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Changes in freshwater zooplankton communities in response to invasive planktivorous fish

A paleolimnological study of temporal beta-diversity

Master's thesis in Natural Resource Management

Supervisor: Sigurd Einum

Co-supervisor: Anders G. Finstad

July 2020

Master's thesis

NTNU
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Lindis

Abstract

The cladocera community response to invasion of planktivorous fish was assessed using a before-after-control-impact (BACI) study design. The hypothesis tested was whether whitefish and perch cause changes in cladocera zooplankton communities. Through paleolimnological methods both contemporary and historical (pre-invasion, approximately 500ybp) Cladocera communities were described in 16 sites. Changes in communities were calculated as temporal beta diversity and were compared between reference and effect sites for lakes containing whitefish, perch or both. The study did not find evidence for a consistent difference in the change in community composition on community level between reference and effects sites. Possible explanation included cladoceras expressing morphological adaptations to predation, as well as adaptations to predatory pressure from trout and charr prior to invasion. The study argues that the fish community might have expressed niche adaptations that could regulate the predatory pressure from whitefish and perch upon the cladocera community that allowed the community to remain resilient. Although no effects of whitefish and perch were detected on the community level, analyses identified effects on some of the individual genera. The thesis yielded novel insights into how communities respond to invasion in a long-term perspective. Since the result were unexpected, this adds to the understanding that invasive species effects can be complex and unpredictable.

Abstrakt

Cladocera samfunnets respons til invasjon av planktivore fisk ble vurdert ved hjelp av et BACI (befor-after-control-impact) studiedesign. Hypotesen som ble testet var om sik og abbor forårsaket en endring i cladocera zooplanktonsamfunnet. Gjennom paleolimnologiske metoder ble både moderne og historiske (pre-invasjon, omtrent 500 år siden) cladocera-samfunn beskrevet for et utvalg på 16 innsjøer. Forandring i samfunn ble beregnet som ending i beta-diversitet over tid og ble sammenlignet mellom referanse- og effektinnsjøer for innsjøer som inneholdt sik, abbor eller begge. Studien fant ikke bevis for en konsekvent forskjell i endringen i samfunnsammensetning mellom referanse- og effektinnsjøer. Mulige forklaringer inkluderte at cladoceraene kunne uttrykt morfologiske tilpasninger til predasjon, samt tilpasninger til predasjon fra ørret og røye før invasjonen skjedde. Studien argumenterer for at fiskesamfunnet kan ha uttrykt nisjetilpasninger i respons til økt konkurranse, som kan ha fungert som en regulator på predasjonen fra sik og abbor på cladocera-samfunnet. Selv om ingen effekt fra sik og abbor ble observert på samfunnsnivå, viste analyser på slektsnivå en effekt for enkelte genus. Denne oppgaven ga ny innsikt i hvordan samfunn reagerer på invasjon i et langsiktig perspektiv. Siden resultatet var uventet, legger dette til forståelsen av at fremmede arter kan være komplekse og uforutsigbare.

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3.0 Introduction

With an accelerating rate of species dispersal affecting ecosystems, there is an increasing interest in collecting information regarding our ecosystems state prior to the anthropocene (Smol, 1992). Throughout modern history, lentic ecosystems such as lakes and rivers have become one of the most threatened types of ecosystem (Dudgeon, et al., 2006). By altering natural barriers, humans have aided in the change of biogeography and allowing for dispersal of species at an unnatural rate (Frederico, Salvador, Andrade, Rosa, & Torquato, 2019). By exercising cautious management, freshwater ecosystems are more likely to yield a sustainable surplus for human consumption and use. Knowledge regarding lentic ecosystems pre-anthropogenic states is however often scarce (Primark, 2014, p.443). There are several examples of how species have been accidentally or intentionally translocated. Fish have in some cases been actively translocated to populate waters as an investment, to later act as a source of food, for recreational activities, or as a biological control upon other species (Lugo, 2006; Withgott & Brennan, 2009).

Introducing new fish species to a freshwater ecosystem can cause a range of effects, often unforeseeable coupled with climate change and altered nutrient composition common in the anthropocene (Primark, 2014 p.176). Consequences of species invasion can vary in magnitude, from affecting one species directly, to indirectly affecting the equilibrium steady state of the native ecosystems (e.g. Jokela, Arnott, & Beinsler, 2017; Bergstrand, 1990; Lugo, 2006). Invasive species with an overlapping niche to native species causes *intraspecific competition*, possibly outcompeting native species (Brönmark & Hansson, 2017, p. 110). Research on ecosystem response suggests that mechanisms to disturbances include concepts such as *resistance* and *resilience*. Different studies define the terms in various ways (Knapp, Matthews, & Sarnelle, 2001; Primark, 2014 p.443).. This thesis will define these terms as “*the degree to which a system is altered when the environment changes*”, and “*the degree and rate of a system’s return to its previous configuration after a perturbation*”. These concepts should be considered when studying ecosystems in a long-term perspective, especially as ecosystem resilience is unlikely be visible in short term studies.

Zooplankton can be described as keystone organisms in limnic ecosystems, due to their abundance and their role as both grazers on bacteria and phytoplankton and as prey for certain species of fish, insects and other zooplankton (Mance, Bernardi, & Giussani, 1987). Prior

studies conducted on invasive planktivores have found varying results on zooplankton communities, usually with effect on either the community size, -structure, -functionality or abundance (e.g. Iacarella, Dick, & Ricciardi, 2015; Knapp, Matthews, & Sarnelle, 2001; Maclennan, Dings-Avery, & Vinebrooke, 2015; Preston, et al., 2017).

Planktivores can affect the zooplankton community in numerous ways (Hanazato & Yasuno, 1989). The *size efficiency hypothesis* (Brooks & Dodson, 1965) predicts that when a planktivore fish is introduced, larger sized zooplankton such as *Daphnia* and *Bosmina* would decrease, possibly releasing resources to cause an increase of smaller sized zooplankton such as *Alonella* (Fryer, 1968). Examples of such effects have been documented in multiple cases where invasive planktivores have been introduced or removed, (e.g. Elser & Carpenter, 1988; Pothoven, Hook, Nalepa, Thomas, & Dyble, 2013; Thorp & Casper, 2003). Several prior studies investigate invasive species at a few sites over a within-year, or year-to-year interval after an invasion (e.g. Pothoven, Hook, Nalepa, Thomas, & Dyble, 2013; Jokela, Arnott, & Beinsler, 2017; Maclennan, Dings-Avery, & Vinebrooke, 2015). Short-term studies are however unlikely to reveal any delayed effects within the community when, or if the system reaches a new state of equilibrium. Complimentary to this argument, Strecker et al. (2011) argued that the effects of predatory invasive species can be particularly pronounced, especially in the early stages following an invasion (Strecker, et al., 2011). This supports the narrative that ecosystems should also be studied in a long-term perspective to unveil any delayed effects. In addition to investigating the effect in sites subjected to invasion, a control should be used for comparison. Comparing the effect sites to nearby similar *reference sites* can aid in excluding confounding effects from the surrounding environment (Primark, 2014, p. 443).

This thesis aims to compare changes in sites with and without invasive planktivorous fish species, with particular focus on whitefish (*Coregonus lavaretus*), as well as exploring the role of perch (*Perca fluviatilis*) as a planktivore over a multiple-century time scale. The null hypothesis is that introduction of the planktivores does not cause changes in cladoceran communities, with the alternative hypothesis being that either one or both planktivores does affect the cladoceran community. By using a before-after-control-impact (BACI) study design (Green, 1979) the long-term effects are more likely to become visible. An expected primary effect is a decrease in larger sized species as a result of selective predation behavior. An expected secondary effect is an increase in smaller sized cladocera species as a response to

the released resources. In some studies, these effects have been found to cause turnovers in species dominance (i.e. Pothoven, Hook, Nalepa, Thomas, & Dyble, 2013; Post & McQueen, 2006). Some short-term studies specifically on whitefish and perch have found that *Bosmina* and *Daphnia* populations decreased in response to the invasive planktivore (Hanazato, Iwakuma, & Hayashi, 1990; Guma'a, 1978). By utilizing multiple effect and reference sites and comparing communities change across a multiple-century perspective, this study design will offer a robust measure of how planktivores affect cladoceran communities over longer time spans.

This thesis is a continuation of S. Eids master thesis “Impact of whitefish introduction on Cladocera communities - A paleolimnological study” from 2019, which similarly sought to understand the impact of whitefish invasion in this area, but which only described the variation among existing communities and thus was unable to describe the temporal changes in communities.

2.0 Materials and method

2.1 Choice of method

To investigate the variation among the sites in response to the two invasive fish species, the change in temporal beta-diversity was quantified and compared between reference and effect sites for the respective treatments. To gain better understanding of the dynamics within the community and how it reacted to invasive species, additional separate analyses was conducted on the genus level. By using a BACI study design the temporal change in effect sites can be investigated and compared to the reference sites (Green, 1979). To assess the cladocera community before (T_1) and after (T_2) invasion, the study utilized historical data through paleolimnology; the study of ecological data integrated in aquatic sediments (Barker, 2009). After an invasion, the ecosystem might experience a period of oscillations as a result of the perturbation, and the effect might not be expressed until years and sometimes decades later (Havel, Kovalenko, Tomaz, & Amalfitano, 2015). Approaching the issue through paleolimnology allows for studying the sites over century time scales and reveal any delayed effects from the introduction of planktivores.

2.2 Study area

The analysis used sediment samples taken from 16 lakes located in Røros municipality, central Norway (Table1). Of the 16 lakes sampled, eight have had whitefish introduced and was used as effect sites, with the remaining eight lakes acting as reference sites. Of the same lakes, six have had perch introduced, and the remaining 10 acted as reference sites for this group. To control for possible interference from either invasive species in the reference sites in the case where both are exhibiting planktivory, perch and whitefish sites were pooled together in a third group referred to as “planktivore” treatment group.

For the majority of the sites, the translocations were unintentional, although some of the sites have been reported to having whitefish intentionally stocked (Korsen, 2004). The area was from the 1600's characterized by increased human activity and settlement due to copper mining operations (Øisang, 1942). Whitefish and perch had only been native to Lake Femunden, south-east of Røros prior to this time period (Huitfeldt-Kaas, 1918; Næsje, Sandlund, & Saksgård, 2010). Due to increased demand for timber in the smelting processes, log flumes were installed between several water bodies to make transportation of logs more efficient. In the year 1715 the first log flume connected the water bodies Femunden and Feragshåen (Jäggi & Johansen, 1997). This process accelerated the dispersal of species, allowing fish such as pike (*Esox lucius*), perch, whitefish, grayling (*Thymallus thymallus*), eelpout (*Zoarces viviparus*) and minnow (*Phoxinus phoxinus*) to migrate and establish in the northern water bodies, which prior to the invasion had mainly been dominated by brown trout (*Salmo trutta*) and arctic charr (*Salvelinus alpinus*) (Huitfeldt-Kaas, 1912; Hesthagen & Østborg, 2002).

similar range to the European whitefish (Huitfeldt-Kaas, 1918). Perch is a generalist species and are known to feed on insects, molluscs, annelids, small fish and zooplankton. In prior studies, perch have been found to feed on zooplankton regardless of size, but primarily in early life stages (~1-year old) (Lorenzoni, Carosi, Pedicillo, & Trusso, 2009, Nurminen, Pekcan-Hekim, & Horppila, 2010)

Table 1: Information about the sampled lakes. Information about species presence is from Artsdatabanken/NINA. Coordinated are given in WGS 84 format. *Lake Gjettjønnå was treated with rotenone in 2017.

Lake name	Planktivores		Fish community	Site information			
	Whitefish	Perch	Additional fish species	Lake surface area (km ²)	Water body ID	Elevation (m.a.s.l)	Coordinates
Abbotjønnå	No	No	Brown trout	0.0215	140171	665	62.42.6043, 11.863968
Dalstjønnå	Yes	No	Brown trout	0.1754	36396	629	62.530252, 11.476555
Feragen	Yes	No	Eurasian minnow, Brown trout, Arctic Charr, Pike	15.7322	127	654	62.553380, 11.868751
Gjettjønnå	No	Yes	*	0.1426	35369	623	62.566547, 11.392367
Gubbtjønnå	Yes	Yes	Burbot, Brown trout	0.051	35445	656	62.469494, 11.793116
Harsjøen	Yes	No	Burbot, Brown trout, Arctic charr	1.4298	247	751	62.572282, 11.656854
Korssjøen	No	No	Pike, Burbot, Brown trout	8.1853	1359	759	62.452792, 11.530222
Langen	Yes	No	Burbot, Eurasian minnow, Brown trout, Arctic charr, Grayling	0.7734	35338	749	62.601313, 11.707582
Langesjøen	No	Yes	Pike, Brown trout, Grayling	0.056606	35516	688	62.427561, 11.855158
Oksloken	No	No	Brown trout	0.0075	140001	658	62.460635, 11.813552
Olaloken	No	No	Brown trout	0.0122	139978	657	62.467540, 11.794377
Ormkåstjønnå	No	No	Pike	0.037	139979	655	62.466712, 11.787776
Rismotjønnå	Yes	Yes	Brown trout, Pike, Eurasian minnow	0.5951	35386	623	62.540510, 11.451635
Røragen	Yes	Yes	Pike, Burbot, Eurasian minnow, Brown trout	1.3448	177	673	62.579607, 11.811254
Storhittersjøen	Yes	No	Burbot, Eurasian minnow, Arctic charr	1.1449	249	721	62.605379, 11.637403
Storkrokattjønnå	No	Yes		0.0776	35529	679	62.422567, 11.875004

2.4 Determining depth

Samples of sedimentary deposits were collected in October 2017 and January 2018. Details about the extraction process can be found in S. Eid (2019). Cores were collected from the deeper parts of the respective lakes, where sedimentation occurs evenly. The samples were divided into 1 cm slices and stored individually. To determine a sediment depth that corresponded to a common time period prior to invasions for each core the sedimentation rate for each respective lake was determined. Pollution from the copper mining smelt process have left traces of metal in the surrounding environment and have become integrated in the sediment deposit layers. A subsample of each slice was freeze dried and homogenized and sent to the University of Umeå, Sweden, where a metal content determination was executed. Peaks in metals like copper, lead, titanium, zirconium, rubidium and aluminum operated as reference points to when mining activity was known to have taken place. Further info about metal content in cores can be viewed in Appendix S.1. Sedimentation rate was calculated for each lake by dividing the distance from the core surface to the reference point, divided by the number of years it took for the deposits to form. This information was used to identify a slice that dated to approximately the year 1500 which represents a time of ca. two centuries prior to invasion allowing for a large margin of error in the dating procedure. The identified slice was then selected for further analysis. Data on contemporary cladocera communities were obtained from Eid (2019), who analyzed upper core layers (0.5-1.5 cm) from the same lakes.

2.5 Preparing samples

Once the relevant sediment depth was determined, a 1mL subsample was extracted from the core using a syringe. The syringe was emptied in a 250mL beaker, and the content was weighted. The sample was diluted in 125mL 10% potassium hydroxide solution and stirred occasionally. The beaker was placed in a water bath and kept at 55 °C for 25 minutes. This process ensured that the sediment deflocculated for easier analysis without damaging cladoceran remains. After 25 minutes the beaker was filled with cool tap water to cease the reaction. The liquid was immediately sieved through a 51 µm mesh, and the remaining sediment left in the sieve was put in a centrifugal tube together with 15mL distilled water. The sample was centrifuged for 10 minutes at 3100 rpm, compressing the material into a pellet. The excess water was removed, and 0,6 mL 96% ethanol was added and mixed with the sample to preserve the remains. To prepare for microscopy analysis, 0.1mL of the sample-

ethanol mixture and 3 drops of heated glycerol-safarin was mixed together on a microscopy slide. A cover glass was immediately added on top. Four replicate slides were prepared for each lake (Eid, 2019). To be able to find the amount of dry sediment in a wet sample a 1mL subsample of each slice of the core was dried completely in a dryer chamber and weighted. The weight lost in the drying process was used to find the percentage dry weight present in a wet sediment sample.

2.6 Microscopy analysis

To ensure that the method of sample preparation and microscope analysis remained similar across projects and datasets, a course for the analysis was given by previous analyst (S. Eid). Analysis of the microscopy slide containing the cladocera remains were done using a light microscope at 200x magnification. When necessary, a 400x magnification were used to obtain details about the remains. The entire area of the slide containing sample was analyzed. Every slide was analyzed by moving horizontally across the slide and moving vertically just out of viewing distance at the edges. Each body part was identified down to the lowest possible taxa (minimum genus), where the highest number of body parts were used to determine the total number of individuals within each taxonomical group for each slide. For identifying the remains, the work of Szeroczynska & Sarmaha-Korjonen (2007) was utilized. Examples of cladocera fragment found in the samples can be viewed in Appendix S2.

2.7 Data analysis

To investigate the community from various aspects two approaches were selected, both on community and genera level. On the community level an analysis of change in beta diversity over the recorded time period is analyzed. On the genus level an analysis on genus responds to treatment with whitefish and perch was conducted.

For the analyses, the sites are split in three groups depending on the presence of planktivore fish. These groups are referred to as treatment groups. A treatment group describes whether the site is functioning as an effect site or reference site based on the presence or absence of whitefish or perch (Table 1). Perch is an opportunist species, it does not necessarily feed on cladocera, but have the potential to exhibit effective planktivory behavior (Nurminen, Pekcan-Hekim, & Horppila, 2010; Guma'a, 1978). Its role as a planktivore should therefore not be assumed or refused. To avoid possible disturbances in the reference sites, sites containing

both perch and whitefish are pooled together in a separate treatment group. This treatment contains both whitefish and perch in the effect sites. The reference sites to the planktivore treatment do not contain any of the planktivory fish, and therefore avoids the possible interference.

2.7.1 Temporal Beta Diversity

An assessment of temporal beta diversity was conducted to reveal whether there was any difference in the change of cladocera communities over time by comparing effect sites to reference sites. If the effect sites changed in a different way from the reference sites, this would indicate an effect from a planktivore. This analysis measures abundance for each taxonomical group as observed individuals divided by the amount of grams of dry sediment in the sample. The change in each species frequency is measured in percentage change on a decimal fraction scale. A pairwise comparison between T₁ (before invasion) and T₂ (after) was conducted for the abundance of all taxonomical groups recorded in each lake. The comparison produced a dissimilarity vector measuring to which extent each species diverged from T₁ to T₂. If a taxon increased in abundance over time, this was considered a *gain* in abundance. Complimentary, if a species decreased in frequency, this was considered a *loss* in species abundance. The sum of these losses and gains produced for each lake was defined as the *temporal community dissimilarity vector*. The alternative hypothesis predicts that larger sized zooplankton would be affected negatively to the suppression from a top down effect. A secondary effect could include the increase in slammer sized zooplankton. The additional losses and gains in species abundance would likely be visible in the community analysis and could indicate if the beta diversity in effect sites differed from the reference sites. The comparison of these vectors between effect and reference sites indicates to which extent the beta diversity differs in response to planktivores across the recorded time period. If the analysis does not detect any differences in temporal beta diversity vectors between the effect and reference sites, this would indicate that the null hypothesis should not be rejected. The data were treated in R studio version 3.6.3 using the package “adespatial” with the function Temporal Beta-diversity Indices, “TBI” (Legendre, 2019; Rstudio, 2020₂). The function assessed if the lakes were mainly dominated by losses or gains in species abundance. The dissimilarity vectors were measured in percentage change on a fraction decimal scale, and 999 permutations were performed.

2.7.2 *T-test*

The dissimilarity vectors for effect and reference sites within each treatment group were compared through a two-sided Welch t-test. In this thesis a significant p-value is determined to be ≤ 0.05 . The objective for the analysis was to assess if the dissimilarity vectors differed significantly when comparing between the effect and reference sites for the respective treatments. This would indicate that the lakes have changed in different ways and support the alternative hypothesis. As the lakes are separated in three ways depending on the presence of whitefish, perch and planktivores, three t-tests were conducted.

2.7.3 *Model selection*

To be able to compare relationships between the amount of individuals pr. unit of sediment sample, the count value for each taxonomical group was divided by the total numbers of cladocera found in one 0.1 mL sample. This allowed for interpreting the percentage presence of a taxon in a sample. The dynamics of the cladocera genera in response to the presence of perch and whitefish, and lake surface area were analyzed using zero inflated generalized linear models (GLM) with mixed effects and an offset (Rstudio, 20201). Of the 24 genera found during the analysis, seven occurred at a sufficiently high frequency to allow for such model to be fitted. A model was developed for sites inhabited by whitefish, which is a known planktivore. Another model was developed for sites containing perch, which is an opportunist and possibly an effective planktivore. To explore the possibility that both species of fish are exhibiting planktivory, sites that contained either perch or whitefish were pooled together in one treatment referred to as “planktivore”. This was done to control for the possibility that either planktivore was disrupting the function of the reference sites. The model fit was cross validated using AIC values. The global model (Equation 1) includes whitefish and perch presence or absence as a predictor variable, as well as lake surface area. Site was included as a random factor.

$$Y(n) = \beta_0 + X_1\beta_1 + X_2\beta_2 + \beta_3X_1X_2 + X_3\beta_3 + \gamma_1 + \varepsilon$$

(Equation 1)

$Y(n)$ denotes the count value of one genus. Negative binominal distribution is assumed. The offset allows for comparing the frequency of each species regardless of the sedimentation rates between the lakes. β_0 indicates the intercept. $X_1\beta_1$ denotes the presence of whitefish and $X_2\beta_2$ indicates the presence of perch. $\beta_3X_1X_2$ presents an interaction term between treatment

and time. $X_3\beta_3$ indicated the lake surface area. The random effect γ_1 denotes random effect of site. ε represents the residuals.

3.0 Results

3.1 Community assessment

Here, results from comparing dissimilarity vector for each lake is presented. Change is measured as decimal fraction on a 0-1 scale. Lakes are displayed as Box-Cox plots, fig. 2.a, 2.b, & 2.c

The plot visualized the shifts in the cladocera communities within each lake. The TBI function revealed that most lakes are dominated by gains in species abundance, with fewer communities being dominated by losses.

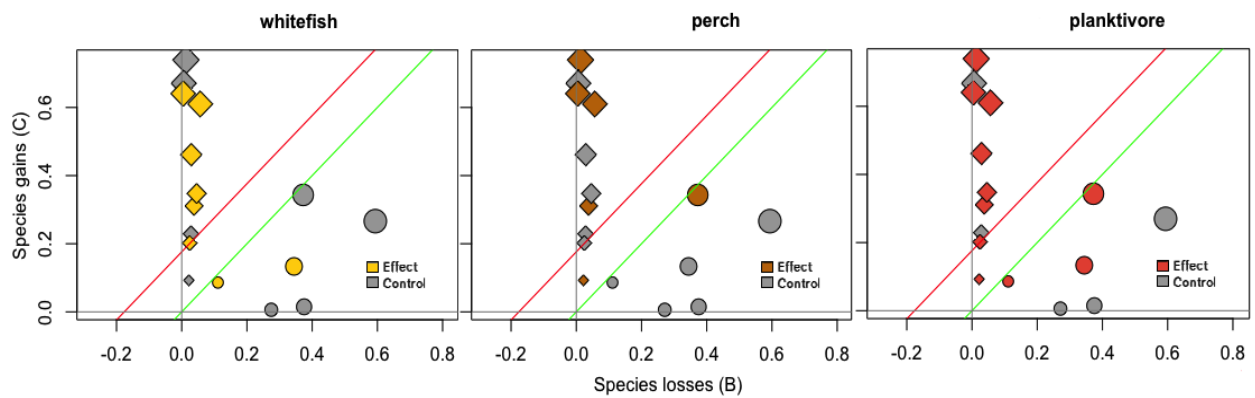


Fig 2.a, 2.b, 2.c: Box-Cox plots illustrating the change within each lake. Colors yellow, brown and red indicate the effect sites for the respective analysis, and grey indicates reference site. Gains is measured on the Y-axis, and losses are measures on the X-axis. The red line indicates the mean change for all lakes. Green line indicates the mean change (red line) for all lakes if losses and gains where equal. The distance between the green and red line indicates that regardless of treatment the lakes are affected over time in a positive direction. Plot 2.c represent the treatments containing both whitefish and perch.

Table 2: Table with percentage losses(B), gains(C), change(D) and temporal vector direction (+/-) for species diversity, used to compose fig. 2.a, 2.b, 2

Temporal vector matrix

Lake name	Treatment Whitefish	Treatment Perch	B (loss)	C (gain)	D (change)	Vector direction
Abbotjønna	Reference	Reference	0.028	0.229	0.257	+
Dalstjønna	Effect	Reference	0.344	0.133	0.478	-
Feragen	Effect	Reference	0.111	0.086	0.197	-
Gjettjønna	Reference	Effect	0.013	0.739	0.752	+
Gubbtjønna	Effect	Effect	0.038	0.311	0.348	+
Harsjøen	Effect	Reference	0.029	0.461	0.491	+
Korssjøen	Reference	Reference	0.006	0.671	0.677	+
Langen	Effect	Reference	0.045	0.347	0.393	+
Langesjøen	Reference	Effect	0.022	0.093	0.115	+
Oksloken	Reference	Reference	0.594	0.266	0.86	-
Olaloken	Reference	Reference	0.271	0.006	0.277	-
Ormkåstjønna	Reference	Reference	0.375	0.015	0.39	-
Rismotjønna	Effect	Effect	0.057	0.61	0.667	+
Røragen	Effect	Effect	0.004	0.641	0.645	+
Storhittersjøen	Effect	Reference	0.024	0.202	0.226	+
Storkrokåttjønna	Reference	Effect	0.372	0.343	0.716	-

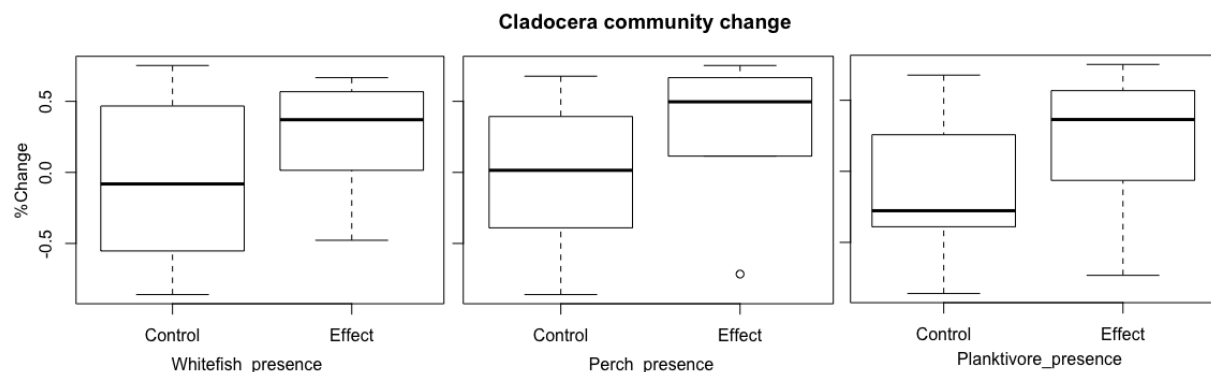


Fig 3.a, 3.b, 3.c: Boxplots illustrating the comparison of temporal dissimilarity vector between the respective treatments, composed from data found in Table 3. Boxplot 3.a illustrates the community response to whitefish presence, 3.b illustrates the community response to perch presence and 3.c illustrates how the cladocera community responds when perch and whitefish are pooled together. Change is measured in percentages on a fraction decimal scale.

3.2 T-test

Here, the results from testing for significant difference in the various groups are presented. When comparing the effect and reference sites depending on whitefish presence, the mean change for reference sites (n=8) was -0.055, and effect sites (n=8) was 0.262. When testing for significant difference between reference and effect sites, the p-value measured to 0.241, which is considered not statistically significant. When comparing the effect and reference

sites depending on perch presence, the mean change for effect sites (n=6) was 0.302 and for reference sites (n=10) was -0.016. The p-value measured to 0.275, which is considered not statistically significant. When comparing the effect and reference sites depending on the presence of either planktivore, the mean change for reference sites (n=11) was -0.119, and effect sites (n=5) was 0.2. When testing for significant difference between reference and effect sites, the p-value measured to 0.241, which is considered not statistically significant. The visualized comparisons for these tests can be viewed in figure 3.a, 3.b, 3.c.

3.3 Genus specific model selection

Here the results from the model selection on genus level is presented. The models were selected by using the function “glmmTMB” (Rstudio1, 2020), a generalized mixed effect model enabling for zero inflation adjustment. A genus specific model was developed for each treatment (Table 3). To visualize the relationship between genera, a barplot containing each genus percentage presence in a sample can be viewed in Fig.4. The models were fitted using treatment, time, treatment-time interaction and lake surface area as predictor variables (Equation 1). A backwards selection was performed where the “anova” function indicated any significance for the predictor variables that likely explained the variation within each genus. The process revealed great variation among the responses. Genus *Alona* was the only genus that was best explained with a null model in every treatment. *Alonella* was best explained by time and lake size in perch and planktivore lakes in addition to treatment in lakes containing whitefish. *Bosmina* was affected by time and treatment with an interaction in all treatment groups. The analysis found that *Chydorus* was not affected by any variable in whitefish and perch treatment groups but expressed a response to time and treatments with interaction in the planktivore treatments. *Acropeus* response was best explained by time and treatment for whitefish and planktivore and was best explained by the null model for sites containing perch presence. *Alonopsis* was affected by time in lakes containing whitefish and lakes containing perch, but also affected by treatment in lakes containing whitefish. When the two treatments were pooled together, there was an effect of treatments and time with interaction. *Daphnia* was best explained by treatments for lakes containing whitefish and was best explained by treatments and time with interaction for perch and planktivore lakes. A visualization of the cladocera response to the various treatment groups can be viewed in Fig. 5.

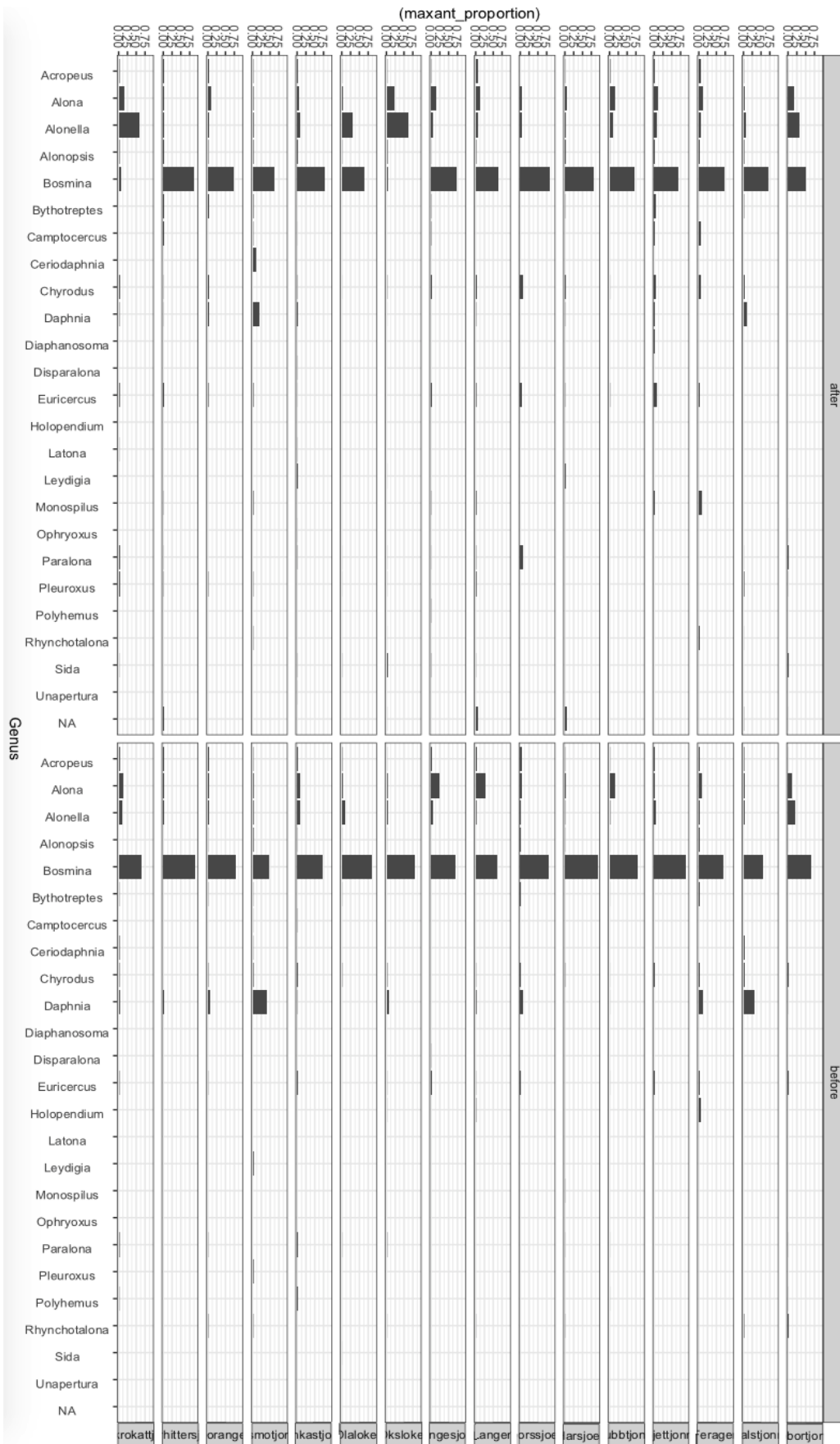


Fig 4: Barplots illustrating the dynamics of dominance between taxonomical groups. Frequency is measured in percentage presence in a 0.1g sample. Labels “before” and “after” refers to time period in terms of the introduction of invasive fish.

Table 3: Table contains results from model selection. Treatments refers to which planktivore is present in the effect sites for the respective analysis. The treatments “planktivore” contains whitefish and/or perch.

Treatment groups

Genus	Whitefish	Perch	Planktivore
Alona	Null model	Null model	Null model
Alonella	Treatment + Time period + Area	Time period + Area	Time period + Area
Bosmina	Time period + Treatment + (Time period: Treatment)	Time period + Treatment + (Time period: Treatment)	Time period + Treatment + (Time period: Treatment)
Chydorus	Null model	Null model	Time period + Treatment + (Time period: Treatment)
Acropeus	Time period + Treatment + (Time period: Treatment)	Null model	Time period + Treatment + (Time period: Treatment)
Alonopsis	Treatment + Time period	Time Period	Time period + Treatment + (Time period: Treatment)
Daphnia	Treatment	Time period + Treatment + (Time period: Treatment)	Time period + Treatment + (Time period: Treatment)

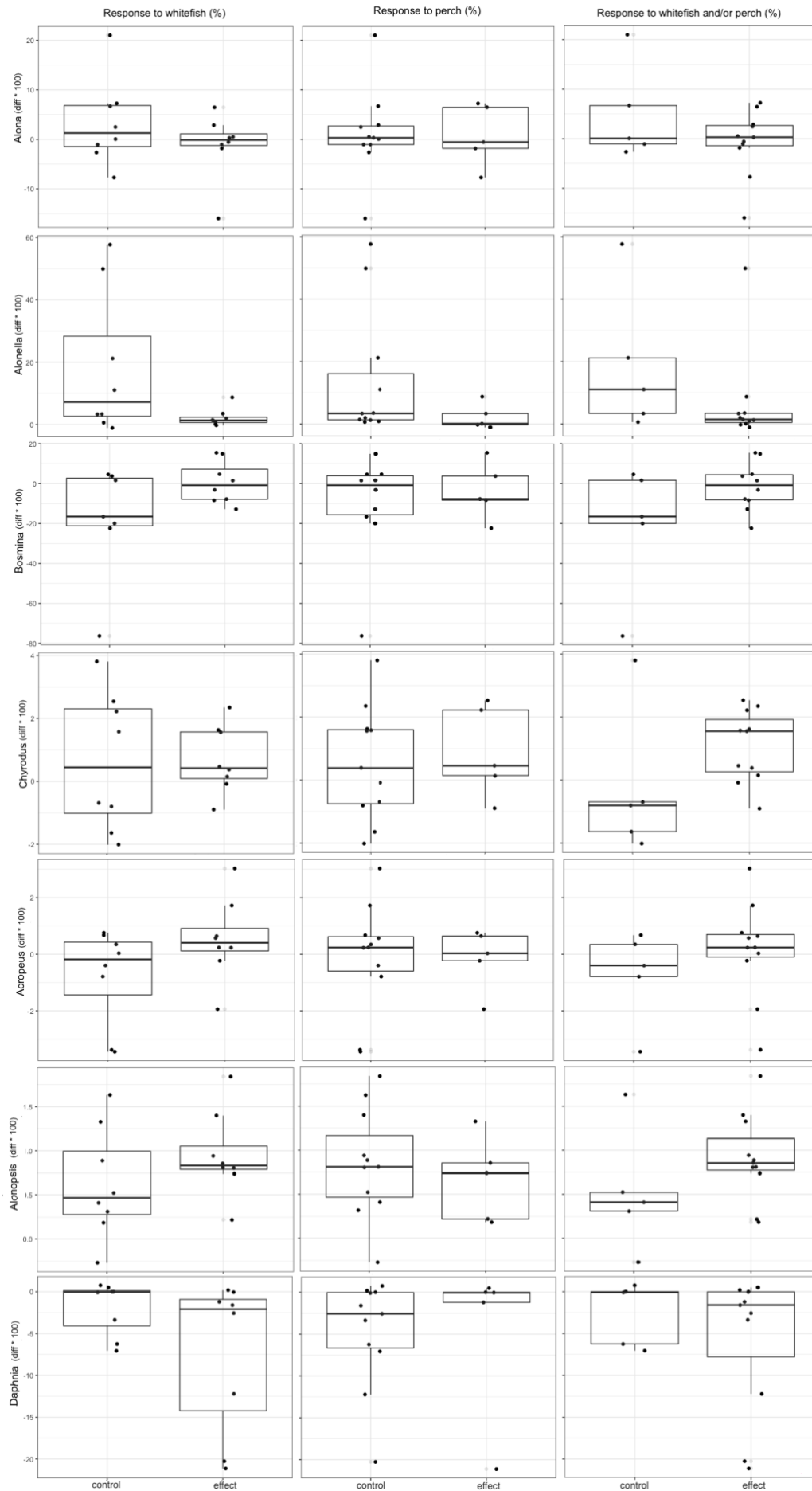


Fig. 5: Boxplots illustrating change in percentage presence in a sample within the genuses between the various treatments. Within each plot, the left side indicates the control sites, and the right side indicates the effect sites.

4.0 Discussion

Here the results from the community analysis and the genus specific model selection are discussed. The analysis conducted on community level found no statistically significant difference when comparing effect and reference sites based on the presence of whitefish or perch. The following discussion will offer various possible explanations to why the community did not respond expectedly to invasion, and if the variation on genus level reflects to these findings. The discussion offers explanations for the results produced by the two approaches, and if they relate to the alternative or the null hypothesis. The analysis investigated how whitefish affect zooplankton communities and also explored the role of perch as a planktivore.

4.1 Genus specific model selection

This analysis was preformed to better understand the dynamics on the taxonomical groups independently of the results on community level. The results from the genus specific model selection found that genera responded to a variety of combinations of the possible explanatory variables (Table 3). Whitefish and perch were listed as a predictor variable for several genuses, such as *Bosmina*, *Acropeus* and *Daphnia*. This might indicate that both whitefish and perch could be affecting the cladocera populations and could therefore disrupt in the function of the reference sites between the treatment groups. It might therefor be more purposeful to discuss the planktivore treatment group. This treatment group does not have potential planktivores present in the reference sites and will consequently be the main focus of this section of the discussion.

Alona was best described by the null model in all treatment groups. This reflects that none of the predictor variables included affects the *Alona* populations. *Alonella* was best explained by time and surface area in the planktivore treatment group. This reflect that the *Alonella* abundance change over time, and that population size is dependent on the size of the lake. Common for the genera *Bosmina*, *Chyrodus*, *Acropeus*, *Alonopsis* and *Daphnia* is that their abundance is best explained with an interaction term between time and treatment. A temporal change itself is not necessarily an indication of a significant event, but more likely due to stochastic events, climate change, eutrophication, or other random events in the surrounding environment. Fitting the model with an interaction term with treatment, this would indicate that population slope depending on time differs from the population slope depending on

treatment. *Bosmina* and *Daphnia* have been found to respond to the presence of a planktivore in prior studies, but no such records have been located for the other genera. None of these effects are reflected on community level, and without knowing the extent of the effect this should not be utilized in evaluation of the hypothesis.

4.2 Community assessment

The results from the temporal beta diversity assessment revealed that there was an overall increase in cladocera frequency in the majority of the sites. It is not unexpected for zooplankton communities to change over time, as mentioned above. Similar results can be found in the section for model selection (Table 3), where several of the genera were fitted with a model including time as explanatory factor. There was no obvious pattern to which sites had an increase or decrease in cladocera frequency (Fig 2.a, 2.b and 2.c). As discussed in section 4.1, perch might be acting as a planktivore in reference sites and should be considered when evaluating the figures. The increase in the majority of the sites may be attributed to an increase in production caused by additional input of nitrogen or phosphorus from the surrounding area. The t-test conducted found no significant difference in temporal community vectors when comparing effect sites to reference sites for either of the treatment groups. This suggests that the null hypothesis should not be rejected.

4.3 Adaptations to predators

This study did not detect an effect from invasive planktivores upon the cladocera community. One possible explanation could be adaptations to predation pressure in the cladoceras. Prior to the invasion, Arctic charr and Brown trout were the dominant species of fish and were present in most of the sampled lakes (Korsen, 2004). Both these fish have a wide range of prey and is known to forage on cladocera (Guma'a, 1978; Nilsson, 1963). The presence of these predators prior to invasion might have adapted the cladocera communities to planktivory. As a possible consequence, the introduction of whitefish and perch might have had a less of an impact long term because the community already have been adapted to the predatory pressure from planktivory. The presence of trout and charr might also have invoked defense mechanisms and adaptations pre-invasion. Cladoceras are able to express morphological adaptations in a within-generation time span (Tollrian & Dodson, 2004). The fish are detected by the zooplankton through chemoreceptors and can provoke phenotypical responses resulting in longer spines on the exoskeleton (Brönmark & Hansson pp.153, 2017). Elongated spines

might be less appealing to predators, and thus lessen the risk of predation (Hanazato & Yasuno, 1989). Rapid phenotypical plasticity could have aided in avoiding heavy predation from planktivores both before and after invasion. Adjusting the life history and behaviors could also decrease the chance of predation. Diel migration and swarming are among the defense mechanisms that can aid in avoiding predators (Brönmark & Hansson, pp.153, 2017). In prior studies, *Bosmina* was found to decrease in carapace size, and mature earlier as a response to planktivore fish (Salo, Walls, Jouko, Rasanen, & Salonen, 1989). This way the cladocera communities might have been adjusted to predation and therefore avoided pronounced effects leading to permanent turnovers and shifts in dominance when the invasion occurred.

4.4 Niche flexibility

By approaching the research question in a multiple-century time perspective, this study presents results which might provide new insights into zooplankton community structures, compared to studies conducted over a shorter time span. The invaded sites might have experienced oscillations in species abundance and community structure early in the invasion process but over time returned to its original state. Since the sites have not been assessed shortly after invasion, the community's short-term response, and therefore resilience is currently unknown. Eid (2019) argued that “*lack of morphological and behavior adaption could explain strong reduction of abundance of certain taxa in the short term but plasticity and evolutionary responses could allow for recovery in the long term*”. The finding of the present study is conflicting to other finding on planktivore impact on cladocera, which have found changes in the community structure and well as decreases in large sized cladocera, and increases in small sized cladocera (Hanazato, Iwakuma, & Hayashi, 1990; Pothoven, Hook, Nalepa, Thomas, & Dyle, 2013).

Since trout and charr also likely posed a predatory pressure on the cladocera community, invasive and indigenous species niches likely overlapped early in the invasion process. *The competitive exclusion principle* predicts that species with overlapping niches would result in the extinction of one competitor (Brönmark & Hansson, 2017, p.110). To avoid extinction, species might have responded with *niche compression*. The compression hypothesis predicts that “*when two species occur together in narrow sympatry, individuals in the overlap zone will use a smaller range of habitats and a larger or unchanged range of prey than individuals in allopatry*” (Dickman, 1986). Avoiding intraspecific dietary competition would depend on

consumers having generalist traits that allows for exercising rapid dietary plasticity, resource partitioning or niche compression (Wootton, pp.199-200; Sánchez-Hernández & Amundsen, 2015). Prior studies on introduced competitor fish have found niche compression and niche segregation to occur in fish communities (Schulze, Droner, Baade, & Holker, 2012; Eloranta, Knudsen, & Amundsen, 2013). An increasing differentiation in dietary resource partitioning might have allowed whitefish and perch to coexist with the indigenous species (Brönmark & Hansson, 2017, p.110). Alternatively, whitefish and perch populations might have been suppressed by other species of fish present in the lakes, and therefore had less of an impact. In a study on fish community in Lake Femund found that whitefish was the main species of prey for trout and charr after reaching a size threshold of 20-30 cm (Næsje, Sandlund, & Saksgård, 1998) which is similar to what Kahilainen & Lehtonen (2002) observed in Lake Muddusjärvi. Salmonids such as trout and charr are considered generalist and opportunist foragers (Sánchez-Hernández & Amundsen, 2015). As trout and charr are secondary piscivores, a niche adaptation might have acted as a top down control on the invasive species and explain why whitefish and perch did not have the expected effect on the cladocera community (Amundsen, 1994; Sandlund, Saksgård, & Næsje, 2019; Næsje, Sandlund, & Saksgård, 1998). A shift to piscivory is favorable when possible due to a positively induced growth rate compared to a diet based on invertebrates (Elliott & Hurley, 2000). By expressing piscivory, trout and charr might have induced a predatory pressure on the invasive planktivores, therefore limiting the population size and effect on the cladocera community. Some studies from non-sampled lakes in the surrounding area gives information about the role of trout in regulating the impact of whitefish. An assessment conducted in Lake Femunden where whitefish is native found that trout are mainly piscivore, and have a diet containing whitefish (69%) and charr (23%) (Sandlund, Saksgård, & Næsje, 2019; Saksgård, Næsje, Sandlund, & Ugedal, 2002). Another assessment on stomach content in trout from Lake Aursunden, Røros found whitefish to be a species of prey to trout in these sites. Other organisms in the trout diet consisted of caddish fly larvae and low levels of cladocera (Johnsen, et al., 2012). This supports the possibility and likelihood that trout might not be utilizing zooplankton as its main source of prey and might be expressing piscivory in response to competition. A shift to piscivory, on the other hand might depend on reaching a certain size threshold as mentioned above. Reaching such a threshold might be less likely due to increased competition and may not always occur (Amundsen, Knudsen, & Bryhni, 2010). Yet, one could argue that resilience and resistance is more likely to occur when the species within the ecosystem are able to express generalist traits and resource partitioning in response to invasive species. These

explanations illustrate how the abundance of a resource can remain static, while the number of consumers can vary. Another similar example of a trophic interaction between the native fish fauna and the invasive species can be found in the Great Lakes, Ontario, where the impact of the invasive zooplankter *Bythotrephes* on the cladocera was likely suppressed by predation on *Bythotrephes* by alewife (*Alosa pseudoharengus*) (Stewart, Johannsson, Holeck, Sprules, & Gorman, 2010). Thus, it seems clear that interactions between an introduced planktivore and native species can shape the effects of the invasive species on their prey. In addition to the native trout and charr, a range of other species are native or have been introduced in the same time period as whitefish and perch (Table 1). Of these species, pike, burbot as well as perch are also able to express piscivory, where burbot and pike are specialized piscivores (McPhail & Paragamian, 2000; Kahilainen & Lehtonen, 2002; Kahilainen & Lehtonen, 2003). In prior studies on predation from burbot, pike, charr and trout, whitefish was found to be the main species of prey (Kahilainen & Lehtonen, 2003). In addition to acting as a planktivore, perch might have acted as a predator upon whitefish, further limiting the whitefish population size. This could be reflected in the results where sites containing perch did not show a significant decrease in cladocerans (Fig. 3.b), but the potential disruption of reference sites should be kept in mind.

Adjustments in the predatory species might have been an ecosystem trait that allows the cladocera community to remain resilient. A study conducted on the resilience and resistance of limnic ecosystem argues that the link between biodiversity and resilience depends on control processes, the composition of species capable of contributing to the processes, and the susceptibility of the species to particular ecosystem stress (Carpenter & Cottingham, 1997). This could be related back to this discussion, where dietary plasticity and niche segregation could be a form key control processes to invasive species. If the fish community developed a predatory pressure upon whitefish, this process might have enabled resilience for the cladocera community.

Another possible explanation to the lack of response in the cladocera community might be that cladocerans have not been predated upon by whitefish and perch. Prior studies have found that perch usually switch from a zooplankton-based diet to benthic food in early life stages and might therefore spend less time of their life feeding on zooplankton (Guma'a, 1978; Lorenzoni, Carosi, Pedicillo, & Trusso, 2009). This could lower the impact on cladocera communities. Whitefish have also previously been found to vary greatly on what species of zooplankton they prey upon where some cases the diet have mainly consisted of

either copepods or cladocera, varying greatly from lake to lake (Rask & Arvola, 1985). If in this study some lakes have been dominated by copepod-preferring whitefish, this might have disrupted the result. As copepods preserve poorly in sediment, this aspect could not be considered in this study.

As shown in this study, for ecosystems to remain unaffected over a prolonged time, it likely possesses some characteristics that allows for adaptation to perturbations. By comparing result of this thesis to the results of other studies on the topic, no common denominators or trends have been identified. This strengthens the view that invasive species affect the ecosystems in highly unpredictable ways. This dissimilarity between study finding also allude to that long-term studies can uncover different results.

4.5 Study limitations

Some limitations apply to the current study. First, it is limited to considering change in abundance only and will not consider any evolutionary or morphological changes in the microscopy- or data analysis to explain the results.

Second, the whitefish is recognized as a polymorph species (Amundsen, Bøhn, & Våga, 2002), and exhibit different feeding behaviors. Since the whitefish morphology and distribution in the sampled sites remain largely unknown, this aspect was not considered in this study.

Third, in a comparison of cladocera remain preservation, Nykänen et al. (2009) stated that some species remains such as *Bosmina* preserved better than i.e.g. *Daphnia* (Nykänen, Vakkilainen, Liukkonen, & Kairesalo.T., 2009). If *Daphnia* remains have disintegrated beyond recognition, this could possibly interfere with the results. The extent of this effect is not currently known, but, some bias due differing conservation were expected.

5.0 Summary

This study investigated the impact of whitefish and perch on cladocera communities. The temporal beta diversity was compared in three treatment groups, and none of the groups produced indication that whitefish or perch is impacting the cladoceran communities in a significant manner. In addition to a community level analysis, the dynamics of cladocera communities was investigated on genus level. *Bosmina*, *Chyrodus*, *Acropeus*, *Alonopsis* and

Daphnia showed indication that the populations were affected by an interaction term between time and treatment in the treatment group containing either perch or whitefish. This study argues that the presence of trout and charr prior to invasion might have mitigated the impact of perch and whitefish. The study also find reason to believe that adaptations among the cladocera and fish community might have allowed the cladocera communities to remain unaffected. Adapting the niche is essential in sympatry. Adaptation among the zooplankton communities might also have contributed the absence of effect from the planktivores.

Suggestions for further research

I have found the use of BACI study designs useful, and I would advocate for its use. To further unveil the mechanisms of resilience to invasive species in lake systems, I would advise that BACI study designs are used in both short-term studies on lentic ecosystems response to invasive species, which would put the short-term effects in contrast to the long-term effects. This way both the immediate and the later effects would become visible. Such knowledge could be valuable in the future of lentic ecosystems facing alien species invasion. I would also suggest further investigating the collected material to study change in zooplankton morphology in response to whitefish invasion. This would aid in explaining the findings mentioned in this thesis.

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S.0. Appendix

S1. Metal determination material.

Results from metal determination process. The graphs illustrate the variation in trace elements from copper mining history left in the sediment core. Peaks in metals was used to determine the time period the slices through the core represents.

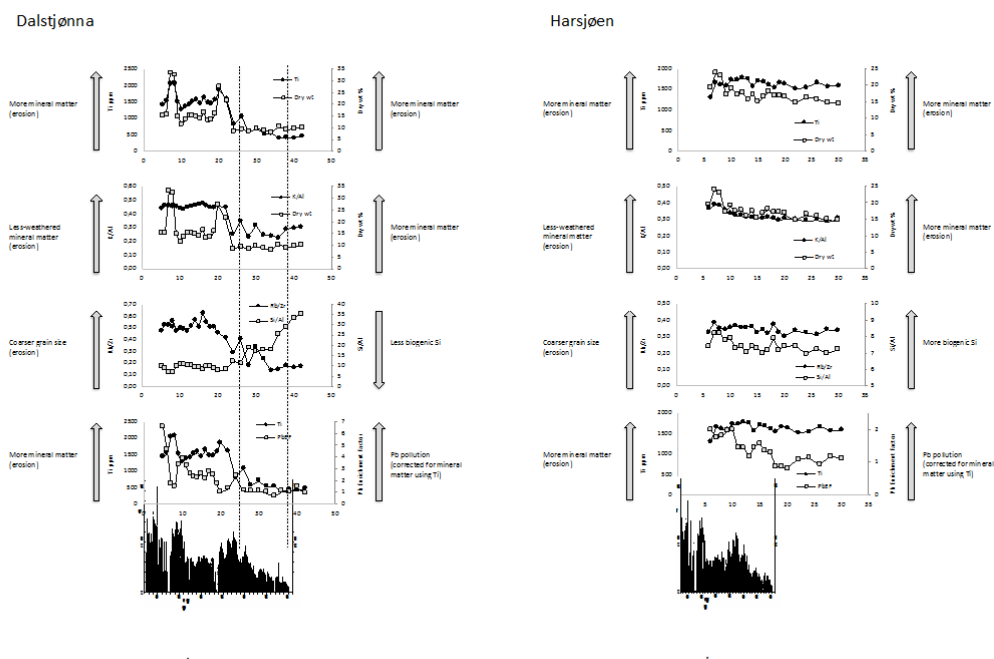
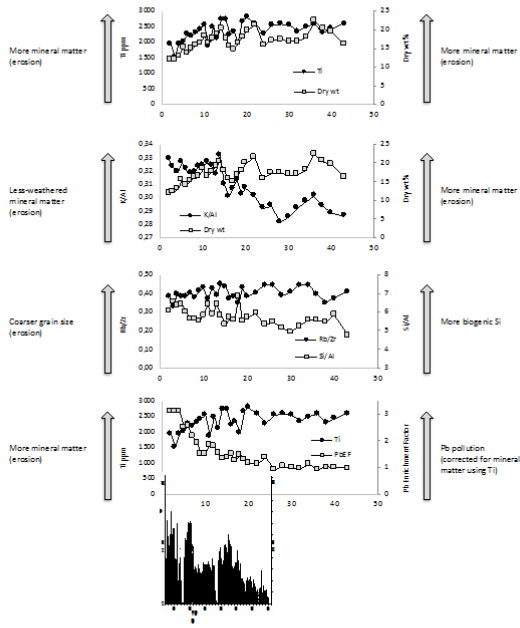
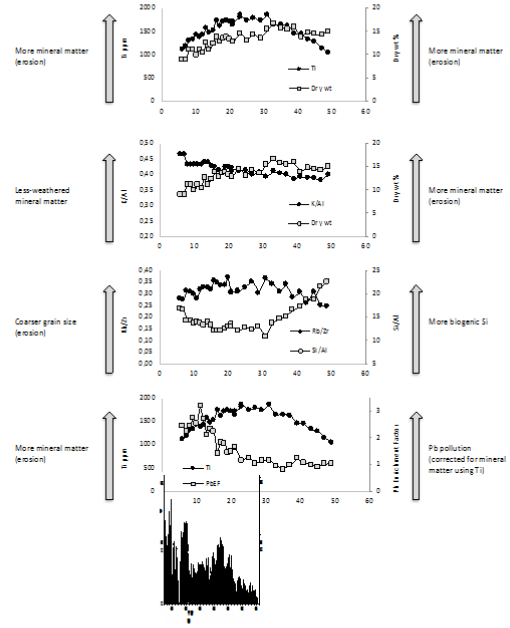


Fig S1.a, S1.b: Examples of metal determination plots from Dalstjønna and Harsjøen.

Storhittersjøen



Langen



Røragen

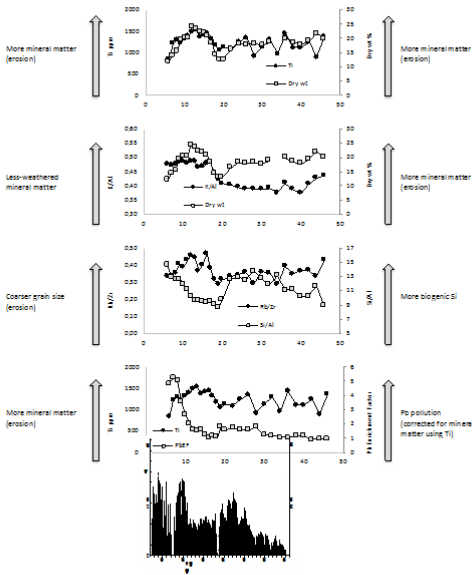


Fig S1.a, S1.b, S1.c, S1.d, S1.e : Examples of metal determination plots from Dalstjøna, Harsjøen, Storhittersjøen, Langen and Røragen.

S2. Pictures from microscopy analysis.

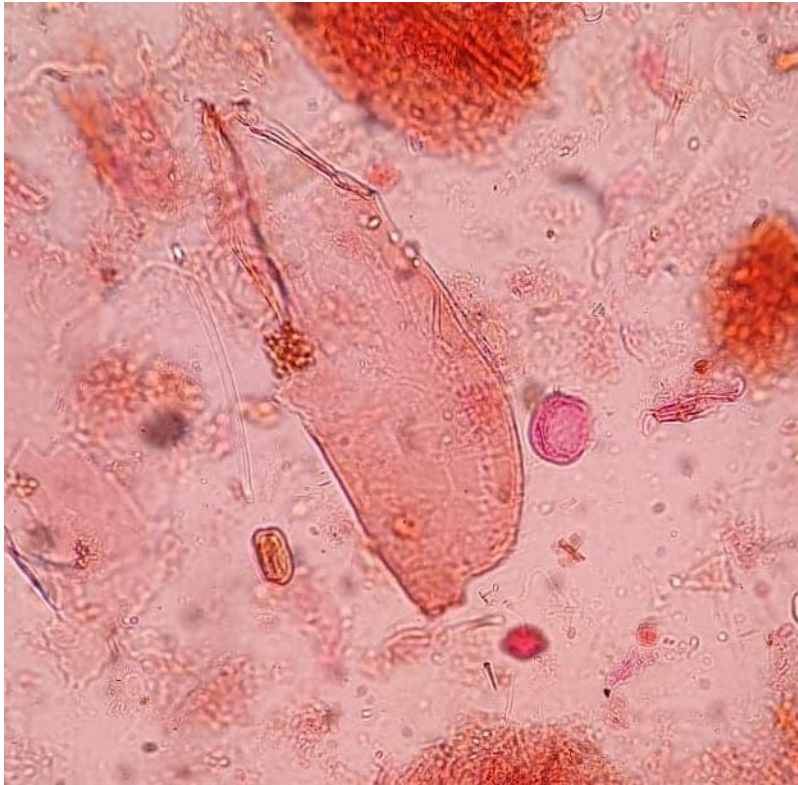


Figure S2.a: Male *Alona affinis* postabdomen.

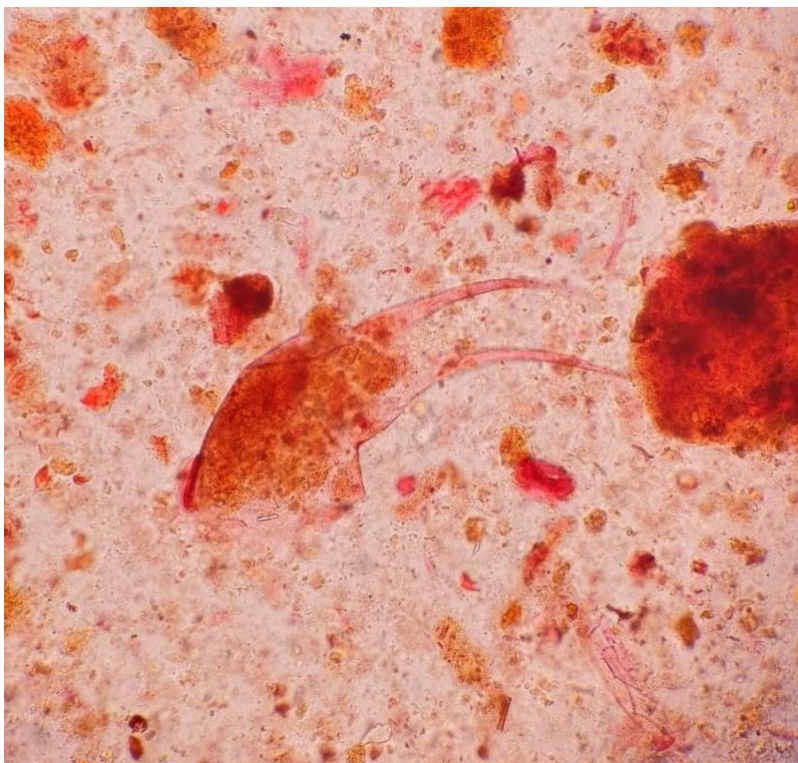


Figure S2.b. Example of *Bosmina* head capsule.



Figure S2.c. Example of *Alonopsis elongata* shell.



Figure S2.d. Cluster of *Bosmina* body parts.