Master's thesis

NTNU
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Biodiversity of benthic invertebrates in regulated and unregulated lakes

Master's thesis in Natural Science with Teacher Education
Supervisor: Gaute Kjærstad
Co-supervisor: Ivar Herfindal & Anders G. Finstad
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Acknowledgements

This master's thesis in biology is written as part of my Natural Science with Teacher Education degree. Working on this thesis, I have acquired both theoretical knowledge about biodiversity and anthropogenic influences on nature, as well as practical skills needed to investigate such matters, both in the field and in the lab. I believe that these are important skills to have as a biologist, but I also believe that these skills could prove valuable in the teaching profession. Sustainable development has been adopted as part of the core curriculum in the Norwegian educational system, and the knowledge and skills I have acquired through my work on this thesis will shape how I teach this curriculum in the future.

I extend my heartfelt thanks to all the people who have helped me out while writing this thesis. Gaute Kjærstad, my main supervisor, for giving me the opportunity to work with this project in the first place, but also for sharing his vast knowledge and skills in both the field and the lab. Ivar Herfindal and Anders G. Finstad, my co-supervisors, who provided invaluable insight for both interpreting my analyses, as well as the writing process. Anette G. Davidsen, for helping me make sense of ”Naturtyper i Norge”. Hanne B. Krogstie and Christianne D. Solvåg for helping me in the field and the lab. Hanne also deserves an extra thanks for providing the map in Figure 1. I must also thank Fredrik Ø. Hanslin for sharing his knowledge on R with me.

Lastly, I will thank all the people who may not have had a direct hand in the making of the thesis, but whom I have had in my corner. I thank the freshwater group at NTNU University Museum for welcoming me into the fold. I thank Anita Kalteborn and all my colleagues in the faunistics course for nurturing my love for insects and taxonomy. And last, but certainly not least, all my family and friends, for your unyielding support.

Vetle Knardahl Rem - Trondheim, June 2024

Abstract

Anthropogenic influences on ecosystems, in particular changes in area usage and associated habitat destruction and fragmentation, are causing global losses in biodiversity. Freshwater ecosystems are under great pressure because of their potential for hydroelectric power production. Most research has been devoted to the effect of hydropower development on riverine systems, and less is known about the effects on lakes and in particular their benthic invertebrates. Therefore, more research on lake impact is needed to further sustainable developments of freshwater systems.

The goal of this study was to investigate the impact of hydropower on lacustrine benthic invertebrate communities, focusing on insects in the orders Ephemeroptera, Plecoptera and Trichoptera (EPT species). This was done by using a control-impact design. EPT species were chosen due to their susceptibility to environmental stressors and role as indicator species. Benthic invertebrates were gathered by "kick-sampling" in six lakes, three lakes impacted by hydropower, and three control lakes without hydropower regulation. The species richness, abundance and Simpson index were the biodiversity metrics used to compare the composition of EPT taxa in the impact and control lakes. In addition, species abundance distributions were made for control and impact lakes. Samples from both spring and fall 2023 were used to provide a temporal aspect to the analysis, both for the described biodiversity measures, but also through a temporal species turnover plot. These analyses were used to establish if and how EPT communities in lakes are impacted by hydropower operations.

This study found that the abundance of EPT species in lakes impacted by hydropower was significantly lower than that of control lakes. However, the species richness and Simpson index did not show a significant effect of hydropower impact. The community composition seemed to be more unstable in regulated lakes, as shown by a higher turnover of species between spring and fall communities in regulated lakes compared to unregulated lakes. A significant interaction was discovered between seasonality and regulation status on the abundance of EPT individuals, which implies that the seasonal increase in EPT abundance is lower in regulated lakes compared to unregulated lakes. The combination of these results indicate that hydropower regulation has a disturbing effect on benthic invertebrate communities in lakes, but that this effect might not be apparent in all measures.

Sammendrag

Menneskelige påvirkninger på økosystemer, særlig endring i arealbruk og tilknyttet habitatødeleggelse og fragmentering, er i ferd med å skape globale tap i biodiversitet. Ferskvannssystemer er spesielt utsatt, siden de har et ettertraktet potensiale for utbygging av vannkraft. Brorparten av forskning på effekten av vannkraft på ferskvannssystemer er viet til elvesystemer, og det finnes mindre kjennskap om hvordan innsjøer og tilknyttede bunndyr påvirkes av vannkraft. I lys av dette er det et behov for mer forskning på hvordan innsjøer påvirkes for å fremme bærekraftig utvikling og bruk av ferskvannssystemer.

Målet med denne studien var å undersøke hvordan vannkraft påvirker bunndyrsamfunn i innsjøer, med et særlig fokus på ordenene Ephemeroptera, Plecoptera og Trichoptera (EPT-arter). Dette ble gjort med et kontroll-inngrep-studie (Control-impact design). EPT-artene ble valgt på grunn av deres ømfintlighet for miljøpåvirkninger og fordi de regnes som indikatorarter. Bunndyr ble samlet med ”sparkeprøver” i seks innsjøer, der tre av innsjøene var påvirket av vannkraftsregulering og tre innsjøer var upåvirket av vannkraftsregulering. Artsrikheten, abundansen og Simpsonindeksen ble brukt som biodiversitetsmetrikker for å sammenligne påvirkede innsjøer med upåvirkede innsjøer. I tillegg ble det laget artsabundansfordelinger for begge innsjøgruppene. Sparkeprøver fra både vår og høst 2023 ble brukt for å gi et bredere tidsperspektiv på analysene av biodiversitetsmetrikkene, og for å undersøke utskiftningen av arter (temporal species turnover). Analysene ble ble brukt for å undersøke om og hvordan EPT-samfunn i innsjøer påvirkes av vannkraftregulering.

Som del av studien ble det oppdaget at abundansen av EPT-arter i innsjøer påvirket av vannkraft er signifikant lavere enn i upåvirkede innsjøer. Det ble derimot ikke funnet en signifikant påvirkning på hverken artsrikheten eller Simpsonindeksen som følge av vannkraftpåvirkning. Artssammensetningen i regulerte innsjøer så ut til å være mer ustabil, som vist av den økte utskiftningen av arter fra vår til høst i regulerte innsjøer sammenlignet med uregulerte innsjøer. Det ble også oppdaget en signifikant interaksjon mellom reguleringstatus og endring i årstid, hvilket impliserer at økningen i abundans fra vår til høst er lavere i regulerte innsjøer enn i uregulerte innsjøer. Resultatene tyder på at vannkraftregulering er en forstyrrende faktor for bunndyr i innsjøer, men at effekten ikke kommer til syne i alle mål.

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1 Introduction

A major part of solving the ongoing climate crisis lies in shifting global energy production away from fossil fuels and towards sustainable, clean, and renewable sources of energy (United Nations, 2015). Hydropower is the most widely used renewable energy source on a global scale, accounting for 16% of global electricity demand (Wasti et al., 2022). Hydropower has low carbon-emissions that are mostly connected to the establishing/building of dams/power plants, and is inexpensive to establish and maintain compared to other renewable energy sources such as wind or solar power (Wasti et al., 2022). It is suggested that further development of hydropower capacity will be necessary to keep global temperatures below 2°C over pre-industrial averages (Wasti et al., 2022). However, a disadvantage with renewable energy sources is their large spatial demands relative to energy output compared to fossil energy sources (Kaza & Curtis, 2014). In the case of hydropower, the spatial impacts are connected to both the creation of reservoirs, as well as hydromorphological impacts in connected lakes and rivers. (Bragg et al., 2003; Kjærstad et al., 2018; Reid et al., 2019). The leading source of biodiversity loss is the destruction and fragmentation of habitats due to changed usage of these areas (Hanski, 2011; IPBES, 2019).

Freshwater ecosystems cover just 2.3% of the earth's surface, but provide several ecosystem services and host an estimated 10% of all described animal species (Postel, Carpenter, et al., 1997; Reid et al., 2019). The monetary value of global ecosystem services provided by lakes alone have been estimated to worth 5.1 trillion USD anually (Li & Tsigaris, 2024). Many ecosystem services provided by lakes are directly connected to lake biodiversity. At the same time, freshwater systems lose biodiversity at a faster pace than both marine and terrestrial systems due to anthropogenic disturbances (Dudgeon et al., 2006).

The release of water from regulated lakes will depend on the demand for energy production, where low energy demand results in low water release and vice versa for high energy demand (Bragg et al., 2003; Kjærstad et al., 2018). For rivers, this results in irregular flow patterns which in turn will alter temperature and sedimentation patterns in the river (Kalff, 2002). Low rates of water release may cause a dewatered shoreline which might otherwise provide shelter or nesting grounds for some species. A regulated lake will show an altered pattern of water level fluctuations compared to an unregulated lake (Bragg et al., 2003; Hofmann et al., 2008). The altered water level fluctuations may furthermore bring alterations to temperature patterns, sedimentation patterns and the flow regime of the lake (Kalff, 2002). Altered temperature patterns may induce a trophic mismatch, or could alter emergence timing in freshwater insects (Nordlie & Arthur, 1981). With increased water level fluctuations, sediments may be degraded and washed away due to increased turbulence, which would negatively impact benthic invertebrates that need the sediment as shelter and a source of food (Kalff, 2002). The primary production that is necessary to support benthic invertebrate communities is also negatively affected by regulation schemes (Bragg et al., 2003). Additionally, when water is drained in winter, the sediment may be subject to freeze induced erosion (Kalff, 2002). On a large time scale, these factors may cause a shift in the entire littoral zone, making it inhospitable to certain species (Hofmann et al., 2008). On a shorter time scale, from spring to autumn for example, the water fluctuation could represent a physical stressor for benthic invertebrates (Hofmann et al., 2008). Establishing regulation for hydroelectric power production thus represents a shift in the abiotic frame of a lake.

The composition of the benthic invertebrate communities in freshwater systems can be used as an indicator of ecosystem health (Wallace et al., 1996). Some orders of aquatic insects are particularly sensitive to perturbations in their habitats, and are commonly used as indicators of ecosystem condition. Species in the orders Ephemeroptera (mayflies), Plectoptera (stoneflies) and Trichoptera (caddisflies), referred to as EPT-species, are commonly used to assess healthiness of freshwater ecosystems (Wallace et al., 1996). In contrast to other measures of ecosystem quality, such as water quality, the use of biota as an index may provide a more nuanced picture of the ecosystem health. Communities of species in an ecosystem will experience the fluctuations that a single hydrology test cannot detect. Perturbations in the abiotic frame of an ecosystem will work as a selective force on the biota, and should the perturbations be too great, some species might disappear from the ecosystem (Hofmann et al., 2008; Smith et al., 1987).

In addition to being sensitive to ecosystem perturbations, EPT-species serve many important functions in their ecosystems (Brönmark & Hansson, 2017). Benthic invertebrates are important for facilitating the energy flow in lacustrine food webs (Brönmark & Hansson, 2017; Nilsson, 1996). EPT-species consume a variety of food, some being predators, other herbivorous, and some detritivorous. In this way, the benthic invertebrates are upcycling nutrients and energy, creating a link between primary production and higher trophic levels, such as fish, birds, or other insect larva

(Nilsson, 1996). Grazing on algae and processing allochthonous carbon may also play part in keeping the trophic level of the lake stable (Brönmark & Hansson, 2017). The winged adult stage of aquatic insects is also of importance, since this represents a mode of dispersal. This is a trait of importance when regarding EPT-species as indicator species, as the traits of a potential habitat is more of a barrier than dispersal to the habitat (Peredo Arce et al., 2021).

Detecting variation in benthic invertebrate communities is central in understanding the impacts of hydropower on freshwater ecosystems. To detect these variations, the composition of benthic invertebrate communities must be measurable. A classic measure of biodiversity is species richness, the number of taxa in a given location (Magurran, 2004). Another useful measure is the species abundance of a location, the number of individuals in all taxa present (Magurran, 2004). Measures of biodiversity may be combined into a single metric, a diversity index. Many diversity indices have been formulated, but the goal of any diversity index is to provide information about the biological diversity of a community (Magurran, 2004).

Given the value of ecosystem services provided by lakes and the increasing demand for development of new hydropower, more knowledge on the benthic invertebrate responce to water level fluctuations is needed. While there exists previous research on hydropower impacts on benthic invertebrates, much of this research is done on riverine systems or on invertebrate communities in temperate or arid areas (White et al., 2011). Less is known about how invertebrate communities in boreal lakes respond to hydropower regulation. In this project, data on the EPT community of regulated and unregulated lakes in central Norway was gathered to assess biodiversity impacts of hydropower development. This was done by comparing different biodiversity measures. Because the composition of benthic invertebrates vary with seasons, data was gathered both in spring and fall to broaden the temporal scope of the study.

2 Materials and Methods

2.1 Study design

A control-impact (CI) design was used to investigate the effect of hydropower regulation on benthic invertebrate biodiversity. Three of the investigated lakes are connected to hydropower and constitute the impact group, while the other three are not connected to hydropower and represent the control. In the control group, two waters (Kilvatnet and Barsetvatnet) are regulated as sources of drinking water, but have water level fluctuation patterns that closely resembles those of unregulated lakes. Since it is assumed that the factors affecting benthic invertebrates are connected to patterns of change in water height, these drinking waters are regarded as ”unregulated” for the purposes of this study.

2.2 Study area

The six lakes of interest are all located within Trøndelag County; Kilvatnet, Stor-Drakstsjøen, Gjølgavatnet, Storvatnet, Roksetvatnet and Barsetvatnet. These lakes were already chosen as part of a larger project, and were chosen based on a selection of criteria. Regulated lakes needed a regulation height above two metres and could not have a history of other impacts, such as rotenone treatments, high runoff from agriculture, etc. Sample locations needed to be comparable in terms of substrate. The locations of the lakes are shown in figure 1.

Based on the Ca^{2+}-concentrations and median grain sizes provided in table 1, the lake bed the lakes were categorized according to ”Naturtyper i Norge” (Edvardsen et al., 2024). Unregulated lakes were all placed in L2-C-13, ”moderat kalkrik grov innsjøsedimentbunn”, while regulated lakes were placed in L16-C-1, ”kalkfattig kronisk fysisk forstyrret innsjøbunn” (Stor-Drakstsjøen), and L16-C-2, ”kalkrik kronisk fysisk forstyrret innsjøbunn” (Gjølgavatnet and Storvatnet). The main difference that separates the two main categories, L2 and L16, is the chronic physical disturbances caused by hydropower regulations (Edvardsen et al., 2024). Grain sizes and Ca^{2+}-concentrations were otherwise in the same bases for local complex environmental variables, except the Ca^{2+}-concentration in Stor-Drakstsjøen. However, it was assumed that the difference in Ca^{2+}-concentration would not significantly impact EPT species.

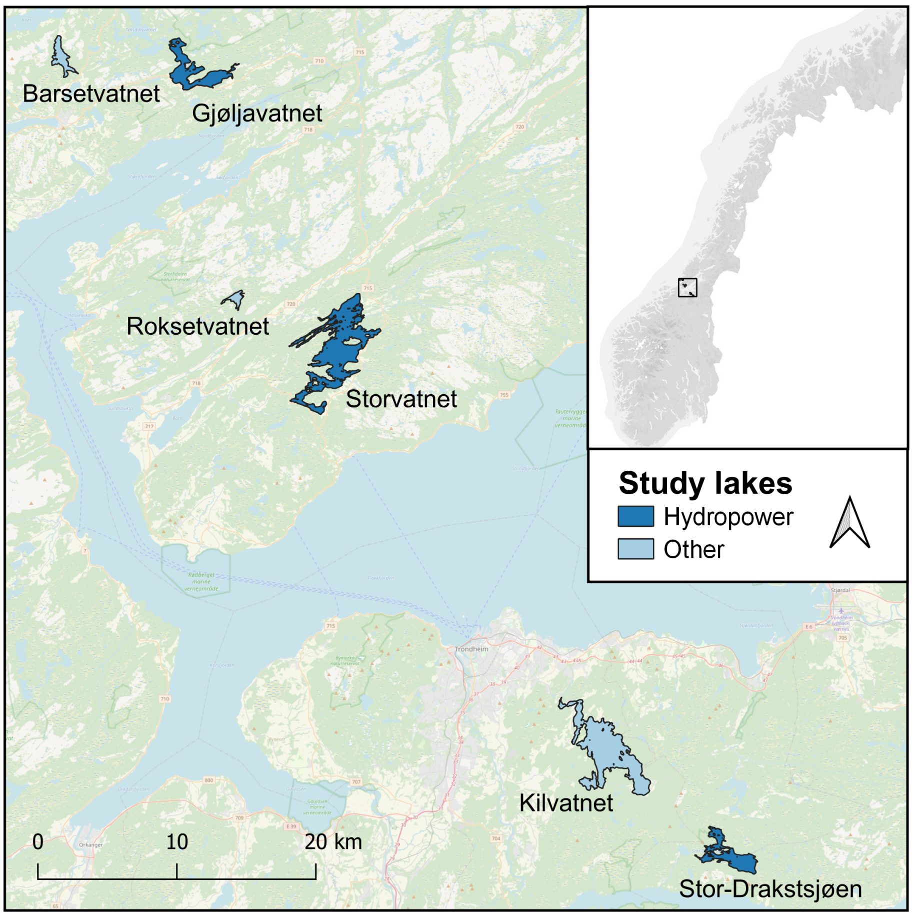

Figure 1: Overview of lake locations in Trøndelag, Norway. Lakes regulated with hydropower (impact lakes) are marked as dark blue, other lakes (control lakes) are marked as light blue.

Figure 2: Overview pictures of unregulated lakes and the corresponding lake bottom. In order from the top, Barsetvatnet, Kilvatnet and Roksetvatnet. The lake bottom is pictured with a $10cm$ long multifunction knife as a reference for scale.

Figure 3: Overview pictures of regulated lakes and the corresponding lake bottom. In order from the top, Gjølgavatnet, Stor-Drakstsjøen and Storvatnet. The lake bottom is pictured with a 10*cm* long multifunction knife as a reference for scale.

Table 1: List of investigated lakes with regulation status, with highest regulated water level (HRV) and lowest regulated water level (LRV) for regulated lakes. In addition, median grain size of the substrate at sampling sites and Ca^{2+}-concentrations (Lime) are provided.

Lake	Ragulation Status	HRV [m]	LRV [m]	Median grain size [cm]	Lime [mg/L]
Gjølgavatnet	Regulated	51.4	47.4	2.72	8
Storvatnet	Regulated	131.9	126.0	2.20	6
Stor-Drakstsjøen	Regulated	51.4	47.4	1.90	2
Barsetvatnet	Unregulated	-	-	2.47	6
Kilvatnet	Unregulated	-	-	1.22	6
Roksetvatnet	Unregulated	-	-	6.37	8

2.3 Field work

Benthic invertebrates were sampled by ”kick-sampling”. This method involves stirring up lake substrate with a foot, ”kicking”, and sweeping the stirred substrate with a net. Here, a net with a $25x25cm$ frame and a mesh size of $0.25mm$ was used. In order to maintain a consistent sampling effort between sampling events, kick-sampling was performed for 1 minute and within approximately 1 m^2 for each replicate. Prior to sampling, the substrate of the sampling area, along with a scale for size, was photographed with a water-proof camera. The camera was also used to locate areas with suitable substrate for kick-sampling, substrate with moderately sized gravel and little to no vegetation. The pictures were later analyzed with ImageJ (Abràmoff et al., 2004) to determine the median grain size of the substrate. Five replicate samples were gathered at each of the six lakes, for a total of 30 samples from each season. Samples were taken from the lakes in spring between May 5th and May 22nd, as well as in fall September 21st and September 25th.

After sampling, the net content was transferred to a white plastic tray filled with lake water to visually inspect the sample before conserving, and to remove any fish. One sample taken at Gjølga was discarded and subsequently resampled due to erroneous kick-sampling. The sample was then strained using a mesh cloth ($0.25mm$ mesh size) to drain water from the sample. To further remove water from the sample, the cloth was gathered up around the sample and gently squeezed. The sample was then moved from the cloth to a jar with 96% ethanol, euthanizing and preserving any collected invertebrates.

The Ca^{2+}-concentration of each lake was tested using a field titration kit

(Aquamerc 111110). These tests, along with the median grain sizes, were used in order to categorize the lake bed according to ”Naturtyper i Norge” (Edvardsen et al., 2024). Measurements are provided in table 1. All equipment that entered the water as part of the sampling, such as the net, buckets, waders and wading shoes, were disinfected with Virkon S before moving between sampling sites in order to avoid spread of organisms between lakes.

2.4 Lab work

In the lab, invertebrates were sorted and identified. Out of the five replicates from each location, three were selected randomly for taxa identification. However, in some cases where the volume of an unsorted sample was notably different from the other chosen samples, it was replaced by a new sample. To reduce the time spent counting non-EPT taxa, a 10% sub-sample was taken from selected samples, and this sub-sample was sorted for all taxa. The rest of the sample was then sorted only for EPT taxa. A sub-sample was taken by placing a chosen sample into a circular metal tray, gently shuffling the contents around with a spoon and forceps as to ”homogenize” the sample contents. Then, a circular metal divider was placed into the tray with the sample, separating 10% from the rest of the sample. The content on the inside of the divider was placed in a separate container using a spoon, forceps and a pipette before sorting and identifying. Spring samples from all lakes were sorted and identified, but due to time constraints, fall samples from two lakes (Gjølgavatnet and Roksetvatnet) were not sorted.

When identifying species in sorted samples, EPT taxa were identified to species level where possible, while other taxa were generally identified to a higher level. Some species are readily identified because they are the lone representative of their order or family in Norwegian lakes. Literature used in the identification process was Rinne and Wiberg-Larsen (2016) for Trichoptera, Engblom (2019) for Ephemeroptera, Lillehammer (1988) for Plecoptera, and Størset (1995) for other taxa.

2.5 Abundance and species richness

For the purposes of this study, the total abundance was expressed as the mean number of EPT individuals found in samples grouped by regulation status and season. The species richness was determined for each location by counting the number of species appearing in any samples sorted for that location. In addition, individuals identified to the genus or family level that are not represented by a different species in the same family or genus were regarded as a species.

2.6 The Simpson index

Species richness does not factor the composition of a community in terms of evenness, which may be investigated using a diversity index. The Simpson index, D, is one such diversity index. Different diversity indices have different strengths and weaknesses, but the Simpson index is regarded by Magurran (2004) as the most robust. In addition, Lande et al. (2000) argues for the use of the Simpson index when using small samples. The Simpson index is given in equation 1.

$$D = \sum_{i}^{S_{obs}} p_i^2, \qquad p_i = \frac{N_i}{N_T} \tag{1}$$

Here, p_i is the proportion of the i-th species of the S_{obs} observed species. p_i is given by $\frac{N_i}{N_T}$, where N_i is the abundance of the i-th species divided by the total abundance of all species, N_T. A lower score on the Simpson index indicates a greater diversity in the community (Magurran, 2004). The score reflects not only the number of species, but how evenly distributed they are. If communities have the same number of species, ones with more similar proportions of species are more diverse (Magurran, 2004). In the current study, the reciprocal $\frac{1}{D}$ was used for ease of interpretation, as this number will increase with increasing diversity.

2.7 Species abundance distributions

Species abundance distributions describe how the abundances of species in a ecological community are distributed (Matthews & Whittaker, 2015). Species abundance distributions were made by using the Sads package in R (Prado et al., 2024). One distribution was made for each combination of regulation status and season, for a total of four distributions. Abundances of species were grouped by regulation status and season, using only abundances of species that were identified to the species level or those of genera or families that were not otherwise represented in the group of locations. Abundances were then grouped by Preston octaves using the octav function from the Sads package (Prado et al., 2024). Then, the fitsad function from the same package was used to estimate the μ and σ parameters for a lognormal distribution for each of the four combinations. μ may be interpreted as the mean of the distribution, and σ as the variance of the distribution (Matthews & Whittaker, 2015). Furthermore, if sampling effort increases, the distribution is expected to shift towards the right as all species should appear in greater numbers (Matthews & Whittaker, 2015). All locations were used for the spring distributions, while only four locations were used for the fall distributions. Thus, only distributions within the same seasons were comparable for the species abundance distributions.

2.8 Species temporal turnover

To investigate turnover in EPT species between the spring and fall sampling events, a species temporal turnover plot was created. This was done by plotting the log transformed abundances of each identified species from the spring against the log transformed abundances from the fall. In order to avoid taking the logarithm of 0, 1 was added to the abundance of each species, and only taxa that were identified to the species level were used. For each plot, an orthogonal regression was made using, which could then be compared to a one-to-one line running through the plot. The orthogonal regression for each lake was made using the odregress function from the pracma package in R (Borchers & Borchers, 2019). Species that are more abundant in the spring than in the fall will appear below the one-to-one line. On the other hand, species that are more abundant in the fall than in the spring will appear above the one-to-one line. If more species are abundant in the spring, the slope of the orthogonal regression will be lower than 1. If more species are abundant in the fall, the orthogonal regression line will have a slope greater than 1. If all species are more abundant in one of the time periods, the slope will be closer to 1, but the intercept in the y-axis will be shifted.

2.9 Statistical analysis

R (version 4.3.1) was used for all data management and statistical analyses (R Core Team, 2021). In order to examine differences in biodiversity measures between impact and control lakes,as well as how they differed between sampling seasons, separate models were created for species richness, total abundance and the Simpson index response. Regulation status and season as predictor variables for these models. The interaction effect between regulation status and season was also investigated to examine whether temporal patterns in the diversity measures differed depending on regulation status. The species abundance distributions were not used in statistical modelling, since those analyses would require bootstrapping and other methods that are outside the scope of this thesis.

Species richness and total abundance are measures that were assumed to be Poisson distributed (Magurran, 2004), and were first modeled using a generalized linear model with a log-linked Poisson distribution. The resulting models for these measures were tested for deviations using the simulateResiduals function from the DHARMa package (Hartig & Hartig, 2017). The dispersion of the models was also tested using the testDispersion function from the same package (Hartig & Hartig, 2017). For the species richness model, there was a quantile deviation detected with simulateResiduals, but the testDispersion returned a dispersion of 1.285 ($p = 0.504$). An alternative model using a negative binomial distribution did not resolve the quantile deviation. Therefore, the Poisson distributed model was kept for the species richness model. For the mean sample abundance model, the simulateResiduals output reported multiple problems with the Poisson distributed model, and testDispersion reported a significant overdispersion of 64.69 ($p < 0.001$). The mean sample abundance was then remodeled using a negative binomial distribution. The simulateResiduals function detected no significant problems with this model, and the testDispersion function reported a dispersion of 0.6055 ($p = 0.584$). Therefore, the alternative model using a negative binomial distribution was kept for the mean sample abundance.

The Simpson index was modeled using a linear model with the default normal distribution.

3 Results

A total of 4265 EPT individuals were sorted and identified, with 1588 from the spring samples and 2677 from the fall samples. From the spring samples, Gjølgavatnet had the highest number of species with 20 species (Figure 4). From the Fall samples, Kilvatnet had the highest number of species with 17 species. The total abundance of EPT individuals in samples from regulated lakes was 104.3 ± 37.1 (s.e.) for spring and 75.8 ± 8.7 for fall. For non-regulated lakes, the numbers were 72.1 ± 9.2 for spring samples and 370.3 ± 70.0 for fall samples. All lakes show an increase in total abundance between sampling events (Figure 5). In all samples Ephemeroptera is the dominant order.

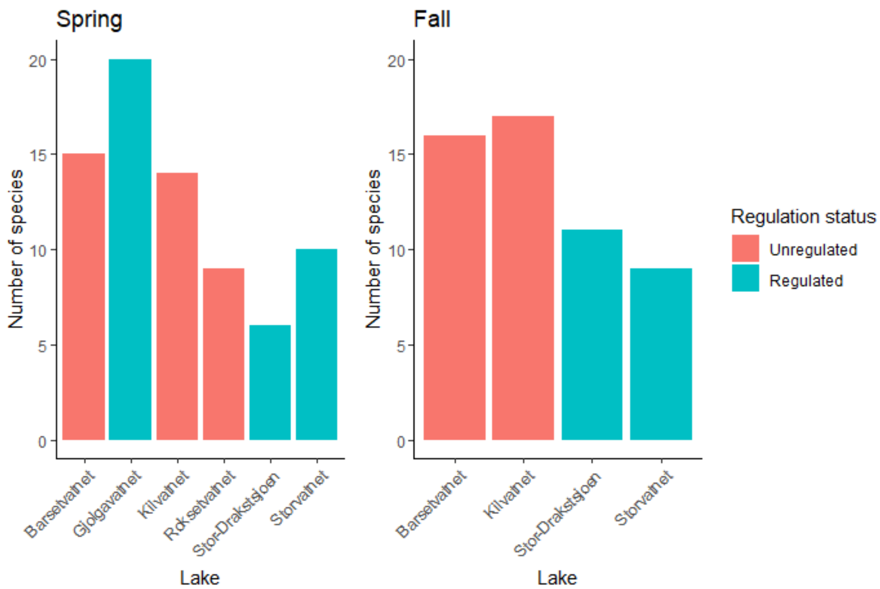

Figure 4: Number of EPT taxa present in samples gathered from all lakes, grouped by season and regulation status.

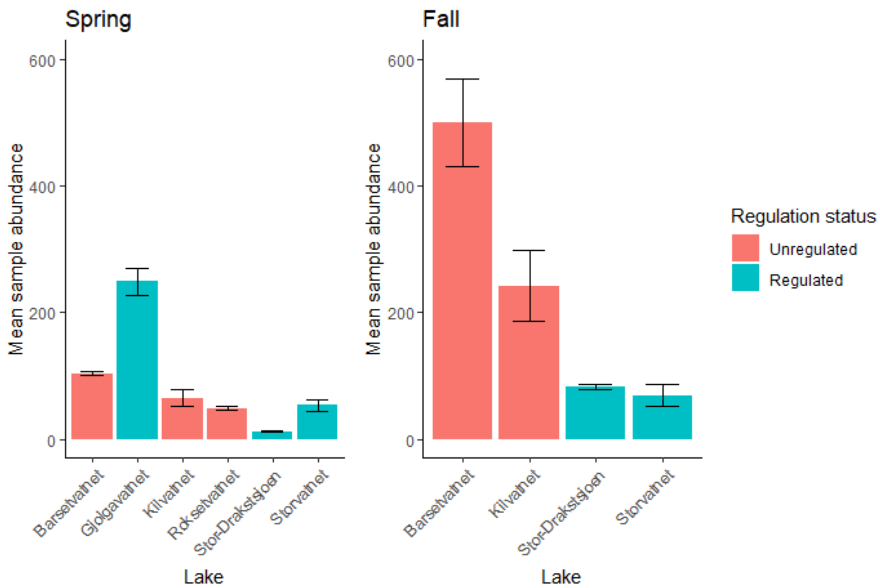

Figure 5: Mean abundances of EPT individuals in samples gathered from all lakes, grouped by regulation season and regulation status. Error bars represent the standard error of the mean.

3.1 Species richness and total abundance

For species richness, there was no statistically significant impact from neither regulation status or change in season (Figure 6). The the number of EPT species is lower in regulated lakes compared to non-regulated lakes for both spring and fall data. Excluding an insignificant interaction term ($p = 0.223$), the generalized linear model detects no significance ($p = 0.184$) in the differences between regulated and unregulated lakes. The species richness increases somewhat from spring to fall, but the model detects no significance ($p = 0.690$).

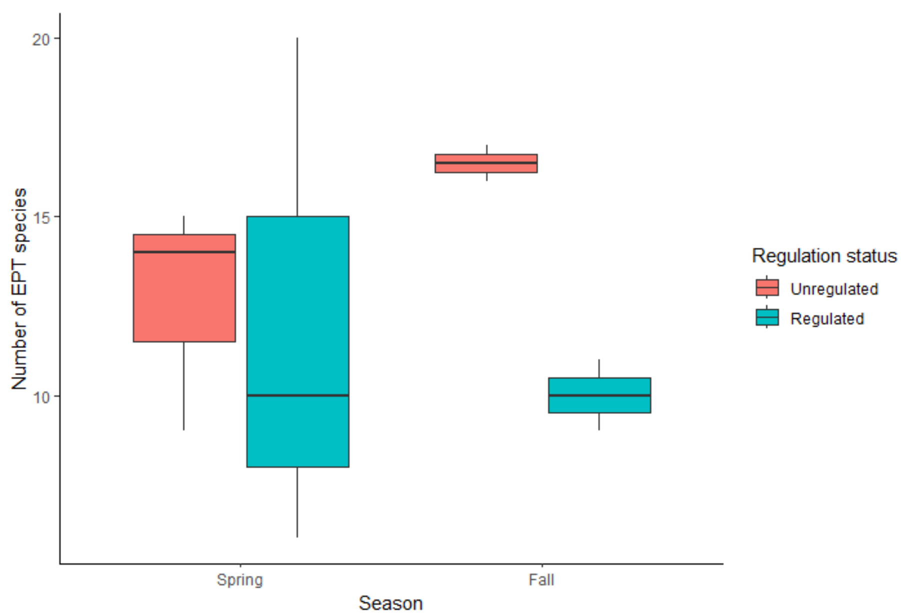

Figure 6: Box plot visualizing the number of EPT species found in regulated and unregulated lakes by season. Horizontal lines are the median, boxes represent the interquartile range, with whiskers covering data within 1.5x interquartile range. Data is grouped by season and regulation status.

For the total abundance of EPT species, both regulation status and change in season proved to be significant factors (Figure 7). The total abundance of unregulated lakes was significantly higher than that of regulated lakes ($p < 0.001$), and the total abundance in all lakes increases from spring to fall ($p < 0.001$). In addition, there was a significant interaction effect between regulation status and season ($p < 0.001$). This implies that the seasonal change in abundance is different between regulated and unregulated lakes.

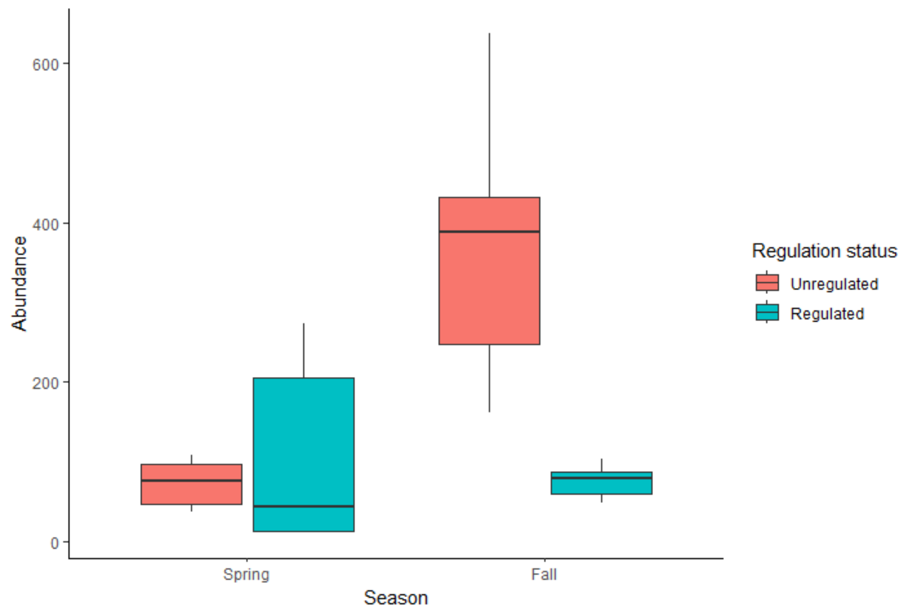

Figure 7: Box plot visualizing the total abundance of EPT species. Horizontal lines are the median, boxes represent the interquartile range, with whiskers covering data within 1.5x interquartile range. Data is grouped by season and regulation status. Regulation status of lakes are marked by colour, with regulated lakes coloured blue and unregulated lakes coloured red.

3.2 The Simpson index

The Simpson index did not differ significantly depending on regulation status of lakes or season (Figure 8). On average, the regulated lakes scored slightly higher on the Simpson index compared to the unregulated lakes, but this difference did not prove significant ($p = 0.658$). The scores also decrease slightly between seasons, but this decrease is statistically insignificant ($p = 0.481$). There is no significant interaction between the change in regulation status and change in season ($p = 0.687$).

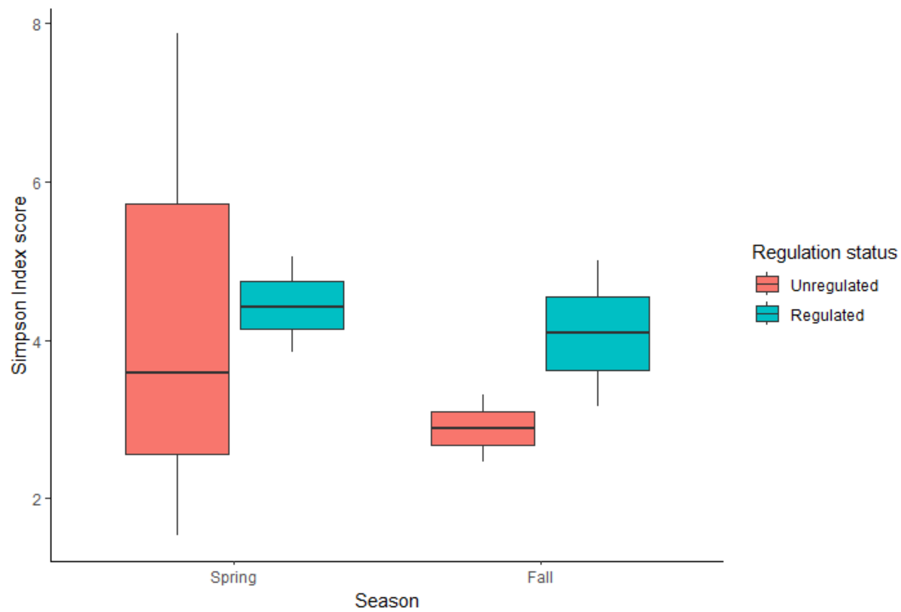

Figure 8: Box plot visualizing the Simpson index score (using $\frac{1}{D}$) calculated for each location. Horizontal lines are the median, boxes represent the interquartile range, with whiskers covering data within 1.5x interquartile range. Data is grouped by season and regulation status.

3.3 Species abundance distributions

The species abundance curves are presented in Figure 9. The lognormal distributions made for the spring samples showed a similar behaviour with a left-shifted peak towards the rare species (spring unregulated: $\mu = 1.127, \sigma = 2.145$, spring unregulated: $\mu = 0.362, \sigma = 2.550$), and a long tail towards the common species (towards the right). For the fall samples, the behaviour was dissimilar between regulation statuses. For the unregulated samples, the behaviour was similar to the spring distributions, with a peak shifted towards the rare species and a long tail ($\mu = -2.073, \sigma = 3.999$). The fall regulated distribution was shifted towards the common species (towards the right) with a short tail ($\mu = 2.616, \sigma = 1.202$). This implies that the species abundances were more similar between lakes with different regulation in spring, and more dissimilar in the fall.

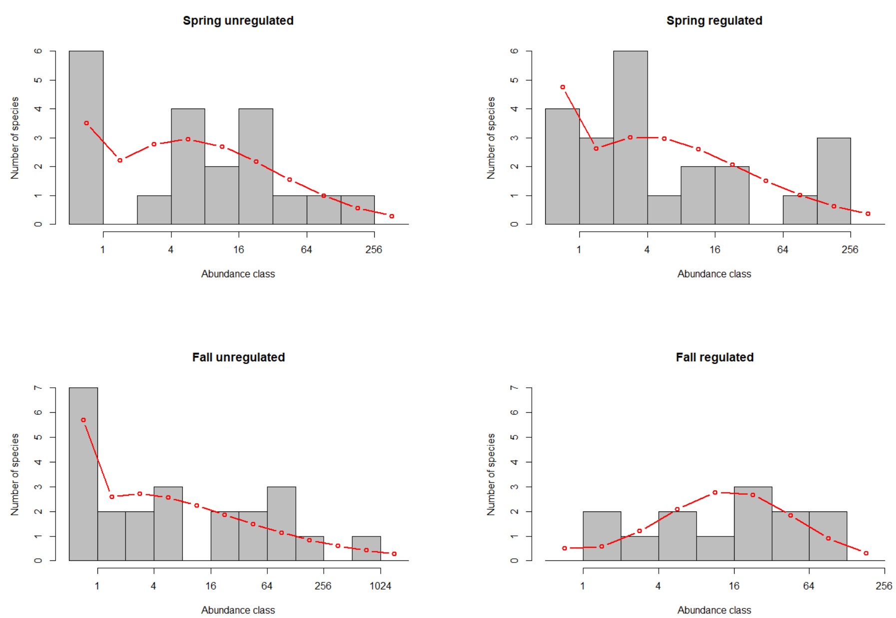

Figure 9: Species abundance distributions (SAD) from species occurrences. Gray bars indicate the number of species in a particular Preston octave, and red lines the represent the fitted lognormal distribution. From left to right, the upper row depicts the SAD for spring unregulated and spring regulated, and the lower row depicts fall unregulated and fall regulated.

3.4 Species temporal turnover

The communities in regulated lakes seemed to be more unstable in composition compared to the communities in unregulated lakes. Figure 10 shows the species temporal turnover for the four lakes that were completely sorted for both spring and fall samples. The red and green lines, that respectively correspond to the unregulated lakes Barsetvatnet and Kilvatnet, are closer to the black dotted line than the blue and purple lines, representing the regulated lakes Stor-drakstsjøen and Storvatnet respectively. The red and green lines are slightly steeper than the dotted black line, indicating that the abundance of some species has increased in abundance. The blue line representing Stor-drakstsjøen is shifted so that it does not intercept near origo, which indicates that all species in that location are more abundant in the fall. The purple line representing Storvatnet shows an entirely different regression from the other lines, indicating a very unstable community where many species found in the spring disappear in the fall, and many of the species found in fall were not present in the spring.

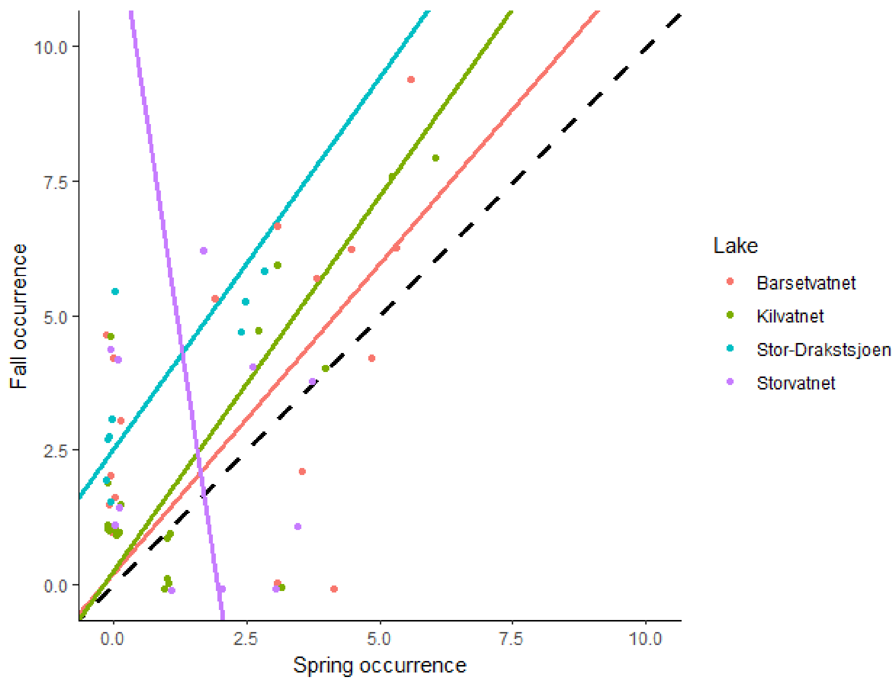

Figure 10: Species fall occurrences plotted against spring occurrences, both log transformed. Coloured dots represent a given species in a certain lake, with different colours representing a different lake. Dots are jittered, as some species may overlap. Regression lines represent an orthogonal regression of species occurence data, and are coloured to match dots. The black dotted line represents a one-to-one relationship of species occurrences, a theoretical location where species turnover is non-existant.

4 Discussion

There was found evidence for biodiversity impacts of hydropower regulation on freshwater fauna based on data on three important benthic taxa, Ephemeroptera, Plecoptera and Trichoptera, in regulated and unregulated lakes in central Norway. The total abundance of EPT species were lower in regulated lakes compared to unregulated lakes. While the abundance increased in both groups of lakes from spring to fall, this increase was significantly lower in regulated lakes. The species richness and Simpson index score did not show a significant difference between regulated and unregulated lakes, but the Simpson index score seemed higher for regulated lakes. The species abundance distributions showed a similar evenness between regulated and unregulated lakes in the spring, but in the fall, regulated lakes showed a more even species abundance distribution. Based on the species temporal turnover, the composition of EPT communities in regulated lakes was more unstable and prone to change with season compared to that of unregulated lakes, who seemed to be more stable with changing seasons. This indicate that disturbance from hydropower impact most species proportionally relatively even.

The total abundance of EPT species was found to be significantly higher in unregulated lakes. The total abundance also increased from spring to fall in both lake groups, but based on the significant interaction effect between regulation status and change in season, the increase in abundance is lower in regulated lakes. This result is supported by Trottier et al. (2019), who found the abundance of macroinvertebrates in reservoirs to decrease with increasing winter drawdown. Because hydropower regulation represents a major disturbing force in the water level fluctuation patterns of lakes, the observed decrease in abundance is expected (Schowalter, 2012). Aroviita and Hämäläinen (2008) did not find a significant effect of regulation on species abundance in a study using a similar group of lakes in Finland, which is contrary to what is found here. A major difference is that the current study used both spring and fall data, whereas Aroviita and Hämäläinen (2008) used only one sampling event in late summer. The total abundance in regulated lakes compared to unregulated lakes was significantly lower in both spring and fall in the current study. This strengthens the result. Additionally, the interannual variation in effect of water level fluctuations can only be evaluated by using multiple sampling events per year. It should, however, be remembered that the current study has a low sample size, using only six lakes. This may influence the interpretation of the study by lowering the probability of discovering real effects of hydropower regulation. The results may also become more prone to effects of atypical environmental conditions.

The species richness of EPT taxa was not significantly different in lakes impacted by hydropower regulation compared to unregulated lakes, nor was richness significantly impacted by the change in season. For the fall samples, the two unregulated lakes show a higher species richness compared to the regulated lakes, but this did not show up as significant in the generalized linear model. Both White et al. (2011) and Aroviita and Hämäläinen (2008) report a significant decrease in species richness in regulated lakes with regulation height greater than $2m$, which contrasts with the results from this study. Both of the aforementioned articles considered all taxa, and did not limit their analyses to EPT only. However, other studies on specific invertebrate groups, such as one study on Odonates by Vilenica et al. (2020), cite hydropower regulation as an important factor in explaining reduced species richness. Thus, the lack of statistical significance in the analyses on species richness in this study was not in concordance with previous studies. The highest EPT species richness was recorden in a regulated lake (Gjølgavatnet) with 20 species. As discussed above, the low number of lakes included in the current study, may amplify the importance of natural environmental factors that cause annual variations in species composition. Because this study used data from only one year, it could not capture such discrepancies.

The Simpson index did not show a significant impact from hydropower regulation regardless of season, but when regarded as a measure of evenness it showed some concordance with the species abundance distributions. The Simpson index tends to increase with increasing species richness and increasing evenness (Magurran, 2004). Given that the number of species recorded in the regulated lakes in the fall was lower than that of the unregulated lakes, the higher Simpson index score of regulated lakes in fall must be a result of the increased evenness of those communities. The σ term from the species abundance distributions could also be regarded as a measure of evenness, as it relates to the variation in specific species abundance (Matthews & Whittaker, 2015). The species abundance distribution for the fall samples showed a greater σ-value for the unregulated lakes compared to the regulated lakes, suggesting that the regulated lakes were more even in their species composition in the fall. In the spring, however, both the Simpson index and the σ-values from the species abundance distributions were more similar between lake groups, suggesting a more similar evenness in spring. Disturbances in ecological systems could give an advantage to some species that thrive under the new and disturbed condition (Schowalter, 2012).

The apparent evenness in the EPT communities of regulated lakes in fall suggest that this is not the case, and possibly that no species are able to thrive and become dominant in regulated lakes. Species abundance distributions are particularly dependent on sample effort, as an increase in abundance of each species might shift the distribution towards the right (Matthews & Whittaker, 2015).

Based on the temporal species turnover in the lakes, unregulated lakes seemed to have a more stable community composition compared to regulated lakes. The temporal species turnover for the investigated lakes show that the unregulated lakes are closer to the one-to-one line, implying that these lakes are more stable in composition over time compared to the regulated lakes. Storvatnet deviates from the other lakes in its orthogonal regression line. In this lake, more so than the other lakes investigated, there are more species that appear in one season and not the other. The unregulated lakes have more species, 8 total, that appear in both the spring and fall samples. In the regulated lakes there are 4 species that appear in both the spring and fall samples. Regardless of regulation status, the species *Leptophlebia vespertina*, *Leptophlebia marginata* and *Heptagenia fuscogrisea*, appear both in spring and fall. These species are univoltine winter species, species that hatch in the fall and grow as nymphs through winter and emerge as adults in the spring or summer (Söderström, 1991). This life cycle adaptation might make these species more resilient in regulated lakes where species are more exposed to freezing/ice and desiccation compared to unregulated lakes (Aroviita & Hämäläinen, 2008).

A strength of this study is the use of data from both spring and fall in order to detect possible temporal effects on the biodiversity measures. Ecosystems and their biota are shaped and impacted by temporal processes, which also holds true for benthic invertebrates (Brönmark & Hansson, 2017; Samways et al., 2010). What is observed one year, might change the next based on random events. Because ecosystems are so dynamic, both Magurran et al. (2010) and Lindenmayer et al. (2012) argues for the value of long term data to capture trends over a longer time scale. In the sense of an ecological timescale this study was short term, but using data from to points of the same year was enough to discover a significant interaction effect between regulation status and seasonality on the abundance of EPT species. Using multiple sampling events per year could also provide insight on how the benthic invertebrate community changes, as evidenced by the temporal species turnover. This study does not cover how the benthic invertebrate community develops over winter, which could be of importance given what is known about winter drawdowns (Trottier et al., 2019).

5 Concluding remarks

In this study, a selection of biodiversity measures were used to investigate if and how hydropower regulation affects benthic invertebrates by comparing regulated and unregulated lakes. Regulated lakes were found to have a significantly lower abundance of benthic invertebrates in the orders Ephemeroptera, Plecoptera and Trichoptera compared to unregulated lakes. There was, however, not found a significant difference in neither species richness nor Simpson index score, which was contrary to what other studies have reported (Aroviita & Hämäläinen, 2008; White et al., 2011). There was found a significant interaction effect between regulation status and seasonality on total abundance, which implied that the expected seasonal increase in EPT abundance would be lower in regulated lakes compared to unregulated lakes. A temporal species turnover analysis indicated that the composition of EPT species was more stable in unregulated lakes, and that regulated lakes had a greater turnover in species between spring and fall. This, in combination with the interaction effect on abundance indicate that hydropower regulation contributes to destabilising benthic invertebrate communities. It could be argued that the health of a freshwater ecosystem can be quantified in terms of vigor, organization and resilience (Costanza & Mageau, 1999). The resilience and organization terms are of particular interest here, as they pertain to how the ecosystem responds to stress and how the composition of species are affected by stress. This implies that the effect of hydropower regulation is detrimental to the overall health of lake ecosystems.

A strength of this study was the use of data from two separate sampling events in order to broaden the temporal scope of the results. This made it possible to evaluate differences in how the composition of species change over the summer in regulated and unregulated waters. Although the sample size was limited, the current study was able to detect the aforementioned interaction effect. However, the results from the current study also highlight the need for longer term studies that capture fluctuations among and within both natural systems and systems with heavy anthropogenic influences.

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