	15	14	19	17	3	45	70	33	0
Control	16	11	12	16	10	23	3	56	18	1	Low	16	10	9	10	7	9	43	14	1	High	16	16	18	20	14	39	61	17	5
Control	17	2	7	16	11	9)	51	42	25	Low	17	0	5	8	7		36	29	17	High	17	3	13	16	15	26	64	57	17
Control	18	10	12	10	3	12	2	56	56	20	Low	18	7	7	9	1	22	38	49	3	High	18	14	15	15	10	22	59	47	30
Control	19	12	12	9	2	49	9	75	1	0	Low	19	6	7	6	0	47	16	2		High	19	15	17	11	3	52	81	6	0
Control	20	10	15	13	11	30	0	66	17	1	Low	20	8	10	10	8	24	40	12	1	High	20	15	20	20	15	48	66	18	2
Control	21	0	4	15	13			2	62	38	Low	21	0	1	8	9		0	48	24	High	21	0	5	18	18		6	58	46
Control	22	11	11	12	10	1		14	57	49	Low	22	7	9	9	5	2	15	42	17	High	22	11	18	18	13	2	16	81	62
Control	23	12	13	10	0	18	8	50	46		Low	23	9	11	7	0	12	34	17		High	23	17	17	17	2	19	47	45	9
Control	24	8	13	13	10	33	3	59	2	2	Low	24	5	10	10	5	24	36	2	2	High	24	10	18	15	11	61	91	3	2
Control	25	10	11	10	11	43	3	63	8	1	Low	25	6	9	12	12	13	38	24	8	High	25	13	13	17	16	60	95	36	4

Channel 6			Dept	th [c	m]	Wa	ter ve	locity	[cm/s]	Channel 6		1	Dept	h [cn	n]	Wat	er vel	ocity	[cm/s]	Channel	5		Dept	h [cr	n]	Wat	er ve	locity	[cm/s]
Discharge	meter	30	60	90	120	30	60	90	120	Discharge	meter	30	60	90	120	30	60	90	120	Discharge	meter	30	60	90	120	30	60	90	120
Control	1	6	8	8	5	66	59	46	24	Low	1	4	3	5	2	59	48	47	12	High	1	13	10	13	8	61	64	51	24
Control	2	8	10	9	6	66	69	3	2	Low	2	8	8	8	1	35	51	12	0	High	2	15	16	13	9	80	84	2	2
Control	3	0	8	11	10		53	66	3	Low	3	0	7	8	7		33	38	13	High	3	10	16	18	15	46	73	52	10
Control	4	6	9	12	7	1	14	71	64	Low	4	1	6	8	4	0	23	66	26	High	4	11	14	17	15	2	3	100	63
Control	5	12	13	13	10	1	23	60	53	Low	5	9	10	10	4	3	47	36	17	High	5	19	19	20	16	2	28	83	40
Control	6	14	14	6	0	28	63	24		Low	6	10	10	2	0	35	41	11		High	6	21	20	14	2	25	70	72	0
Control	7	13	16	12	12	38	58	9	1	Low	7	8	10	10	9	29	26	3	1	High	7	18	21	19	18	42	75	7	1
Control	8	5	9	12	11	28	51	44	10	Low	8	2	7	9	8	12	29	30	14	High	8	10	14	18	18	49	63	52	9
Control	9	4	10	10	12	1	53	58	43	Low	9	2	7	9	8	0	30	48	33	High	9	9	15	20	18	9	62	78	37
Control	10	11	12	11	0	25	51	53		Low	10	6	8	8	0	17	36	43		High	10	17	18	18	0	28	67	45	
Control	11	7	12	12	9	46	64	14	2	Low	11	5	10	10	6	17	45	9	1	High	11	15	19	18	15	52	82	8	1
Control	12	10	13	17	16	22	48	29	1	Low	12	6	10	12	8	0	29	25	0	High	12	17	21	21	19	39	57	35	3
Control	13	0	7	12	11		0	62	40	Low	13	0	6	10	8		1	46	26	High	13	4	11	20	18	0	2	81	55
Control	14	16	10	12	13	5	20	56	28	Low	14	10	9	10	8	0	22	39	6	High	14	20	19	21	18	1	10	59	48
Control	15	12	18	12	3	27	50	58	0	Low	15	9	13	11	1	19	43	12	0	High	15	19	22	18	5	20	65	68	0
Control	16	14	15	17	12	28	49	15	1	Low	16	10	13	12	11	20	37	6	1	High	16	17	21	20	18	31	69	25	3
Control	17	0	9	10	11		50	41	21	Low	17	0	7	8	8		30	29	13	High	17	4	16	21	16	4	64	52	18
Control	18	9	10	11	7	34	45	51	19	Low	18	5	8	8	4	23	44	43	9	High	18	13	18	18	12	25	62	50	29
Control	19	12	11	2	0	49	62	0		Low	19	8	10	1	0	41	51	0		High	19	18	20	7	0	51	86	2	
Control	20	11	13	13	12	40	59	15	1	Low	20	10	10	12	9	28	47	7	2	High	20	16	19	19	16	44	75	7	0
Control	21	0	0	11	12			61	22	Low	21	0	1	10	7		0	47	17	High	21	0	0	20	18			66	29
Control	22	11	13	15	12	1	2	55	46	Low	22	10	12	12	10	1	1	35	41	High	22	16	19	20	18	1	1	54	51
Control	23	12	13	9	0	17	42	52		Low	23	10	12	8	0	7	27	44		High	23	18	18	11	0	16	65	86	
Control	24	12	15	13	11	43	50	3	1	Low	24	9	12	11	11	22	28	1	2	High	24	17	17	18	15	59	70	7	4
Control	25	12	12	19	18	45	52	8	2	Low	25	13	14	18	16	19	33	7	1	High	25	17	20	22	20	50	68	26	1

Channel / Sample	1/1	1/2	1/3	1/4	1/5	1/6
13:00	March 17th					
Ephemeroptera	4	2	3	8	7	5
L. marginata			1	3		1
L. vespertina	1		1	1	3	
Ephemerella sp.						
Baetis sp.	3	2		2	2	2
Heptagenia sp.			1	2	2	2
Plecoptera	11	5	5	15	21	56
Trichoptera	21	13	3	2	1	18
Simuliidae	1	6		14	1	9
Ceratopogonidae						
Chironomidae	41	48	37	64	89	4
Elmidae	1	1		1	1	
Turbellaria						
Lymnaeidae				3	2	2
Oligochaeta			1	1		
A. aquaticus	8	5	4	8	7	3
Odonata						

Appendix 4: Winter Surber samples

Channel / Sample	2/1	2/2	2/3	2/4	2/5	2/6
13:00	March 16th					
Ephemeroptera	1	15	15	18		6
L. marginata		1				
L. vespertina	1					
Ephemerella sp.			1			
Baetis sp.		8	4	11		
Heptagenia sp.		6	10	5		
Plecoptera	3	7	5	5		10
Trichoptera	1		1			
Simuliidae			2	1	2	83
Ceratopogonidae	1					
Chironomidae	69	121	66	63	105	64
Elmidae						
Turbellaria		8	1	3	4	
Lymnaeidae				3		
Oligochaeta					2	
A. aquaticus	15	22	6	5	15	1
Odonata						

Appendix 4 (continue)

Channel / Sample	3/1	3/2	3/3	3/4	3/5	3/6
13:00	March 21th					
Ephemeroptera	16	25	22	14	3	49
L. marginata		1	1	3		
L. vespertina				2		
Ephemerella sp.		1		1		
Baetis sp.	5	10	9	1		16
Heptagenia sp.	11	12	12	7	3	33
Plecoptera	6	8	16	10		44
Trichoptera			1			1
Simuliidae	6	1		2	1	37
Ceratopogonidae				1		
Chironomidae	56	52	36	108	51	74
Elmidae						
Turbellaria		1			3	
Lymnaeidae	1	1		3	1	2
Oligochaeta				1	5	
A. aquaticus	26	10	8	31	29	8
Odonata						

Channel / Sample	4/1	4/2	4/3	4/4	4/5	4/6
13:00	March 21th					
Ephemeroptera	22	39	16	53	13	40
L. marginata			2		2	2
L. vespertina		1	4	1	1	
Ephemerella sp.					1	3
Baetis sp.	6	13	3	7	5	20
Heptagenia sp.	16	24	6	45	4	15
Plecoptera	18	26	8	37	9	129
Trichoptera	4	8	3	5	1	6
Simuliidae	3			4	2	12
Ceratopogonidae						
Chironomidae	43	81	112	42	91	94
Elmidae						
Turbellaria	3	1	1			
Lymnaeidae			1		1	
Oligochaeta						
A. aquaticus	2	20	5		13	4
Odonata						

Appendix 4 (continue)

Channel / Sample	5/1	5/2	5/3	5/4	5/5	5/6
13:00	March 16th					
Ephemeroptera	9	25	32	28	32	20
L. marginata						
L. vespertina		2				
Ephemerella sp.						
Baetis sp.		12	9	5	8	8
Heptagenia sp.		11	23	23	24	12
Plecoptera	4	10	7	20	27	44
Trichoptera		2	4	12	7	2
Simuliidae		1	9	53	20	11
Ceratopogonidae						
Chironomidae	17	42	46	57	122	163
Elmidae					2	1
Turbellaria		3	1			
Lymnaeidae		3			3	5
Oligochaeta						
A. aquaticus	2	7	2	5	13	2
Odonata						

Channel / Sample	6/1	6/2	6/3	6/4	6/5	6/6
13:00	March 16th					
Ephemeroptera	14	36	3	32	4	12
L. marginata		1			2	2
L. vespertina		2	2		1	
Ephemerella sp.						1
Baetis sp.	8				1	2
Heptagenia sp.	6	33	1	32		7
Plecoptera	10	55	1	29	3	14
Trichoptera	6	9	3	4	4	3
Simuliidae	2	2				1
Ceratopogonidae						
Chironomidae	75	48	115	54	120	99
Elmidae			1			1
Turbellaria		3	4	2		
Lymnaeidae		2	3	2	1	
Oligochaeta					3	
A. aquaticus	3	12	22	7	20	6
Odonata					1	

Channel / sample	1/1	1/2	1/3	2/1	2/2	2/3
13:00	June 9th	June 9th	June 9th	June 8th	June 8th	June 8th
Ephemeroptera	3	1	1	1	2	3
L. marginata						
Ephemerella sp.	3					
Baetis sp.						
Caenis sp.			1	1	2	3
Heptagenia sp.						
Plecoptera	1	1	1		5	
Trichoptera	22	22	18		5	
Simuliidae					11	
Ceratopogonidae			3			1
Chironomidae	34	43	78	10	68	61
Elmidae			4		7	11
Turbellaria	1			2	4	
Nematoda						
Lymnaeidae	1		1			1
Oligochaeta				1		1
A. aquaticus	11	20	16	14	15	36
Hydrachnidae					1	

Appendix 5: Summer Surber samples

Channel / sample	3/1	3/2	3/3	4/1	4/2	4/3
13:00	June 9th					
Ephemeroptera	3	12	22	1	8	2
L. marginata						
Ephemerella sp.			6			
Baetis sp.	2	3	6	1	1	
Caenis sp.		6	10		3	2
Heptagenia sp.	1	3			4	
Plecoptera		1	3	2		
Trichoptera	4	13	24	2	10	2
Simuliidae	5	54	422	7	49	1
Ceratopogonidae						
Chironomidae	20	101	62	8	11	25
Elmidae	3	14		2	4	2
Turbellaria						
Nematoda			1	1		
Lymnaeidae						1
Oligochaeta						4
A. aquaticus	1	24	11	7	3	25
Hydrachnidae						

Appendix

Appendix 5 (continue)

Channel / sample	5/1	5/2	5/3	6/1	6/2	6/3
13:00	June 8th					
Ephemeroptera	2	7	30	1	3	11
L. marginata					1	
Ephemerella sp.		2				
Baetis sp.	1	1	5			
Caenis sp.	1	4	21	1	2	8
Heptagenia sp.			4			2
Plecoptera		1	1			
Trichoptera	2	16	23		6	20
Simuliidae		10	21			1
Ceratopogonidae					1	
Chironomidae	15	63	81	7	14	33
Elmidae	2	2	7	2		5
Turbellaria	1					1
Nematoda						
Lymnaeidae						
Oligochaeta					5	
A. aquaticus	3	17	6	24	82	32
Hydrachnidae						

Appendix 6: Winter daytime drift

Channel / Sample	1/1	1/2	1/3	2/1	2/2	2/3
13:00	March 17th	March 17th	March 17th	March 16th	March 16th	March 16th
Ephemeroptera		2	2	1	2	2
B. rhodani						
B. muticus						
H. dalecarlica						
H. sulphurea						
L. marginata				1		1
L. vespertina		2	2		2	1
C. horaria						
Plecoptera					1	1
Trichoptera						
Simuliidae	1	1	1		1	
Chironomidae	4	4	5	14	4	19
Chaoboridae				1	1	2
A. aquaticus					1	

Channel / Sample 13:00	3/1 March 16th	3/2 March 16th	3/3 March 16th	3/1 March 17th	3/2 March 17th	3/3 March 17th
Ephemeroptera	1	3	2		3	2
B. rhodani					1	1
B. muticus						
H. dalecarlica						
H. sulphurea			1			
L. marginata	1				1	
L. vespertina		3	1			1
C. horaria					1	
Plecoptera		1	2			
Trichoptera					1	
Simuliidae				1	1	1
Chironomidae	1	3		6	1	2
Chaoboridae	1	1	2			
A. aquaticus			1	1		

Appendix

Appendix 6 (continue)

Channel / Sample	4/1	4/2	4/3	4/4	4/5	4/6
13:00	March 16th	March 16th	March 16th	March 17th	March 17th	March 17th
Ephemeroptera	2	5	5		4	2
B. rhodani						
B. muticus					2	
H. dalecarlica						
H. sulphurea						
L. marginata		1			1	
L. vespertina	2	4	5		1	2
C. horaria						
Plecoptera	1			1	1	3
Trichoptera					1	
Simuliidae						1
Chironomidae	3	4	3	10	2	4
Chaoboridae		1		1	1	
A. aquaticus	1		3	1		

Channel / Sample	1/1	1/2	1/3	2/1	2/2	2/3
13:00	March	March	March	March	March	March
	17th	17th	17th	16th	16th	16th
Ephemeroptera		1	1	2	5	5
B. rhodani						
B. muticus		1				
H. dalecarlica						
H. sulphurea						
L. marginata				1		1
L. vespertina			1	1	5	4
C. horaria						
Plecoptera	1	1			1	1
Trichoptera						
Simuliidae						
Chironomidae	3	9	4	9	15	23
Chaoboridae		2		1	3	2
A. aquaticus						2

	1/1	1/2	1/3	2/1	2/2	2/3
01:00	March 17th	March 17th	March 17th	March 16th	March 16th	March 16th
Ephemeroptera		2	2	2	2	4
B. rhodani						
B. muticus						1
H. dalecarlica						
H. sulphurea						
L. marginata		1		2	1	2
L. vespertina		1	2		1	1
C. horaria						
Plecoptera	1			1	1	1
Trichoptera	1					
Simuliidae	1	1				
Chironomidae	2	7	2	4	7	2
Chaoboridae			1	4	12	6
Elmidae						
Turbellaria					1	
A. aquaticus				1		
Collembola						
Hydracnidae						

Appendix 7: Winter nighttime drift

	3/1	3/2	3/3	3/1	3/2	3/3
01:00	March 16th	March 16th	March 16th	March 17th	March 17th	March 17th
Ephemeroptera	4	3	5	2	1	1
B. rhodani			1	1		
B. muticus	1			1		
H. dalecarlica		1				
H. sulphurea						1
L. marginata		1	1			
L. vespertina	3	1	3		1	
C. horaria						
Plecoptera		2		1		1
Trichoptera						
Simuliidae	3		1	5	3	3
Chironomidae	2	1	2	1	1	3
Chaoboridae	7	13	16		2	1
Elmidae	1					
Turbellaria	1			1		
A. aquaticus	1		4		1	
Collembola						
Hydracnidae						

Appendix 7 (continue)

	4/1	4/2	4/3	4/1	4/2	4/3
01:00	March 16th	March 16th	March 16th	March 17th	March 17th	March 17th
Ephemeroptera		2	1	1	5	
B. rhodani						
B. muticus					1	
H. dalecarlica						
H. sulphurea		1				
L. marginata		1	1	1	1	
L. vespertina					3	
C. horaria						
Plecoptera	1	1				
Trichoptera						
Simuliidae		1				
Chironomidae		1		1		
Chaoboridae	1	3	4		1	
Elmidae						
Turbellaria		1				
A. aquaticus			1			
Collembola						
Hydracnidae						

	5/1	5/2	5/3	6/1	6/2	6/3
01:00	March 16th					
Ephemeroptera	2	2	3	2	1	3
B. rhodani	2	2	0	2	1	Ū
B. muticus			1	1	I	
H. dalecarlica						
H. sulphurea						
L. marginata	2			1		1
L. vespertina		2	2			2
C. horaria						
Plecoptera		2				
Trichoptera						
Simuliidae		2				
Chironomidae	4	4	5	2	3	3
Chaoboridae	9	19	9		3	18
Elmidae						
Turbellaria						
A. aquaticus	1	1				
Collembola						1
Hydracnidae		1				

Channel / Sample	1/1	1/2	1/3	2/1	2/2	2/3
13:00	June 8th					
Ephemeroptera			2	1	2	
E. ignita			1			
H. sulphurea						
L. vespertina						
Baetis sp.					1	
Caenis sp.					1	
Plecoptera					2	
Trichoptera				2	1	
Simuliidae	1					
Ceratopogonidae	3		3	8	5	1
Chironomidae	3		32	29	27	16
Hydrophilidae						1
Elmidae						
Turbellaria					1	
Nematoda						
Oligochaeta						
A. aquaticus					1	1
Hydracnidae						

Appendix 8: Summer daytime drift

Channel / Sample	3/1	3/2	3/3	3/1	3/2	3/3
13:00	June 8th	June 8th	June 8th	June 9th	June 9th	June 9th
Ephemeroptera	1		1		1	2
E. ignita						1
H. sulphurea						
L. vespertina					1	
Baetis sp.			1			1
Caenis sp.	1					
Plecoptera				1		
Trichoptera	2	1	1			1
Simuliidae	19	28	24	12	28	15
Ceratopogonidae						1
Chironomidae	26	12	18	17	22	15
Hydrophilidae						
Elmidae						
Turbellaria	1	2			2	1
Nematoda						1
Oligochaeta				3		
A. aquaticus	4	2	2	1	6	7
Hydracnidae						

Appendix 8 (continue)

Channel / Sample	4/1	4/2	4/3	4/4	4/5	4/6
13:00	June 8th	June 8th	June 8th	June 9th	June 9th	June 9th
Ephemeroptera	1	1	0	1	2	
E. ignita						
H. sulphurea		1				
L. vespertina					2	
Baetis sp.						
Caenis sp.	1			1		
Plecoptera		1			1	
Trichoptera	2	3	1	3	4	4
Simuliidae	9	15	11	9	9	9
Ceratopogonidae						
Chironomidae	16	22	28	12	29	36
Hydrophilidae						
Elmidae	3	1	2		1	2
Turbellaria	1					
Nematoda		3				1
Oligochaeta						
A. aquaticus	6	15	4	5	6	4
Hydracnidae						

Channel / Sample	5/1	5/2	5/3	6/1	6/2	6/3
13:00	June 8th					
Ephemeroptera	2		2	1	24	24
E. ignita	2		1	1		
H. sulphurea						
L. vespertina						
Baetis sp.			1			
Caenis sp.					24	24
Plecoptera		1			1	2
Trichoptera				3	4	8
Simuliidae	2	3	3	1	4	4
Ceratopogonidae						
Chironomidae	18	7	14	18	47	28
Hydrophilidae						
Elmidae					4	4
Turbellaria	2			2	3	5
Nematoda			1			
Oligochaeta			3		7	4
A. aquaticus				4		1
Hydracnidae			1		1	

Channel / Sample	1/1	1/2	1/3	2/1	2/2	2/3
01:00	09.jun	09.jun	09.jun	08.jun	08.jun	08.jun
Ephemeroptera			1	1		
E. ignita						
Baetis sp.						
B. rhodani						
B. muticus				1		
Heptagenia sp.						
Caenis sp.						
Plecoptera				2		
Trichoptera	2		3		2	1
Simuliidae			8	10	2	2
Ceratopogonidae						
Chironomidae	6	1	10	15	3	11
Chaoboridae				2		
Corixidae						
Argulus						
A. aquaticus						
Collembola						3
Haliplidae					1	1
Hydrophilidae						1
Elmidae						
Turbellaria				1		
Nematoda						
Oligochaeta	1					
Hydracnidae				1		

Appendix 9: Summer nighttime drift

Appendix 9 (continue)

Channel / Sample	3/1	3/2	3/3	3/1	3/2	3/3
01:00	08.jun	08.jun	08.jun	09.jun	09.jun	09.jun
Ephemeroptera		4			2	2
E. ignita						
Baetis sp.		1				
B. rhodani						1
B. muticus		1				
Heptagenia sp.						
Caenis sp.		2			2	1
Plecoptera						
Trichoptera	1	3	5	1	6	1
Simuliidae	7	18	29	18	27	14
Ceratopogonidae						1
Chironomidae	2	23	16	1	22	23
Chaoboridae						
Corixidae		1				
Argulus						
A. aquaticus	3	2		2	2	4
Collembola						
Haliplidae		1				
Hydrophilidae						
Elmidae					1	2
Turbellaria			1			6
Nematoda						
Oligochaeta						
Hydracnidae			1			1

Appendix 9 (continue)

Channel / Sample	5/1	5/2	5/3	6/1	6/2	6/3
01:00	08.jun	08.jun	08.jun	08.jun	08.jun	08.jun
Ephemeroptera		1		10		5
E. ignita		1				
Baetis sp.						
B. rhodani						
B. muticus						
Heptagenia sp.						
Caenis sp.						
Plecoptera		1		3		9
Trichoptera		1	2			
Simuliidae	1	1	3			1
Ceratopogonidae						
Chironomidae	8	21	5	2	2	14
Chaoboridae						
Corixidae						
Argulus						
A. aquaticus		1				
Collembola						
Haliplidae						
Hydrophilidae						
Elmidae						
Turbellaria						1
Nematoda						
Oligochaeta						
Hydracnidae						