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Effects of introduced planktivorous fish on the seasonal dynamics of freshwater zooplankton

Master's thesis in Natural Resources Management

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Silje

ABSTRACT

Introduced planktivorous fish in freshwater may have a substantial effect on the food-web by acting as a top-down controlling agent on zooplankton, with potentially cascading effects on lower trophic levels. However, such an effect of introduced planktivores is unlikely to be constant throughout the season and may rather influence the seasonal dynamics of their prey. As the zooplankton follows a seasonal succession pattern regulated by abiotic and biotic factors, it is crucial to understand the effects and consequences introducing non-native planktivorous fish will have on the seasonal dynamics of zooplankton, to better manage freshwater ecosystems. To study this, I went on six field trips during June-October, where I conducted vertical zooplankton hauls, sampled water for lake chlorophyll α concentration, and took abiotic measurements of 12 lakes with or without the introduced planktivorous species European whitefish (*Coregonus lavaretus*) and European perch (*Perca fluviatilis*), in Central Norway. With this data I compared patterns of density-dependent population growth and seasonal changes in demographics of the freshwater crustacean *Daphnia spp.* based on the lakes fish community. In addition, by using the Bray-Curtis dissimilarity Index, I tested for differences in the seasonal dynamics of zooplankton community composition between lakes with and without the invasive planktivores. Results show that it was not possible to distinguish between the two lake types based on the apparent strength of density dependence in *Daphnia spp.* growth rates. In contrast, there was a clear difference in the seasonal fluctuation in *Daphnia spp.* body size between the lake types, with a larger size range, mean size and fluctuation in size in the absence of planktivorous fish. The seasonal change in zooplankton community composition in lakes based on fish community showed a bigger change between consecutive sampling events in the planktivorous lakes compared to the non-planktivorous lakes, with both lake types changing the most in spring, and with decreasing change through the season. However, only towards the end of the season did I see a difference between the zooplankton community composition based on the fish community, as the composition became more similar when compared within lake type than between lake types. Patterns earlier in the season showed no effect of fish community on the differences in zooplankton community composition between lake types, indicating that other factors than planktivorous fish are stronger driver of succession of in the start of the season.

ABSTRAKT

Introdusert planktivore fisk i ferskvann kan ha en betydelig effekt på næringsnettet ved å fungere som en kontroll ovenfra og ned på zooplankton, med mulige kaskadeeffekter på lavere trofiske nivåer. Imidlertid er det usannsynlig at en slik effekt av introduserte planktivore vil være konstant gjennom hele sesongen og kan heller påvirke den sesongmessige dynamikken til byttet deres. Ettersom zooplanktonet følger et sesongmessig suksesjonsmønster regulert av abiotiske og biotiske faktorer, er det avgjørende å forstå virkningene og konsekvensene introduksjon av ikke-naturlige planktivore fisk vil ha på den sesongmessige dynamikken til zooplankton, for å bedre kunne forvalte ferskvannøkosystemer. For å studere dette dro jeg på seks feltturer i løpet av juni-oktober, hvor jeg gjennomførte vertikale zooplanktontrekk, tok prøver av vann for klorofyll α -konsentrasjon og tok abiotiske målinger av 12 innsjøer med eller uten de introduserte planktivore artene europeisk sik (*Coregonus lavaretus*) og europeisk abbor (*Perca fluviatilis*), i Midt-Norge. Med disse dataene sammenlignet jeg mønstre av tetthetsavhengig populasjonsvekst og sesongmessige endringer i demografien til ferskvannskrepsdyret *Daphnia spp.* basert på innsjøenes fiskesamfunn. I tillegg, ved å bruke Bray-Curtis ulikhetsindeks, testet jeg for forskjeller i sesongdynamikken i zooplanktonsamfunnets sammensetning mellom innsjøer med og uten de introduserte planktivore fiskene. Resultatene viser at det ikke var mulig å skille mellom de to innsjøtypene basert på styrken av tetthetsavhengighet i vekstraten hos *Daphnia spp.* Derimot var det en klar forskjell i sesongsvingningene i kroppsstørrelsen hos *Daphnia spp.* mellom innsjøtypene, med et større størrelsesspekter, gjennomsnittlig størrelse og svingninger i kroppsstørrelse ved fravær av planktivore fisk sammenlignet innsjøene med planktivore fisk. Sesongvariasjonen i zooplanktonsamfunnets sammensetning i de ulike innsjøtypene viste en større endring mellom påfølgende feltrunder i innsjøene med planktivore fisk sammenlignet med de ikke-planktivore innsjøene. Begge innsjøtypene endret seg mest om våren, og med avtagende endring gjennom sesongen. Likevel så jeg ikke en forskjell i sammensetning av zooplanktonsamfunnet basert på innsjøtype før mot slutten av sesongen. Ulikheten i zooplankton sammensetningen ble da mindre innad i innsjøtypene sammenlignet med ulikheten mellom innsjøtyper. Mønstret tidligere i sesongen viste ingen effekt av fiskesamfunn på ulikheten i zooplankton sammensetningen mellom innsjøtypene, noe som tyder på at andre faktorer enn predasjonstrykket fra planktivore fisk er en sterkere driver for suksesjon av zooplanktonet i starten av sesongen.

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Introduction

With the ever-increasing environmental changes caused by human activity, nature is experiencing immense pressure with native ecosystems being increasingly transformed into landscapes dominated by humans (Kim & Byrne, 2006). Both on a global and local scale, changes in species composition, abundance, and ecosystems diversity, are leading to a loss of biodiversity and the ecosystem services they provide us (Walsh et al., 2016). Of the many drivers for change in nature, the spread of non-native species -with their potential of becoming invasive- is seen as one of the strongest ones, leading to a homogenisation of ecosystems and thus a loss of biodiversity and ecosystem services on a global and local scale (Díaz et al., 2019; Toussaint et al., 2016). Freshwater ecosystems, as one of the most exploited ecosystems in the world, are losing biodiversity at a higher rate than most terrestrial ecosystems (Dudgeon et al., 2006). This is partly due to their relatively high biodiversity, but also due to their fundamental role for the functioning of human societies, by contributing with a range of ecosystem services like drinking water and being a source of food and recreational activities (Dudgeon et al., 2006; Walsh et al., 2016). Translocation of freshwater fish species, which can be intentional through fish stocking and recreational practices, or unintentional through secondary distribution or use of live bait, is an increasing threat for the decreasing number of undisturbed freshwater systems (Hesthagen & Sandlund, 2004; Strayer, 2010). Thus, understanding the consequences of such translocations should be of high priority for management of freshwater ecosystems.

The consequences of introducing new fish species into a freshwater system can be vast, depending on the type of species that are being introduced, the composition of native species in the system, and at which trophic level the introduced species belongs to (Strayer, 2010). The introduction of planktivorous fish may cause large cascading effects in freshwater food webs, by efficiently feeding on, and thus reducing the abundance of herbivorous zooplankton (Brooks & Dodson, 1965; Carpenter et al., 1985; Hanazato & Yasuno, 1989). The central placement of zooplankton in the freshwater food web is what causes changes in the zooplankton communities to potentially lead to cascading effects on the rest of the system (Bartrons et al., 2020; Zhang et al., 2013; Zollner et al., 2003). The presence of efficient zooplankton predators, such as planktivorous fish species, can reduce the zooplankton biomass and alter the species composition through top-down (TD) control by predation pressure and size-selection of prey (Carpenter et al., 1987; Dahlhansen, 1995; Northcote, 1988; Zhang et al., 2019). Depending on the nutrient loading in the system, zooplankton

can also be controlled bottom-up (BU), by limitation of available phytoplankton (Carpenter et al., 1985; Mcqueen et al., 1986; Sommer et al., 1986; Straškraba, 1965). The size or digestibility of available phytoplankton also effects the composition of the zooplankton because the size of particles that zooplankton are able to consume are linked to morphological traits, such as body size and feeding strategies (Burns, 1968; Hall et al., 1976).

The above considerations suggest that pronounced changes to the food web can be expected when planktivorous fish are introduced to localities where they were previously absent. However, these responses may manifest differently during different periods of the plankton growth season. Through the season, the relative strength of TD control by predation pressure and BU control by resource availability vary on its effect on the zooplankton (Carpenter et al., 1985; Sommer et al., 1986). Within a window set by abiotic factors, temporal variation in predation pressure and resource limitation can lead to a seasonal succession pattern of the zooplankton community composition and size distribution, as described in the PEG-model (Hu et al., 2019; Sommer et al., 1986; Zhang et al., 2019). In the beginning of spring, increasing temperatures and light conditions lead to rapid growth of phytoplankton (Sommer et al., 1986). Herbivorous zooplankton density increases fast following the phytoplankton bloom. The quickly increasing zooplankton biomass will in nutrient limited lakes deplete the phytoplankton resources completely, resulting in a period of strong BU control on the zooplankton by a high competition pressure for resources during summer known as the “clear water phase” (Brooks & Dodson, 1965; Carpenter et al., 1985; Sommer et al., 1986). During the clear water phase, a rapid decrease in zooplankton abundance and biomass occurs, caused by increased competition for limited resources and resulting reduced fecundity, and thus recruitment to the population in addition to higher mortality rates due to starvation. With the decrease in zooplankton biomass following the clear-water phase, the phytoplankton is released from grazing and may increase in abundance, which may be associated with a second peak in zooplankton abundance. Finally, as autumn progresses, temperatures and light conditions worsen, and the abundance of both phytoplankton and zooplankton decreases (Carpenter et al., 1987; Sommer et al., 1986). In lakes containing planktivorous fish, the zooplankton will in addition to the BU control in the clear water phase also experience a strong TD control by predation. Higher temperatures causes the fish to increase their feeding rates, and in addition they may increase in total biomass due to rapid growth of the 0+ cohort (Carpenter et al., 1985). Thus, both BU and TD effects may contribute to a decrease in zooplankton population

abundance (Vanni et al., 2009). Compared to the absence of planktivores, the presence of an effective predator may reduce the zooplankton biomass in the summer before they get affected by the increasing competition for resources (Gliwicz & Pijanowska, 1989; Zaret, 1980). This competition release could lead to phytoplankton biomass staying high enough for the zooplankton not to be as drastically affected by increased competition, which would otherwise lead to a decrease in reproduction and an increase chance for starvation. As TD control by predation will help keep the zooplankton biomass low, under the carrying capacity of the phytoplankton resource through the season (Zaret, 1980), it could possibly lead to zooplankton growth rates being less affected by density-dependent competition for resources. As temperatures decline towards autumn and thus the predation pressure, the release of TD control gives the zooplankton a chance to increase shortly a second time in fall before decreasing as temperature goes below their thermal optimum (Gliwicz & Pijanowska, 1989; Sommer et al., 1986).

In addition to influencing patterns of density dependence, the change from BU to TD regulation of zooplankton when experiencing invasion by a planktivore fish may also influence the seasonal dynamics of zooplankton populations' demographic structure (Dawidowicz & Pijanowska, 1984; Pourriot, 1983). In many previous studies, biomass and abundance have been used to measure the trophic effects planktivorous predators, such as fish, and phytoplankton has on the zooplankton community (Carpenter et al., 1987; Hairston & Hairston, 1993; Hansson et al., 2004; Persson et al., 1992). But studies have also shown that due to the size selectiveness of planktivorous fish and zooplankton when it comes to prey, the biomass of zooplankton on a finer taxonomic level are not always negatively correlated with an increase in predation pressure (Cyr & Curtis, 1999; Heneghan et al., 2016), or positively correlated with an increase in phytoplankton (Persson et al., 2007; Yuan & Pollard, 2018). The changes in population demographics, such as individual size distribution, can in the absence of planktivorous fish be expected to be influenced by their resources. Trends in individual size have therefore been suggested to be a better measure to indicate which trophic control is at play (Braun et al., 2021; Hall et al., 1976; Zhang et al., 2013). With the increasing competition for phytoplankton in the clear water phase, the mean size of individuals in zooplankton populations tend to increase. This has been argued to be because bigger individuals have a lower metabolic rate per unit body mass compared to smaller individuals, and can feed on a broader size range of phytoplankton (Bonecker et al., 2011; Brooks & Dodson, 1965; Burns, 1968; Cyr & Curtis, 1999). Others have suggested that the superiority of larger individuals is due to increased

predation pressure of smaller sized individuals by a larger biomass of planktivorous invertebrates in the absence of invertebrate-feeding fish (Dodson, 1974; Yan & Pawson, 1997). Thus, if zooplankton in lakes without planktivorous fish are more strongly regulated by their resources, the size distribution should reflect this by increasing when resources are low and competition high (i.e., in the clear water phase), and decrease when competition goes down due to more available resources (i.e., towards the second peak in zooplankton). Conversely, the presence of a planktivorous fish may shift zooplankton size distributions towards dominance by smaller sizes (Ogorelec et al., 2021; Post & McQueen, 1987; Vanni, 1986). This is due to size selectivity of planktivorous fish, which makes them prefer older and larger sized zooplankton in favour of smaller ones (Brooks & Dodson, 1965). Lakes with planktivorous fish often see this dominance of smaller zooplankton when predation pressure is high (e.g. during summer), but in periods when predation pressure falls (e.g. towards autumn), the zooplankton tend to increase in mean body size (Post & McQueen, 1987; Zhang et al., 2019). In some high productivity (eutrophic) lakes, this shift to a smaller sized and less effective grazing zooplankton community structure can lead to an uncontrolled growth of phytoplankton and toxic algae (Ersoy et al., 2019; Ogorelec et al., 2021).

A final effect of invasion by planktivorous species is that it may influence the seasonal zooplankton community dynamics (Gliwicz & Pijanowska, 1989). As explained, predation and resource availability may affect the zooplankton community, and together with the change in temperature, they are what drives the succession patterns of zooplankton communities, changing them through the season (Allan, 1977; Jensen, 2019). Both predation and resource limitation lead to a less diverse zooplankton community, by decreasing the range of the size structure, either to larger species by BU control, or smaller species by TD control (Yan & Pawson, 1997; Zhang et al., 2019). Following the spring bloom of phytoplankton there is an exponential growth of herbivorous zooplankton with short generation time feeding on the smallest and most easily handled phytoplankton (Persson et al., 1993). Later in the season these are outcompeted by the more specialised herbivorous zooplankton with longer generation time (Brooks & Dodson, 1965; Hall et al., 1976; Sommer et al., 1986). Due to the high pressures by the trophic controls of limited resources and predation pressure following the phytoplankton bloom in spring, it has been seen that the zooplankton community changes the most in the start of the season, and is expected to change less after the decrease in biomass following the spring bloom (Rogers et al., 2020; Sommer et al., 1986).

In the present study I addressed all these three categories of potential effects (i.e., strength of density dependence and seasonal dynamics of size-structure in a focal taxon, and seasonal change in zooplankton community structure) of invasive planktivores on the seasonal dynamics of freshwater zooplankton. I did a comparative study including twelve freshwater lakes with different fish communities in central parts of Norway, which were sampled six times in the period of June to September in 2021. The lakes were inhabited by introduced planktivorous fish species European whitefish (*Coregonus lavaretus*) and/or European perch (*Perca fluviatilis*), or only inhabited by the non-planktivorous fish species brown trout (*Salmo trutta*) or Northern pike (*Esox lucius*). To see if there were possible seasonal differences in the zooplankton community between lakes with different fish communities, I tested and compared the effect of the fish community on (i) the density dependence of population growth, (ii) the seasonal dynamics of body size, and (iii) the differences in the seasonal dynamics of zooplankton communities. For (i) and (ii) I focused on *Daphnia spp.* because these are highly efficient grazers on phytoplankton, and are commonly preferred as prey by planktivorous fish in freshwater (Brooks, 1968). In addition, this group was present in most lakes throughout the season. For (iii) I tested whether the difference in the zooplankton community composition and the changes in this throughout the season depended on lake type, using the Bray-Curtis dissimilarity Index.

Material and methods

Study area

Samples were gathered from lakes in Røros and Holtålen municipalities in Trøndelag, Norway (Fig. 1). In total, twelve lakes were selected to form two lake type groups based on information about their fish communities, gathered from the Norwegian Biodiversity Information Centre. Six lakes were categorized as containing planktivorous fish based on the recorded presence of European whitefish and/or European perch. These are regional invasive species that were introduced to lakes in the area during the 18th century as a result of a growing human population and mining operations in the area (Huitfeldt-Kaas, 1918). Prior to this, whitefish and perch were only native to Lake Femunden, but got spread unintentionally through log flumes connected to surrounding lakes. Later, in the early 1900s, several lakes in the area were also intentionally stocked with whitefish (Sandlund et al., 2013). The remaining six lakes were categorized as non-planktivorous and contained only brown trout or Northern pike. While pike is considered a specialised piscivore, feeding mainly on smaller fish (Beaudoin et al., 1999), brown trout is observed to have a more varied diet, which includes zooplankton in periods when zooplankton densities are high (Schei & Jonsson, 1989). Brown trout is however not thought to be an efficient predator of zooplankton compared to whitefish and perch, which are more specialized on feeding on smaller invertebrates like zooplankton (Eloranta et al., 2011; Guma'a, 1978).

To verify the existing fish community data, water samples were taken from each lake for an accompanying study that analyses the fish community in lakes based on eDNA (M. Majaneva, unpublished data). In the cases where the two sources of information were inconsistent, we obtained recent observations from local anglers. In one of the lakes (L. Åbbårtjønna) where previous records suggested presence of only brown trout, only perch were observed in the eDNA analyses. Thus, the status of this lake was changed to the planktivorous lake type group. One lake (L. Dalstjønna) changed status from containing introduced whitefish to only containing brown trout based on eDNA results and angler records, and therefore was moved to the non-planktivorous lake type group.

In addition to whitefish and/or perch, a supplementary variety of fish were present in the planktivorous lake types. This included brown trout, pike, arctic char (*Salvelinus alpinus*), burbot (*Lota lota*), common minnow (*Phoxinus phoxinus*), and European grayling (*Thymallus thymallus*) (Table 1).

Data on abiotic factors in the lakes classify all the lakes as oligotrophic, low productivity lakes (Table A1). Measures taken were conductivity (7.7-95.0 mS), dissolved oxygen (8.18-10.45 mg/L), pH (6.57-7.90), and nitrogen (4.4-10.0 µg/L) and particulate phosphorus (1.45-3.00 µg/L).

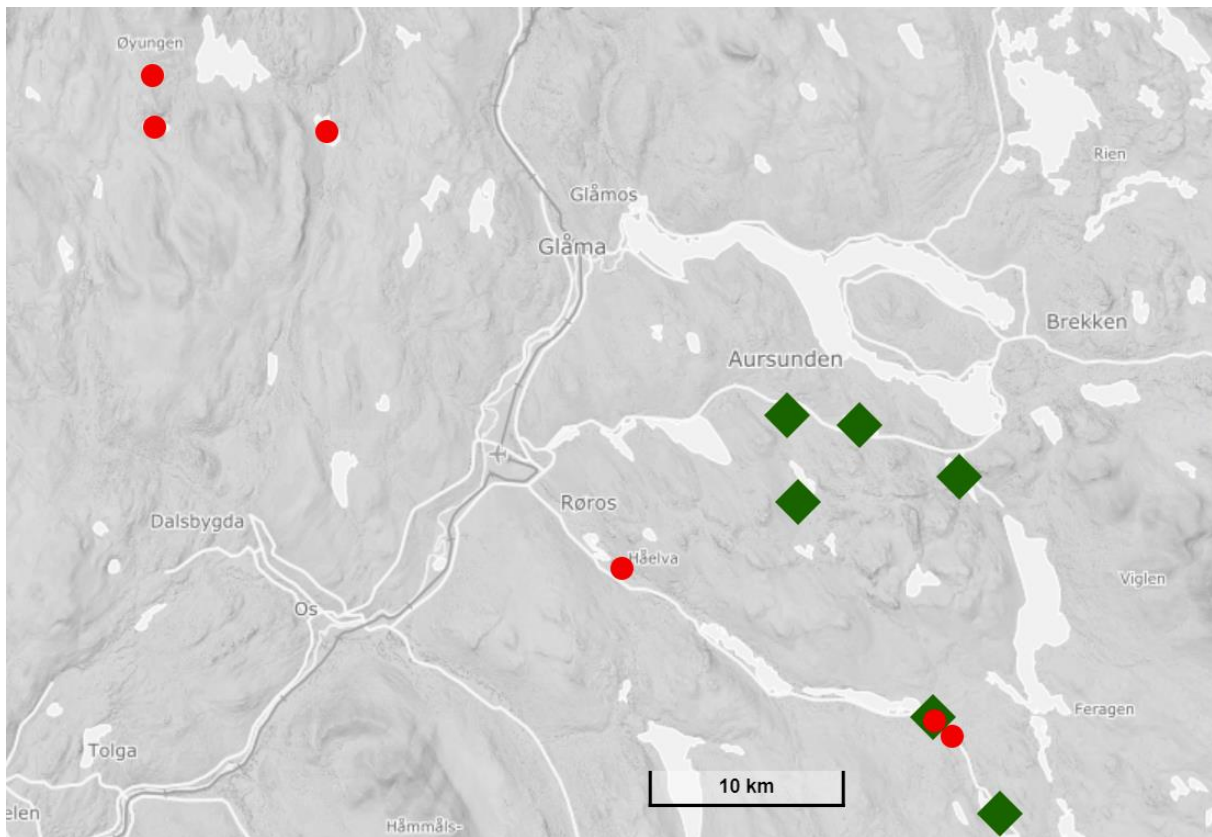


Figure 1: Map showing the area of Røros and Holtålen municipality, with the locations of the sampled lakes. ■= lakes with planktivorous fish (whitefish and/or perch), and ●= lakes with only non-planktivorous fish (brown trout or pike).

Table 1: Information about the lakes sampled. Fish community data were gathered from sightings registered at the Norwegian Biodiversity Information Centre (<https://artskart.artsdatabanken.no/>, visited at 10.11.2020), eDNA samples and recent angler records. Fish species present in each lake are listed by common name, coordinates of lake center point (in latitude/longitude), lake elevation (in meters above sea level), lake area (in km²) and the unique national serial number from the lake database of The Norwegian Water Resources and Energy Directorate (<https://www.nve.no/>, visited at 10.11.2021).

Information about fish community			Information about site			
Lake Name	Lake Type Category	Fish Present	Coordinates	Elevation	Lake area	Lake ID
Røragen	Planktivorous	Brown trout, Burbot, Minnow, Perch, Pike, Whitefish	62.5818° N 11.8056° E	673	1,3448	177
Langen	Planktivorous	Arctic charr, Brown trout, Burbot, Perch, Minnow, Grayling, Whitefish	62.5996° N 11.7169° E	749	0,7734	35338
Harsjøen	Planktivorous	Arctic charr, Brown trout, Burbot, Whitefish	62.5735° N 11.6565° E	751	1,4298	247
Storhittersjøen	Planktivorous	Arctic charr, Burbot, Minnow, Grayling, Whitefish	62.6054° N 11.6364° E	721	1,1449	246
Åbbærtjønnna	Planktivorous	Perch	62.4258° N 11.8646° E	666	0,0218	140171
Oksloken	Non-planktivorous	Pike	62.4606° N 11.8134° E	658	0,0087	140001
Olaloken	Non-planktivorous	Brown trout	62.4674° N 11.7945° E	652	0,0123	139978
Gubbtjønnna	Planktivorous	Brown trout, Burbot, Perch, Whitefish	62.4692° N 11.7918° E	651	0,0517	35445
Dalstjønnna	Non-planktivorous	Brown trout	62.5295° N 11.4757° E	629	0,1754	35396
Elgtjønnna	Non-planktivorous	Brown trout	62.7444° N 10.9772° E	871	0,1329	35150
Elgsjøen	Non-planktivorous	Brown trout	62.7228° N 10.9849° E	818	0,5815	35203
Hessjøen	Non-planktivorous	Brown trout	62.7253° N 11.1534° E	722	1,0337	884

Sampling

Lakes were sampled six times each, with approximately three-week intervals during the period June-September of 2021. Vertical zooplankton hauls and filtration of water for chlorophyll α extraction were conducted during each sampling event. All lakes were sampled at each sampling event, except for L. Hessjøen where strong winds prevented sampling during the 6th sampling event.

Zooplankton samples

Six vertical zooplankton hauls were conducted at each of the twelve lakes per sampling event. In each lake I attempted to identify the deepest location based on echosounder sampling and surrounding topography, and the same location was used for all zooplankton hauls within a lake. The zooplankton hauls, taken from 1m above the bottom of the lake up to the surface, used a zooplankton net with diameter 30 cm and mesh size 95 μm , and with the speed of the hauls being approximately 0.5 m/sec. The content from each zooplankton haul was transferred into individually marked 50 ml tubes, and 0.5 ml Lugol's solution was added and mixed into each tube before storing.

Phytoplankton samples

Water samples were taken at 1 m depth from each lake per sampling event. The collected water was first filtered (250 μm) to remove zooplankton. Then, two samples of this filtrate (2000 – 6000 ml, volume depending on phytoplankton content as assessed by colouring of the filters) were filtered through 20 μm -filters with vacuum. Finally, the filtrate from these two samples were divided into three samples (200 – 1000 ml) and filtered using GF/F-filters. All filters were put in individual colored glass vials and wrapped in tin foil. These were stored at 4 °C until being brought into the lab (i.e., 1-2 days), after which they were kept at -18 °C until analyzed.

Temperature measurements

Temperature data were collected throughout the entire sampling period by using temperature data-loggers (HOBO Pendant by Onset Computer Corporation) that were deployed at 1 meter depth in each lake in October 2020 and were collected during the last sampling event. Temperature was logged at 6-hour intervals.

Lab

Chlorophyll extraction

4mL cold methanol were added to the coloured glass vials with the 20 µm- and GF/F-filters, which were then centrifuged for 2 seconds and placed at -18 °C for 24 hours for extraction. After extraction, the filtrate was centrifuged again and filtered through a 0.2 µm-filter. Two ml of the extracted filtrate was transported to a glass vial, and the chlorophyll content was measured using a fluorometer (Trilogy Laboratory Fluorometer by Turner Designs), using a Chl_A-na module (Chlorophyll α, not acidified).

Calculations of µg chlorophyll-α/ L were done by using the given formula:

$$\frac{\mu g \text{ chl } \alpha}{\text{liter}} = \frac{(FL - BL) * f * E * 1000}{V * 1000} \quad (I)$$

, where FL is the sample reading, BL the reading of a 100% methanol blank, f is the calibration factor (0.47), E is the extraction volume in ml, and V is the filtrated volume in ml.

Dry biomass

One of the six zooplankton samples from each lake per sampling event was used to measure total dry biomass of zooplankton. The whole sample was emptied into a dish and dried at 50°C for 24 hours before being weighed, with an accuracy of ±0.1 mg.

Zooplankton sorting and counting

Three of the six zooplankton samples from each lake per sampling event were sorted and counted. A subsample of up to 10 ml was taken from each sample, except when it contained less than 150 individuals, in which case the whole sample was analysed (up to 50 ml). Individuals were identified down to species level (*Bythotrephes longimanus*, *Cyclops scutifer*, *Holopedium gibberum*, *Polyohemus pediculus*, *Diaphnosoma brachyurum*, *Leptodora kindtii*) or genus level (*Bosmina* spp., *Daphnia* spp., *Heterocope* spp., *Ceriodaphnia* spp., *Chydorus* spp., *Arctodiaptomus/Acanthodiaptomus* spp.) using a stereo microscope. After being sorted and counted, up to 50 individuals from each of the three samples per lake per sampling event were put into separate Eppendorf tubes containing 70% ethanol for further processing.

Quantification of body size and population growth of *Daphnia spp.*

A total of three species belonging to *Daphnia* were identified: *D. longispina*, *D. galeata*, and *D. cristata*. Since not one single species were present in all lakes in all sampling events, and due to difficulty in identifying juvenile individuals to species level, the three species were grouped together to investigate the effects of the fish community on their combined seasonal dynamics with respect to total abundance and individual body size.

Pictures and size measurements

Pictures were taken of the sorted *Daphnia spp.* individuals from each lake per sampling event for size measurements. All individuals from a single Eppendorf tube were transferred to a petri dish which was placed on a light pad with constant light intensity. Pictures were taken using a Nikon D3500 on a stand, using manual settings kept constant through all pictures. Pictures were analysed using a standardized method with the IMAGEJ-software (v1.53.e). A global scale was set for the pictures based on a picture of a scale taken with the same settings as the pictures of the daphnids. The original picture (Fig. 2A) was set to image type 8-bit (Fig. 2B), and a bandpass filter was added, filtering structures between 3 and 200 particles, suppressing noise and using a tolerance of direction on 5% (Fig. 2C). Next, the threshold was adjusted, moving the upper threshold to a value where clear stripes and noise appear in the picture (Fig. 2D), before moving the threshold down 15 steps to remove noise. This was done using default, B&W settings (Fig. 2E). Lastly, particles within the petri dish were analysed, with particle size set to 0.0005-infinity mm² and circularity set to 0.20-1.00 (Fig. 2F). The minimum size was set based on the typical size measured from what was considered newly born juveniles.

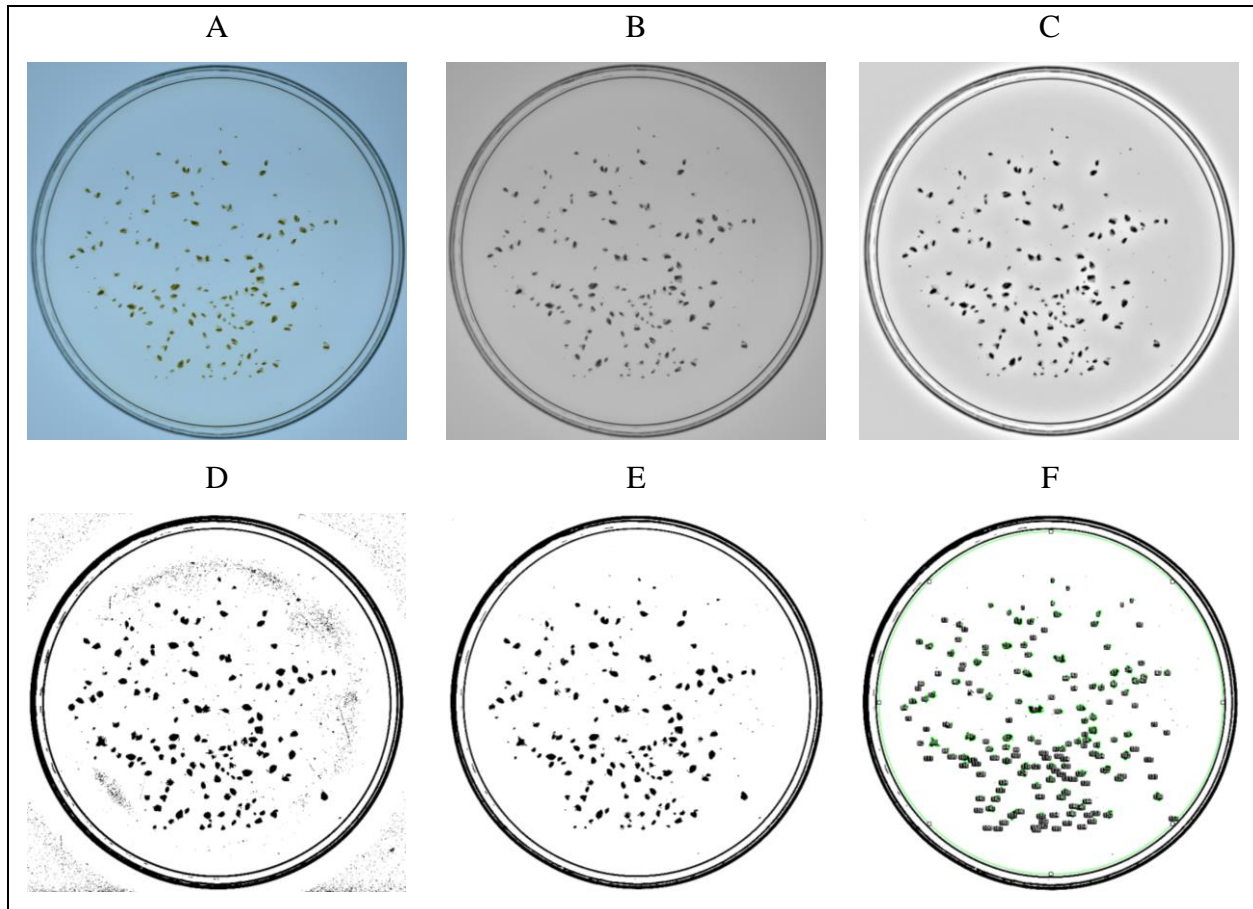


Figure 2: Showing the different steps (A-F) in the picture analysis measuring the area of individual *Daphnia spp.*, using the IMAGEJ-software. A: original picture, B: set to image type 8-bit, C: bandpass-filter added, D-E: adjusting the threshold, and F: analysing particles.

Size data

Estimation of the area of individual *Daphnia spp.* was based on analyses of the ImageJ data (see above). A total of 8982 particles were identified in all the images, while the total counted number of individuals in these samples was 5362. Manual inspection of images showed that the smallest particles identified consisted of detritus or eggs that had fallen out of mature individuals. Thus, the 3620 smallest particles were removed in the initial step. I then conducted the following procedure to ensure that only actual individuals had been measured for size for each sample.

1. In samples where the manual count was lower than the number identified from the image analysis, the excess, smallest particles were assumed to be detritus/eggs and removed.
2. In pictures where manual counts were higher than the number identified from the image analysis this was likely due to the loss of individuals during processing and prior to taking the image. Thus, in such cases all particles were used in estimation of size.

Based on the general allometry between area and volume of isometrically growing organisms, a proxy for individual biomass (BM) was calculated based on the particle's measured areas (A) as $BM = A^{2/3}$. A proxy for total biomass of *Daphnia spp.* (TBM) was then calculated for each of the three samples, based on the mean BM for all measured individuals from the same lake and sampling event, multiplied with the manually counted number of daphnids in the corresponding sample.

Growth rate calculations

Population growth rates of *Daphnia spp.* between two consecutive sampling events $p-1$ and p for a given lake were calculated both in terms of total biomass and total number of individuals. The total biomass growth rate (BioGR) for each period was calculated as:

$$BioGR = \frac{\ln(TBM_p/TBM_{p-1})}{T} \quad (I)$$

, where T is the time of the period in cumulative degree days. The cumulative degree days is calculated as mean temperatures for the period multiplied with the number of days. The use of the cumulative number of degree days is intended to control away effects of water temperatures on growth rates. Although this relationship shows increasing curvilinearity as temperatures become sufficiently high and approaches optimality (Giebelhausen & Lampert, 2001; Lampert & Trubetskova, 1996), the range in temperature observed among periods in my study lakes (Table A2) were well below reported optimal temperatures for population growth in these *Daphnia* species (Smirnov, 2017). Thus, I assume linearity in this relationship for this calculation. The numeric growth rate (NumGR) for each period was calculated as:

$$NumGR = \frac{\ln(N_p/N_{p-1})}{T} \quad (II)$$

, where N_{p-1} and N_p are the number of daphnids at the beginning and the end of a period between two sampling events, respectively.

Statistical analysis

All statistical analysis were done using the RStudio-software, version R.3.6.2 (RStudio Team, 2021). L. Olaloken was excluded in the analysis of density-dependence and size dynamics of *Daphnia spp.* due to their absence in most samples (only a single individual was observed in all samples combined).

Population growth rates of *Daphnia spp.*

In models of *Daphnia spp.* population growth rates (both biomass and numeric) I first explored three different measures of density in separate models. These were (i) TBM at the start of the period, (ii) total dry weight of all zooplankton at the start of a period, and (iii) a Competition Index that is calculated as the ratio between TBM and mean chlorophyll α content in the GF/F-filters. Only values from the GF/F-filters were included, as only these considered particles that were small enough for consumption by the daphnids. Whereas models with density effects (i) and (iii) considers the isolated effects of intraspecific competition, density effect (ii) considers the sum of intra- and interspecific competition. These three measures of density were set as an explanatory variable in separate models together with lake type and an interaction between these, and with the random effect of the individual lakes (Lake ID). Model comparison of these linear mixed effect models (LME) was used to determine which of the three density measures that gave the best models based on the Akaike Information Criterion with correction for small samples (AICc).

The *lme* function from the *nlme* package (Pinheiro et al., 2022) was used for the modelling, with the models using alternative fixed effects structures being fitted with maximum likelihood (ML). By using the *dredge* function from the *MuMIn* package (Bartón, 2022), five sub-models with different fixed terms were drawn from the original model, which then were compared based on their AICc- values. The best models were refitted with restricted maximum likelihood (REML) for parameter estimates (Table A3-A4) and inspection of residuals for homoscedasticity, linearity, and normal distribution (Fig. A2-A5).

Body size of *Daphnia spp.*

To analyse the difference in seasonal change of individual size in *Daphnia spp.* between the lake types, LME was used to model the individual area of the daphnids, with the main effects of sampling event and lake, and an interaction between these, and with Lake ID as a random effect. Again, with the given variables, five sub-models with different fixed terms were drawn from the

original model, which then were compared based on their AICc- values. The best model was refitted with REML for parameter estimates (Table A5) and inspection of residuals for homoscedasticity, linearity, and normal distribution (Fig. A6-A8).

Zooplankton community composition

The change in community composition within and between the two lake type categories were investigated and compared using the Bray Curtis dissimilarity Index (BCI), calculated using the *distveg* function in the *vegan* package (Oksanen et al., 2022). BCI carries out a pairwise comparison of the zooplankton community composition using the relative abundance of species. Each comparison receives a value from 0-1 based on the dissimilarity of the two compared community compositions, where 0 equals to the two having identical relative species abundance and 1 is equal to no common species found.

To investigate the difference in community composition *between* the two lake types through the season, a pair-wise comparison of all samples from all lakes was conducted for each sampling event, based on the relative abundance of each species/ genus in the samples. A linear mixed effect model was fitted, with BCI as the response variable, sampling event and contrast type (indicating if compared samples came from the same or different lake types) as fixed effects, and the random effect of lake pair (there were data from three samples per lake per sampling event, resulting in nine BCI values per lake pair per sampling event).

To examine how the species composition changed *within* the two lake types through the season, BCI values were calculated for all sample pairs from the same lake between two consecutive sampling events. A linear mixed effect model was fitted, with the BCI values as the response variable, lake type and time interval as fixed effect, and the random effect of Lake ID.

Model comparisons were conducted using AICc-values, both for the *between-* and *within-* lake type comparisons. The best models were refitted with REML for parameter estimates (Table A6 & A7) and inspection of residuals for homoscedasticity, linearity, and normal distribution (Fig. A9-A14).

Results

Population growth rates of *Daphnia spp.*

From the model comparison that addressed which of the density measures that best explained the variation in the biomass growth rate (BioGR) of *Daphnia spp.*, it was the model with total biomass (TBM) of *Daphnia spp.* at start of a period that had the lowest AICc-value and explained most variation compared to the two other density measures (Table 2). For the numeric growth rate (NumGR) it was the Competition Index that had the lowest AICc-value and explained most of the variation (Table 2). For both types of population growth, AICc-values were fairly similar for these two measures of density, whereas models using total zooplankton biomass performed considerably worse (Table 2). Further analyses of the density dependence of BioGR and NumGR used the corresponding best measures of density as identified here.

Table 2: Results from model comparison shows which of the three density measures that best explain the variation in BioGR and NumGR separately. Three models with BioGR or NumGR as response variables were compared with the given fixed effects based on their AICc-value. All models had Lake ID as a random effect.

	AICc
Fixed effects in BioGR model	
Total <i>Daphnia spp.</i> biomass * Lake type	-430.0
Competition Index * Lake type	-429.0
Total zooplankton biomass * Lake type	-425.7
Fixed effects in NumGR model	
Total <i>Daphnia spp.</i> biomass * Lake type	-422.7
Competition Index * Lake type	-423.2
Total zooplankton biomass * Lake type	-420.8

Biomass growth rate

Based on the AICc-value, the model that only included TBM of the *Daphnia spp.* as an explanatory variable was the best model to explain the variation seen in BioGR (Table 3). Thus, there was no clear pattern that distinguishes the effect of density dependence in the BioGR between the two lake types. There was considerable variation among individual lakes in the strength of effect of TBM of *Daphnia spp.* at the start of a period on BioGR for the *Daphnia spp.* (Fig. 3). However, the overall trend in all the lakes was that when the TBM of *Daphnia spp.* at the start of a period increased, the BioGR decreased (Table 5).

Table 3: Results from model comparison explaining the variation seen in BioGR as a function of TBM of *Daphnia spp.* at start of a period and lake type, with the random effect of Lake ID. K: number of estimated parameters in the model, AICc: corrected AIC-value, Δ AICc: difference between AICc the best model and the model compared to it, W_i : probability of the model.

Model	Fixed Variables	K	AICc	Δ AICc	W_i
1	Total <i>Daphnia spp.</i> biomass	4	-430.0	0.00	0.540
2	Total <i>Daphnia spp.</i> biomass + Lake Type	5	-428.2	1.73	0.227
3	Total <i>Daphnia spp.</i> biomass * Lake Type	6	-426.9	3.06	0.117
4	Intercept	3	-425.7	4.22	0.066
5	Lake Type	4	-425.2	4.77	0.050

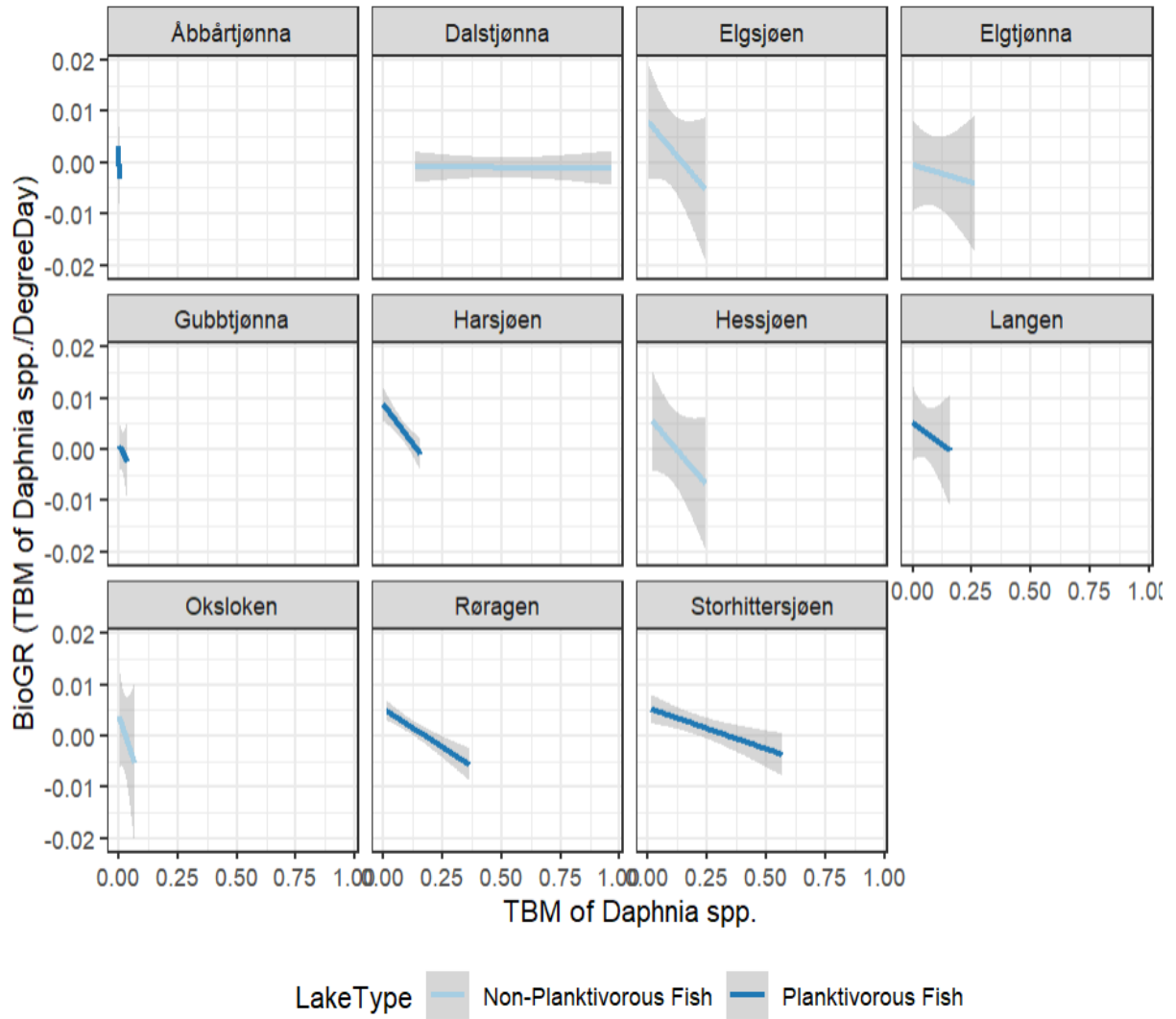


Figure 3: Effect of total biomass (TBM) of *Daphnia spp.* at start of the period on the biomass growth rate (BioGR) of *Daphnia spp.* in the individual lakes based on their different lake types; non-planktivorous fish or introduced planktivorous fish.

Numeric growth rate

Based on the AICc-value, the model that only included the Competition Index as an explanatory variable was the best model to explain the variation seen in NumGR (Table 4). Thus, as for BioGR, there was no clear pattern that clearly distinguishes the strength of density dependence in the NumGR between the two lake types (Fig. 4). The overall trend in all the lakes was that when the competition index of the *Daphnia spp.* increased, the NumGR went down, resulting in a negative numeric growth rate for the *Daphnia spp.* (Table 5).

Table 4: Results from model comparison explaining the variation seen in NumGR as a function of the Competition Index and lake type, with the random effect of Lake ID. K: number of estimated parameters in the model, AICc: corrected AIC-value, Δ AICc: difference between AICc the best model and the model compared to it, W_i : probability of the model.

Models	Fixed Variables	K	AICc	Δ AICc	W_i
1	Competition Index	4	-423.2	0.00	0.651
2	Competition Index + Lake Type	5	-420.8	2.34	0.202
3	Competition Index * Lake Type	6	-418.9	4.29	0.076
4	Intercept	3	-417.8	5.37	0.045
5	Lake Type	4	-416.7	6.43	0.026

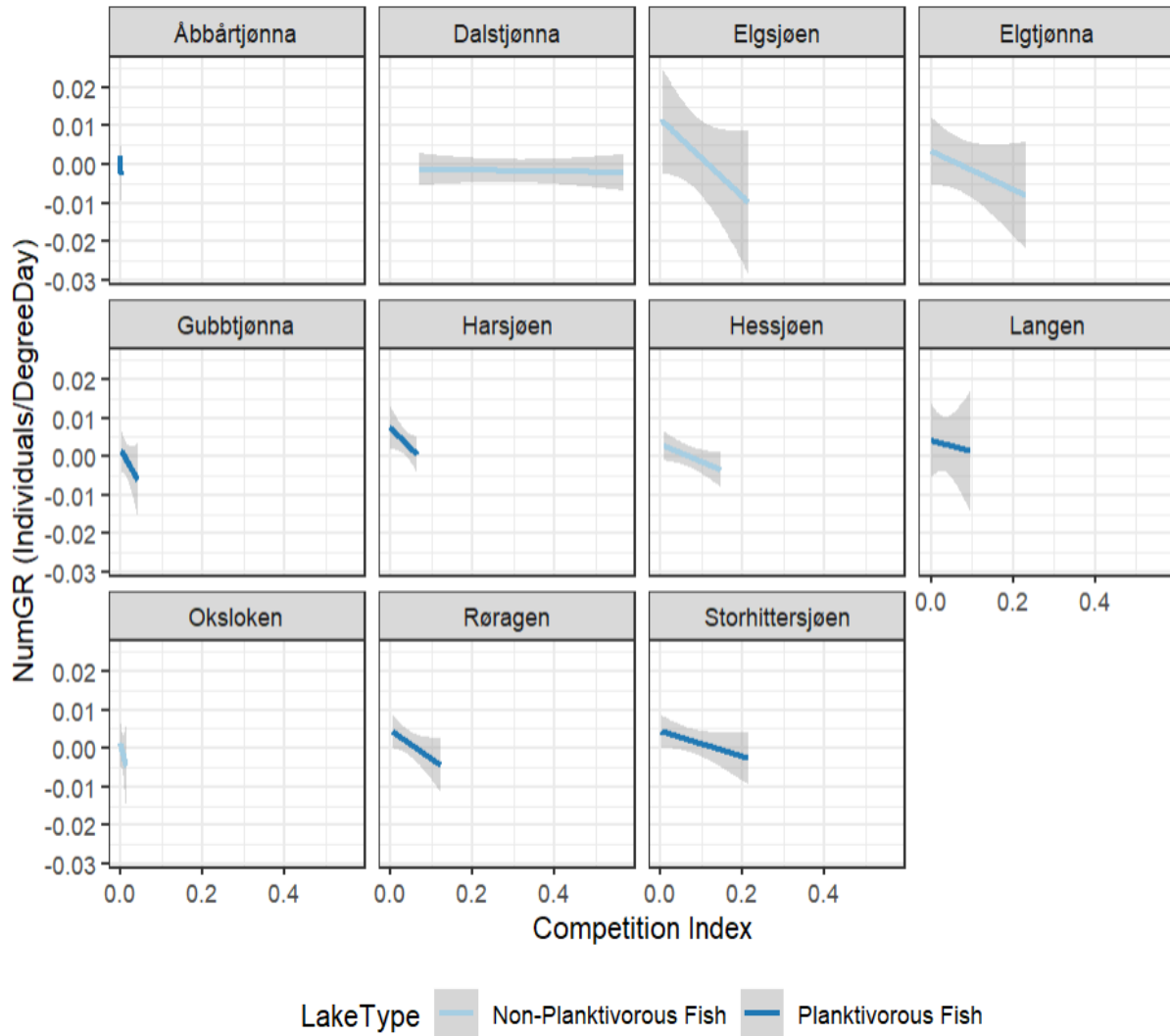


Figure 4: Effect of the Competition Index on the numeric growth rate (NumGR) of the *Daphnia spp.* in the individual lakes based on their different lake types; non-planktivorous fish or introduced planktivorous fish.

Table 5: Parameter estimates (fit with REML) for the best model describing the variation observed in BioGR and NumGR. Both models had the random effect of Lake ID.

	Estimate	SE
Biomass growth rate (BioGR)		
<i>Fixed effects</i>		
Intercept	0.00208	0.00068
Total <i>Daphnia</i> spp. biomass	-0.00781	0.00302
<i>Random effects (SD)</i>		
Lake ID	4.4367 x10 ⁻⁷	
Residual	0.00424	
Numerical growth rate (NumGR)		
<i>Fixed effects</i>		
Intercept	0.00196	0.00071
Competition Index	-0.01518	0.00538
<i>Random effects (SD)</i>		
Lake ID	2.5955x10 ⁻⁷	
Residual	0.00443	

Seasonal dynamics of body size in *Daphnia spp.*

Based on the AICc-value, the model including sampling event, lake type and the interaction between these as explanatory variables was the best model to explain the variation in individual size in *Daphnia spp.* through the season (Table 6). There was a clear difference in patterns of how individual size in the *Daphnia spp.* fluctuates through the season between lakes belonging to the two lake types (Fig. 5). Daphnids in lakes with introduced planktivorous fish stayed relatively small and differed little in mean size between sampling events. In comparison, the daphnids in lakes with non-planktivorous fish reached larger sizes and fluctuated considerably more in mean size throughout the sampling period.

Table 6: Results from model comparison explaining the variation seen in individual size in *Daphnia spp.* as a function of sampling event and lake type, with the random effect of Lake ID. K: number of estimated parameters in the model, AICc: corrected AIC-value, Δ AICc: difference between AICc the best model and the model compared to it, W_i : probability of the model.

Models	Fixed Variables	K	AICc	Δ AICc	W_i
1	Sampling Event * Lake Type	14	-40515.4	0.00	1.000
2	Sampling Event + Lake Type	9	-40309.4	205.99	0.000
3	Sampling Event	8	-40305.5	209.46	0.000
4	Lake Type	4	-40010.1	505.29	0.000
5	Intercept	3	-40006.4	508.96	0.000

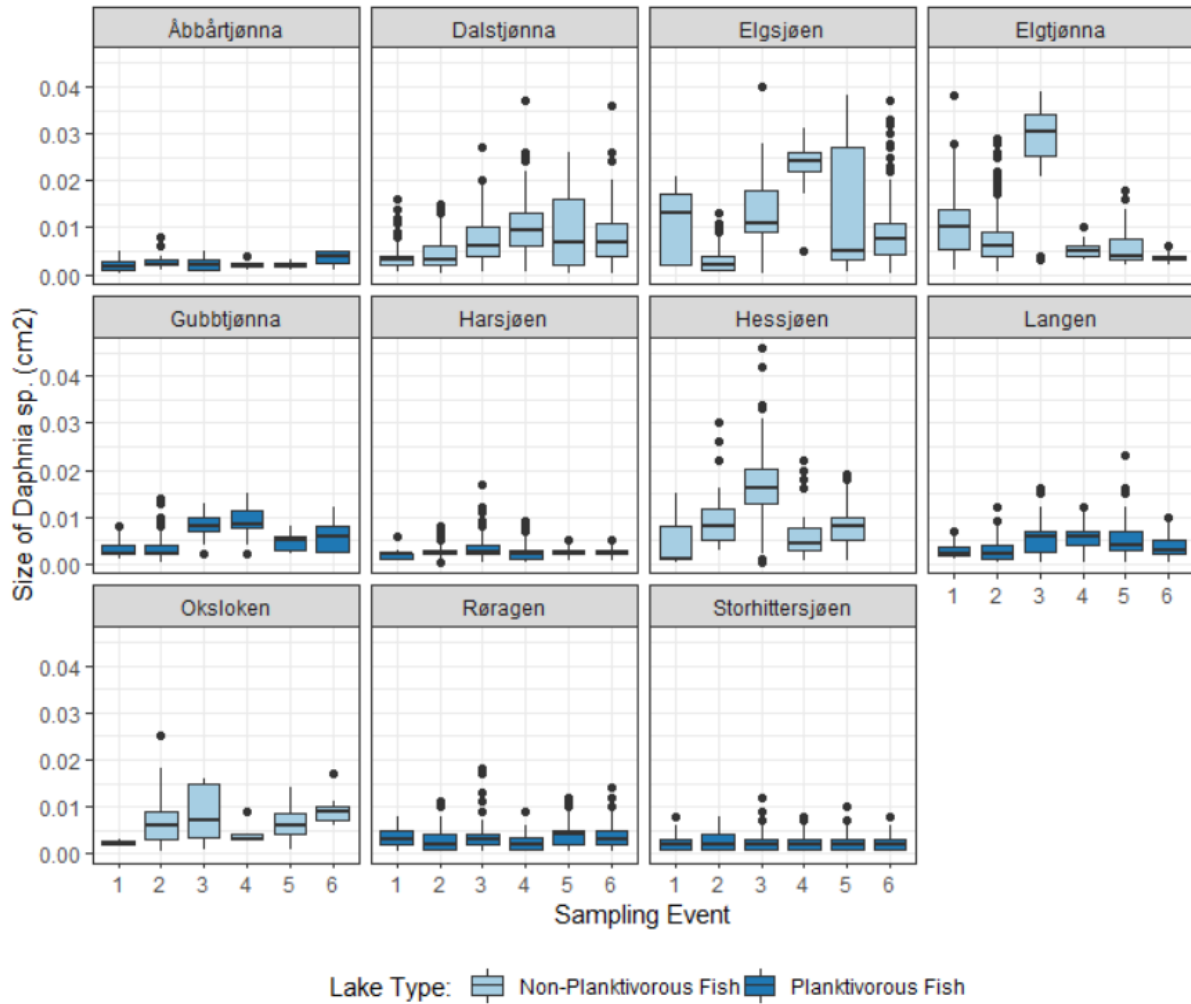


Figure 5: Individual size (area, cm²) of *Daphnia spp.* during different sampling events in the individual lakes based on their different lake type; non-planktivorous fish or introduced planktivorous fish.

Zooplankton community composition

The zooplankton community varied much both in abundance (Fig. 6) and in composition (Fig. 7) between the sampled lakes. In many of the lakes there was a substantial amount of copepods, especially *Cyclops scutifer*, through most parts of the season.

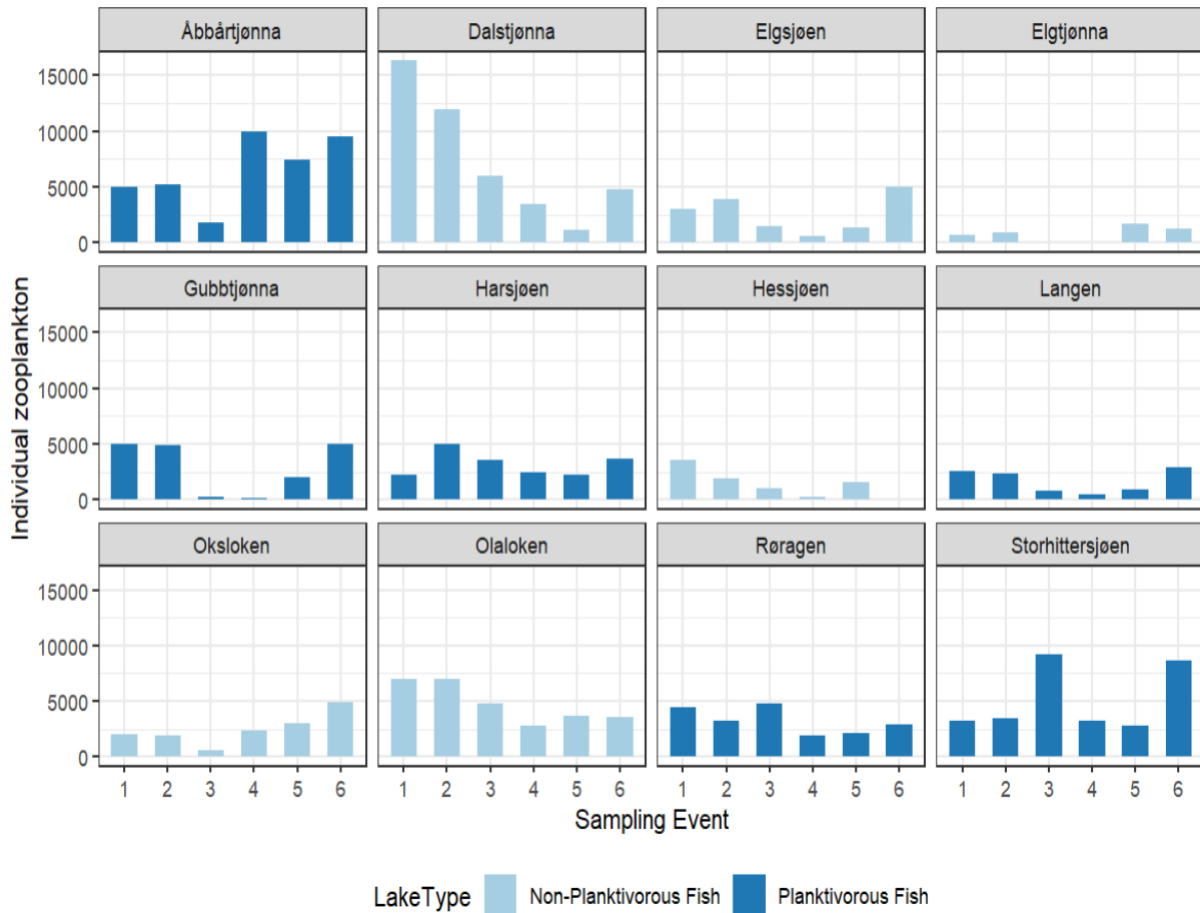


Figure 6: Number of zooplankton in samples during different sampling events in the individual lakes based on their different lake type; non-planktivorous fish or introduced planktivorous fish. Based on mean individual number in samples.



Figure 7: Proportion of the zooplankton species/genus during different sampling events in the individual lakes based on their different lake type; non-planktivorous fish or introduced planktivorous fish. Based on the mean individual number from samples.

Between lake type differences

Based on the AICc-value, the model that included the interaction between sampling event and contrast type as explanatory variables was the best to explain the variation in the Bray-Curtis dissimilarity Index (BCI) in the *between lake type* analysis (Table 7). For measures of dissimilarity between lakes the overall trend was for it to increase from the start to the mid-season, before declining again towards the end of the season (Fig. 8). The effect of contrast-type, i.e., whether two lakes were in the same or different fish community categories also changed throughout the season. In early- and mid-season, dissimilarity between two lakes did not depend on whether they were from the same or different fish community categories. In contrast, late in the season the community composition of a given lake was more similar to that of other lakes within the same fish community type (*same lake type*) than to that of lakes of the other fish community type (*different lake type*) (Fig. 8).

Table 7: Results from the model comparison explaining the variation in the BCI of zooplankton communities as a function of sampling event and contrast type (within vs between lake type comparison), with the random effect of lake pairs. K: number of estimated parameters in the model, AICc: corrected AIC-value, Δ AICc: difference between AICc the best model and the model compared to it, W_i : probability of the model.

Models	Fixed Variables	K	AICc	ΔAICc	W_i
1	Sampling Event * Contrast Type	14	-2085.7	0.00	1.000
2	Sampling Event + Contrast Type	9	-1968.2	117.56	0.000
3	Sampling Event	8	-1965.0	120.77	0.000
4	Contrast Type	4	-395.6	1690.10	0.000
5	Intercept	3	-392.4	1693.37	0.000

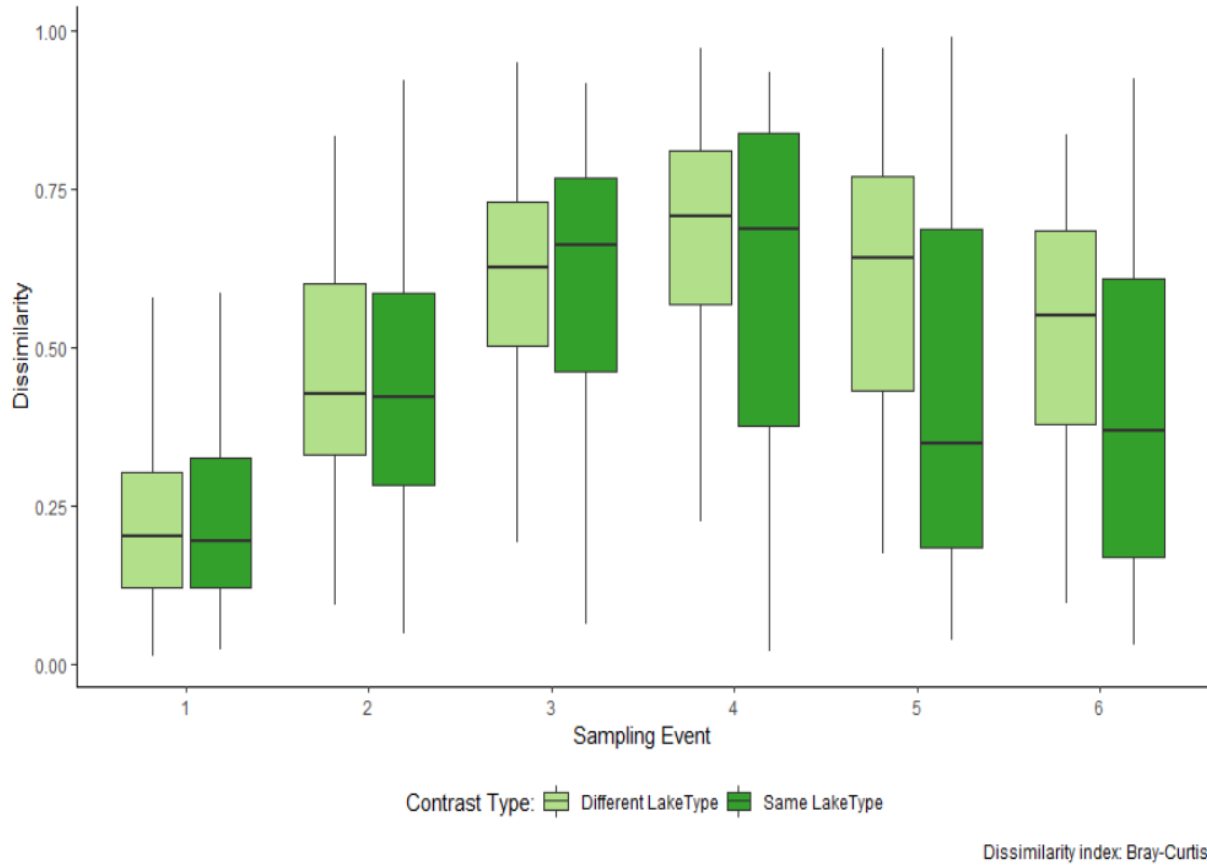


Figure 8: Difference in dissimilarity (BCI) of the zooplankton community composition through the season, based on contrast type of the sample pair (tells if the compared samples are from different lake types or from the same lake type). Using the Bray-Curtis dissimilarity Index based on the relative abundance of the species in each sample.

Within lake type differences

Based on the AICc-value, the model including the interaction between sampling event and lake type as explanatory variables was the best model to explain the variation in BCI in the *within lake type* analysis (Table 8). The temporal change in community composition between two sampling events changed more in the beginning of the sampling season, with the change between sampling event becoming smaller through the season (Fig. 9). Furthermore, the general pattern was that the community composition of lakes with introduced planktivorous fish changed more over time than the composition of lakes with only non-planktivorous fish, particularly early in the season.

Table 8: Results from the model comparison explaining the variation in the BCI of zooplankton community composition as a function of sampling event and lake type, with the random effect of Lake ID. K: number of estimated parameters in the model, AICc: corrected AIC-value, Δ AICc: difference between AICc the best model and the model compared to it, W_i : probability of the model.

Models	Fixed Variables	K	AICc	ΔAICc	W_i
1	Sampling Event * Lake Type	12	-366.9	0.00	0.994
2	Sampling Event	7	-356.0	10.97	0.004
3	Sampling Event+ Lake Type	8	-354.7	12.20	0.002
4	Intercept	3	-291.7	75.26	0.000
5	Lake Type	4	-290.4	76.56	0.000

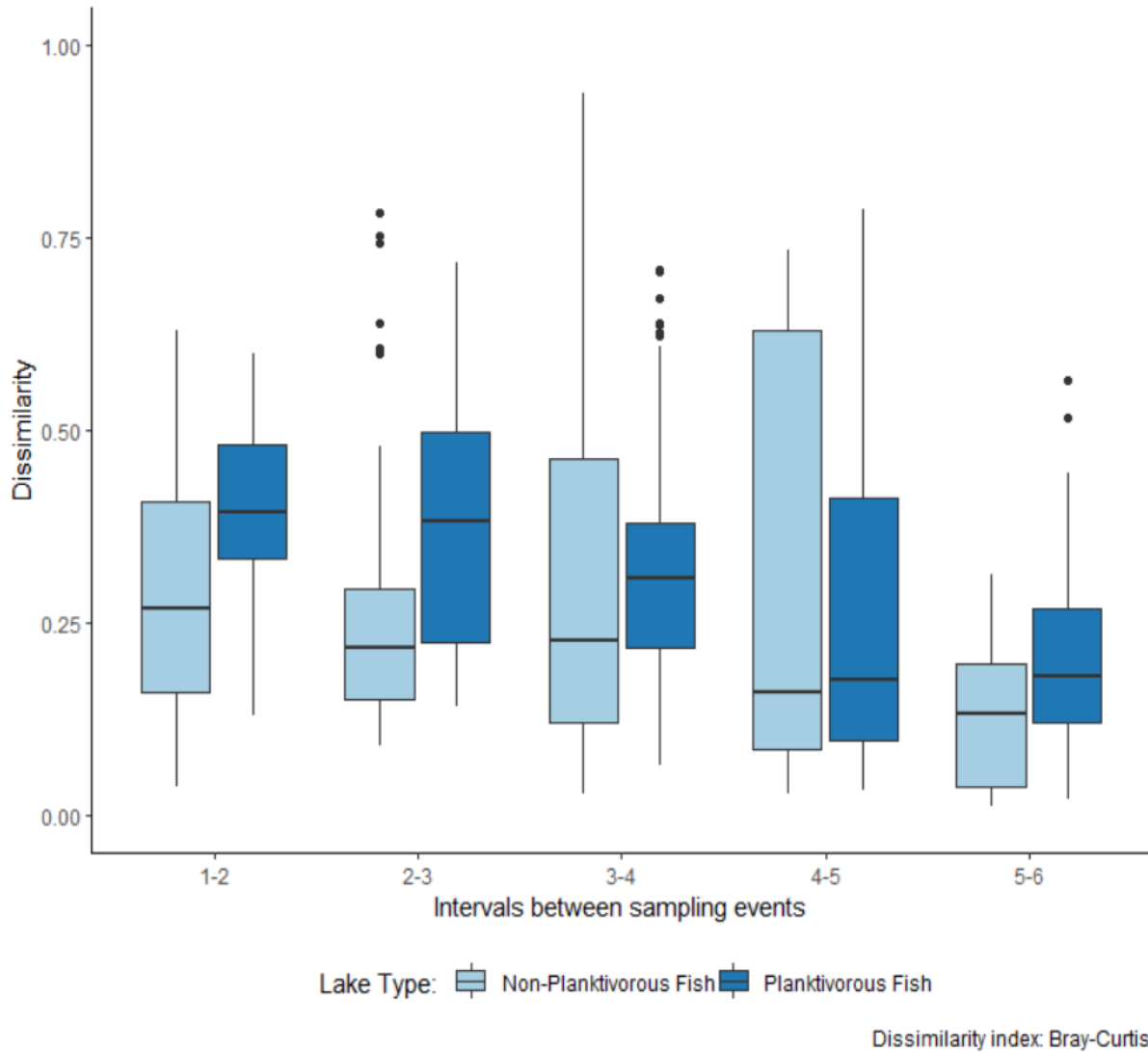


Figure 9: Difference in dissimilarity (BCI) of the community composition in samples within two lake types through the season; non-planktivorous fish or introduced planktivorous fish. Using the Bray-Curtis dissimilarity Index based on the relative abundance of the species in each sample.

Discussion

In this comparative study of lakes with different fish communities I investigated the effects that the introduced planktivorous fish European whitefish (*Coregonus lavaretus*) and European perch (*Perca fluviatilis*) has on the zooplankton. The effects that were tested for were on (i) the density dependence of population growth, (ii) the seasonal dynamics of body size, and (iii) the differences and seasonal dynamics in the zooplankton community. Only *Daphnia spp.* were used to investigate (i) and (ii), as these are a commonly preferred prey species of planktivorous fish and were abundant through the season (Brooks, 1968). The results from the study showed no effect of the introduced planktivores on the density dependence of population growth of *Daphnia spp.*. The seasonal dynamics of body size did however depend on the fish community. In lakes with planktivorous fish, the individual size of daphnids were smaller and fluctuated less than in lakes without planktivorous fish. Furthermore, I saw a divergence in the zooplankton community composition towards the end of the growth season, when the community composition became more similar between lakes within the same lake type (presence/absence of introduced planktivorous fish) compared to between lake types. Finally, my results show that seasonal changes in zooplankton community composition was largest early in the season, and that lakes with introduced planktivorous fish changed more through the season than those without planktivores.

Differences in population dynamics of *Daphnia spp.*

Studies on the effect of TD control of planktivorous fish on zooplankton have shown that competition between zooplankton for resources will decrease, as the predator will reduce the prey population before they overuse their resources (Nicolle et al., 2011). One could then hypothesize that in the current study, the *Daphnia spp.* would be less effected by competition for resources in the lakes with presence of a planktivorous fish, and that this would translate into differences in the strength of density-dependent population growth between the two lake types. However, my results showed no support for such an interaction.

One possible explanation for this could be linked to behavioural responses of zooplankton to visually hunting predators. In lakes with planktivorous fish, zooplankton have been observed to migrate down to the darker, colder, and thus less productive parts of the water column during daytime to avoid planktivorous fish in the upper layers where they are more vulnerable due to better visibility (Loose & Dawidowicz, 1994). The trade-offs for protection are lower growth rates

and fecundity due to lower temperatures and limited food resources (Pangle et al., 2007). If this behaviour to a sufficient extent reduces mortality, their populations may still reach abundances that reduces food availability even in the presence of planktivorous fish. One potential effect of this could then be that as their abundance increases, individuals have to stay longer in the upper layer to feed before migrating to safety, which would cause increased exposure to predation and create density-dependent population growth. However, I have no data on the temporal patterns in vertical distribution to evaluate the potential for such a mechanism. Another possible explanation is that the increase in density of zooplankton and increase in predation pressure happen to occur in parallel, without there being a causal relationship between the two. In addition to an increasing fish biomass following egg hatching in spring, fish are ectothermic, meaning that they have a higher metabolic rate and therefore consume prey at a higher rate with increasing water temperatures (Kestemont & Baras, 2007). At the same time, population abundance of *Daphnia spp.* is expected to be at a minimum early in the spring following hatching of resting eggs, after which it will increase due to clonal reproduction. Under this scenario, increased *Daphnia spp.* density and increased predation rate will be correlated even if they are not causally related.

Even though there were no clear indications that the fish community would affect the BioGR and NumGR of *Daphnia spp.*, the overall trend in all lakes were that both BioGR and NumGR were negatively affected when the density of daphnids at the beginning of a period increased. This decrease in the growth rates of *Daphnia spp.* is in line with what is described in the PEG-model, saying that the increase in *Daphnia spp.* density will lead to increased competition for limiting resources among the daphnids, linked to the chlorophyll α concentration (Braun et al., 2021; Carpenter et al., 1985; Sommer et al., 1986; Zhang et al., 2019). Other studies have suggested that using chlorophyll α as a measure of food abundance might give an unprecise indication of the amount of good quality food left in the lake, as grazing by effective herbivores will rapidly change the phytoplankton assemblage by consuming high quality food first (Kerfoot et al., 1988). If chlorophyll α concentration is a weak measure for the amount of edible food for *Daphnia spp.* it might explain why inclusion of the chlorophyll α concentration (Competition Index) as an explanatory variable only gave a little more explanation to the models for density-dependent population growth. To get a more precise indication on the amount of good quality food in the lakes, one should for future studies also consider the species and size of phytoplankton.

Knowing the abundance of different sized phytoplankton, and not only the chlorophyll α concentration, could also help to better understand of how intra vs. interspecific competition affected the density-dependent population growth rate of the *Daphnia spp.*. In this study, intraspecific competition had a larger effect than the interspecific competition, as the models with total dry weight of zooplankton gave weaker models compared to those including TBM of *Daphnia spp.*. Through the season in many of the lakes, a large proportion of the zooplankton community consisted of copepods (*Cyclops scutifer*). *Daphnia spp.* and copepods have different ways of feeding. *Daphnia spp.* are filter feeders restricted to a smaller size range of particles (1-30 μm), compared to copepods that selectively feeds on larger particles if available (Sommer & Sommer, 2006). These differences in feeding mechanisms and food preference results in less overlap in resource use and thus less interspecific competition given that there is a large abundance of different sized phytoplankton. Interspecific competition could still be affecting the density-dependent population growth of the *Daphnia spp.* To get a better picture of the effect of interspecific competition on the *Daphnia spp.*, it could help to focus on species which have similar feeding mechanisms and therefor more overlapping niches, such as other species of filter feeders.

Based on the larger effect of intraspecific competition on the density-dependent population growth of *Daphnia spp.*, it could indicate that there is a stronger grazing pressure on the smaller size-range of phytoplankton. The high efficiency of filter feeding zooplankton to graze down high-quality phytoplankton lead to an increasing concentration of low-quality food for the zooplankton (Ogorelec et al., 2021; Sommer et al., 1986). When high-quality food gets reduced, daphnids must go over to grazing on phytoplankton of a lower quality, with worse nutritional value and longer handling time to meet their energetic requirements. The increased use of suboptimal food sources causes a drop in the fecundity of daphnids because less energy is being invested in reproduction, leading to a negative impact on the population growth rate (Carpenter et al., 1985; Nicolle et al., 2011).

Differences in demographic changes of *Daphnia spp.*

As it has been suggested, to get a better understanding of how the presence of planktivorous fish affects the seasonal succession of the zooplankton community, one should look into difference and change in zooplankton size (Braun et al., 2021). A general observation is that planktivorous fish have an effect on the zooplankton demographic structure, such as individual size, both in

manipulative setups (Nicolle et al., 2011), and in observational studies in nature (Badosa et al., 2007; Braun et al., 2021; Zhang et al., 2019). This was also apparent in the current study, which showed a clear difference in the seasonal change of individual size in *Daphnia spp.* between the two lake types. In general, the daphnids in lakes without planktivorous fish had a broader size range through the sampling season. In addition, mean individual size fluctuated more between sampling events in the absence of planktivorous fish. In lakes with introduced planktivorous fish however had a smaller mean size, smaller size range and showed less variation in individual size by staying consistently small throughout the season. These trends are consistent with both the size efficiency hypothesis (SEH, Broods & Dodson, 1965), as well as size selective predation.

The SEH proposes that when competition for resources is high, the smaller individuals are outcompeted by the larger individuals (Brooks & Dodson, 1965; Hall et al., 1976). This is because the upper limit of particle size filter-feeders can ingest is linked to body size, making them able to feed on algae and particles of larger sizes, which are often less depleted (Cyr & Curtis, 1999). In this regard, the SEH can explain the lower abundance of smaller and younger individuals during certain periods of the season in the absence of planktivorous predators. Another explanation for the observed pattern is that in the absence of planktivorous fish predation pressure from invertebrate planktivores increase, which typically prey on the smaller sized daphnids (Hanazato & Yasuno, 1989). However, none of the invertebrate planktivores that have previously been suggested to cause such effects (e.g., *Chaoborus*) were observed in my samples, suggesting that this was not causing the observed trends. Size-selective predation may be more likely to explain the consistent small size of *Daphnia spp.* in the lakes with planktivorous fish, which typically prefer the larger sized individuals (Liu et al., 2020; Zimmer et al., 2001). In addition, TD control by planktivorous predation is a more continuous pressure on the zooplankton through the season compared to the BU control from density-dependent competition, which can peak several times (Sommer et al., 1986). Due to this more stable predation pressure through the season, the daphnids will stay small due to size specific selection by the fish, and therefore show less fluctuation in size compared to daphnids in the non-planktivorous lakes.

One of the non-planktivorous lakes, L. Oksloken, deviated somewhat from the other lakes within that category in terms of seasonal dynamics of size structure. Specifically, it showed a smaller size range of individual daphnids and had weaker fluctuations in size through the season compared to

the other lakes without planktivorous fish. One explanation for this could be the abiotic state of this lake compared to the rest. During the first sampling event in early June, it had one of the lowest pH-, conductivity-, and oxygen content levels (see Table A1). Compared to the other non-planktivorous lakes which had a pH ranging from 7.23-7.53, L. Oksloken had a pH of 7.06, and the nearby L. Olaloken which had a pH of 6.57 lacked *Daphnia spp.*. This suggests that abiotic conditions may be close to the tolerance limit for *Daphnia spp.* in L. Oksloken, and that both their abundance and size distribution may have been affected by this. A negative relationship between mean size in *Daphnia spp.* and pH has previously been described, with the optimum conditions being between 7.9 and 8.3 (El-Deeb et al., 2011). Limiting abiotic conditions are also supported by the observation that L. Oksloken was the lake with the highest mean chlorophyll α concentration through the sampling season, despite the absence of planktivores and with P-levels being similar to the other lakes (Table A1, Fig. A1).

The fact that there is such a strong difference between the two lake types regarding the change in individual size, and a lack thereof regarding apparent density dependence, suggests that the former is a better measure than the latter for inferring effects of planktivores on their zooplankton prey. As discussed above, the observed correlation between *Daphnia spp.* population abundance and population growth may or may not represent a causal relationship in the presence of planktivores. Thus, data on the individual level may be easier to interpret with respect to the effect of the planktivores on the seasonal dynamics. My results suggest that in the absence of planktivores, *Daphnia spp.* go through periods of strong resource limitation during certain periods of the season, as indicated by the increase in their mean size. In contrast, in the presence of planktivores, *Daphnia spp.* experience an overall decrease in mean size and little to no seasonal variation in size. These types of patterns, in addition to the nutrient loading in the lake, must be taken into consideration in the management of lake systems, as large zooplankton has been seen more effective in reducing algae blooms in highly productive lakes compared to smaller zooplankton (Cyr & Curtis, 1999; Ogorelec et al., 2021).

Differences in zooplankton community composition

The presence of planktivorous fish have previously been shown to have substantial effects on the structure of the zooplankton community compared to that of lakes with an absence of planktivorous fish (Carpenter et al., 1985; Persson et al., 1993; Zhang et al., 2019). Studies with

different density of planktivorous fish show the ability to shift the size structure of zooplankton communities towards smaller species, and in high predator densities exclude larger sizes of zooplankton completely (Carpenter et al., 1987; Dahlhansen, 1995). My data show how such effects on community composition result from invasive whitefish and perch, but that such an effect is only apparent during certain periods of the season. The plankton succession model from the Plankton ecology group (PEG-model) posits that winter works as a reset for the composition of the zooplankton community, with only a limited range of species actively overwintering while most others overwinter as resting eggs (Sommer et al., 1986). This is consistent with my results showing that the dissimilarity between lakes was low and independent of lake type at the first sample. For this sample, all lakes had the greatest abundance of the copepod *Cyclops scutifer*, which typically overwinter as nauplii and mature and reproduce during summer (Boers & Carter, 1978). Also present in several of the lakes during the first sampling was the smaller cladoceran *Bosmina spp.* which is often seen in larger density early in spring before they are outcompeted by larger herbivorous zooplankton like *Daphna spp.* (Kerfoot et al., 1988).

The zooplankton community of both lake types changed most during the two first intervals, having a dissimilarity in community composition of over 0.25 between sampling event 1 and 2, and almost as much between round 2 and 3. Throughout the rest of the season the community changed with decreasing magnitude between sampling events. This is consistent with previous literature that has suggested that the largest change in zooplankton composition is thought to be happening during the clear water phase, due to the strong selective pressures from food limitation and/or increasing planktivorous fish biomass. (Carpenter et al., 1985; Sommer et al., 1986). The large change within both lake types in the beginning of the season was divergent in nature, leading to an increasing dissimilarity among lakes, where the zooplankton community composition went from being under 0,25 dissimilar during sampling event 1, to having a dissimilarity of almost 0,75 during sampling event 4. Furthermore, the direction of this divergence among lakes was independent of lake type during this period, such that the dissimilarity among two lakes did not depend on whether they were within the same or different lake type up to and including sampling event 4. This indicates that the presence of planktivorous fish did not have a strong systematic effect on the zooplankton community composition during this period. Rather, it is possible that differences among lakes in seasonal progression of abiotic factor such as temperature may drive such different patterns of zooplankton succession (DeMott, 1983).

Towards the end of the sampling season, i.e., from sampling event 4 to 6, the temporal change in community composition decreased further for both lake types. Yet, the changes that occurred during these two periods appear to be more strongly linked to lake type, with the result that there was an increasing divergence in community composition between lake types. During the two last sampling events most lakes saw an increase in the zooplankton abundance, potentially reflecting a positive effect of a second bloom of high-quality algae or relaxed predation pressure from the fish. Typical species for this period are smaller ones like *Bosmina spp.* that earlier may have been outcompeted by the larger zooplankton (Gliwicz & Pijanowska, 1989). This increase in late fall is however short, as many species decline with the rapidly declining temperatures (Sommer et al., 1986). There was also an increasing biomass of *Cyclops scutifer* mostly consisting of smaller sized nauplii, which are thought to make out next season's population after overwintering. The larger amount of daphnids in some of the lakes, and the small proportion of males and ehippia (own observations) during the last sampling events could indicate that environmental conditions had not become sufficiently limiting for them to switch from clonal to sexual reproduction (Zhang et al., 2016). This also indicates that not the full plankton season were sampled during this study, which could be seen as a limitation in terms of not getting the full seasonal pattern of the change in zooplankton community composition.

While the mean dissimilarity in zooplankton community composition indicates that the zooplankton community is more similar within a lake type than between lake types by the end of the season, there is substantial variation in community composition among lakes within lake types throughout the season. In addition to the presence or absence of planktivorous fish, the zooplankton community in lakes is largely affected by the abiotic factors of their system, where temperature alone have been suggested to be a driver of zooplankton succession in lakes (Jensen, 2019; Sommer et al., 1986). Different species have different preferences and tolerance for pH, oxygen-content, temperature, and type of phytoplankton they feed on, which will be different among lakes depending on factors such as lake area, nutrient runoff into the lake, and the bedrock and climate in the area (Hu et al., 2019). These in-lake differences may have led to the sometimes-large variance seen in the within lake type comparisons (Fig. 9). Some of the lakes with the same fish communities were very different, e.g., L. Hessjøen and L. Oksloken, in terms of abiotic factors such as lake area, depth and conductivity. These differences would most likely affect their species composition. Temperatures were also a lot higher in L. Oksloken compared to L. Hessjøen. As

temperature have a strong effect on succession rates in the plankton community, it can also have led to the communities being compared at different “stages” in their succession.

Conclusion

This study looked at what effects introduced planktivorous fish might have on the seasonal dynamics of zooplankton by comparing trends in the zooplankton in lakes without planktivorous fish to that of lakes with whitefish and/or perch. On a population level, the presence of planktivorous fish had mixed effects. No effect of the fish community on was found in the density dependence of *Daphnia spp.* population growth, which might be due to different trophic controls affecting the population when its density increases are at work in the different lakes. The presence of planktivorous fish had on the other hand large effects on the size structure of the *Daphnia spp.* through the season. Larger sized daphnids and pronounced seasonal fluctuation in the absence of planktivorous fish may be explained by periods of intense competition for resources. The smaller sized daphnids with little seasonal fluctuation in the presence of planktivorous fish is consistent with size selective predation pressure from the fish. The fish community had an effect on the amount of change in zooplankton community composition, where the zooplankton community in planktivorous lakes changed more during the season than it did in the non-planktivorous lakes. However, between lake type analyses indicates that there was great variation in all lakes during the first part of the season, independently of the fish community in the lake. Only towards the end of the season did communities in the two categories of lakes diverge.

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APPENDIX

Table A1: Abiotic measures from the individual lakes. Conductivity (in millie Siemens), oxygen content (in mg oxygen per liter), pH measured in water from 1 meter depth during first sampling event (June 2021). Particular phosphorus (in microgram per liter) and nitrate + nitrite (in microgram per liter) measured from 0.2 filters after filtering >20 ml lake water and since frozen in October of 2020.

Lake Name	Conductivity (mS)	O ₂ -content (mg O ₂ / liter)	pH	Phosphorus PO ₄ (µg/L)	Nitrate NO ₃ +NO ₂ (µg/L)
Røragen	95	10.45	7.78	3.00	6.60
Langen	80.2	9.77	7.90	2.60	10.50
Harsjøen	35.5	9.98	7.64	1.90	8.05
Storhittersjøen	55.6	10.34	7.74	2.85	10.00
Åbbårtjøenna	20.1	9.30	7.09	1.45	5.45
Oksloken	17.8	8.85	7.06	2.65	8.40
Olaloken	7.7	8.18	6.57	1.65	6.15
Gubbtjøenna	20.6	9.70	7.17	1.80	5.35
Dalstjøenna	41.7	9.40	7.52	2.20	5.45
Elgtjøenna	22.2	9.82	7.23	1.80	6.25
Elgsjøen	27.5	10.45	7.30	2.00	4.40
Hessjøen	31.4	9.70	7.53	2.20	17.8

Table A2: Mean temperature (T) in period in °C leading up to a sampling event. (d): number of days in period. Estimated Day of Ice Melting (DIM): estimated start of plankton growing season, as the first day in the year where temperatures in the lake increased with 0.4 °C over the span of three days.

Lake Name	DIM	T (d) <i>Sampling event 1</i>	T (d) <i>Sampling event 2</i>	T (d) <i>Sampling event 3</i>	T (d) <i>Sampling event 4</i>	T (d) <i>Sampling event 5</i>	T (d) <i>Sampling event 6</i>
Røragen	11/05	6.80 (29)	13.90 (21)	17.81 (21)	15.67 (21)	12.17 (24)	9.95 (21)
Langen	15/05	6.88 (25)	14.71 (21)	18.00 (21)	16.00 (21)	12.09 (23)	9.70 (23)
Harsjøen	14/05	5.88 (26)	14.71 (21)	18.33 (21)	15.95 (21)	12.43 (23)	10.00 (23)
Storhittersjøen	13/05	6.26 (27)	14.29 (21)	18.38 (21)	16.14 (21)	11.88 (24)	10.22 (23)
Åbbårtjønnna	12/05	8.75 (28)	15.57 (21)	19.00 (21)	17.14 (21)	13.35 (23)	10.67 (24)
Oksloken	11/05	9.31 (29)	16.48 (21)	19.57 (21)	17.29 (21)	12.87 (23)	10.50 (24)
Olaloken	11/05	8.72 (29)	15.57 (21)	19.33 (21)	17.90 (21)	14.13 (23)	11.33 (24)
Gubbtjønnna	15/05	8.88 (25)	15.10 (21)	18.67 (21)	17.71 (21)	14.61 (23)	11.88 (24)
Dalstjønnna	12/05	9.41 (29)	15.60 (20)	19.27 (22)	17.68 (19)	13.96 (23)	11.28 (25)
Elgtjønnna	25/05	6.44 (16)	12.71 (21)	17.09 (22)	15.70 (20)	11.26 (23)	9.18 (22)
Elgsjøen	15/05	5.15 (26)	13.38 (21)	17.41 (22)	16.40 (20)	11.70 (23)	9.59 (22)
Hessjøen	14/05	6.41 (27)	12.86 (21)	17.68 (22)	16.15 (20)	11.87 (23)	9.59 (22)



Figure A1: Chlorophyll α concentrations extracted from the GF/F-filters during each sampling event.

Population growth rates for *Daphnia spp.*

Table A3: Model comparison explaining the variation seen in BioGR as a function of the three different density measures and Lake Type category, with Lake ID as random effect. K: number of estimated parameters in the model, AICc: corrected AIC-value, Δ AICc: difference between AICc the best model and the model compared to it, W_i : probability of the model.

Models	Fixed variables	K	AICc	Δ AICc	W_i
<i>Total Daphnia spp. biomass</i>					
1	Total Daphnia spp. biomass	4	-430.0	0.00	0.540
2	Total Daphnia spp. biomass + Lake Type	5	-428.2	1.73	0.227
3	Total Daphnia spp. biomass * Lake Type	6	-426.9	3.06	0.117
4	Intercept	3	-425.7	4.22	0.066
5	Lake Type	4	-425.2	4.77	0.050
<i>Competition Index</i>					
1	Competition	4	-429.0	0.00	0.479
2	Competition * Lake Type	6	-427.1	1.94	0.182
3	Competition Index + Lake Type	5	-427.0	2.00	0.176
4	Intercept	3	-425.7	3.29	0.093
5	Lake Type	4	-425.2	3.84	0.070
<i>Total zooplankton biomass</i>					
1	Intercept	3	-425.7	0.00	0.315
2	Lake Type	4	-425.2	0.55	0.239
3	Total zooplankton biomass	4	-425.0	0.73	0.219
4	Total zooplankton biomass + Lake Type	5	-424.6	1.15	0.177
5	Total zooplankton biomass * Lake Type	6	-422.1	3.68	0.050

Table A4: Model comparison explaining the variation seen in NumGR as a function of the three different density measures and Lake Type category, with Lake ID as random effect. K: number of estimated parameters in the model, AICc: corrected AIC-value, Δ AICc: difference between AICc the best model and the model compared to it, W_i : probability of the model.

Models	Fixed variables	K	AICc	ΔAICc	W_i
<i>Total Daphnia spp. biomass</i>					
1	Total Daphnia biomass	4	-422.7	0.00	0.628
2	Total Daphnia biomass + Lake Type	5	-420.6	2.09	0.221
3	Total Daphnia biomass * Lake Type	6	-418.1	4.59	0.063
4	Intercept	3	-417.8	4.87	0.055
5	Lake Type	4	-416.7	5.94	0.032
<i>Competition Index</i>					
1	Competition Index	4	-423.2	0.00	0.651
2	Competition Index + Lake Type	5	-420.8	2.34	0.202
3	Competition Index * Lake Type	6	-418.9	4.29	0.076
4	Intercept	3	-417.8	5.37	0.045
5	Lake Type	4	-416.7	6.43	0.026
<i>Total zooplankton biomass</i>					
1	Total zooplankton biomass	4	-420.8	0.00	0.445
2	Total zooplankton biomass + Lake Type	5	-420.0	0.75	0.305
3	Intercept	3	-417.8	2.97	0.101
4	Total zooplankton biomass * Lake Type	6	-417.6	3.19	0.090
5	Lake Type	4	-416.7	4.03	0.059

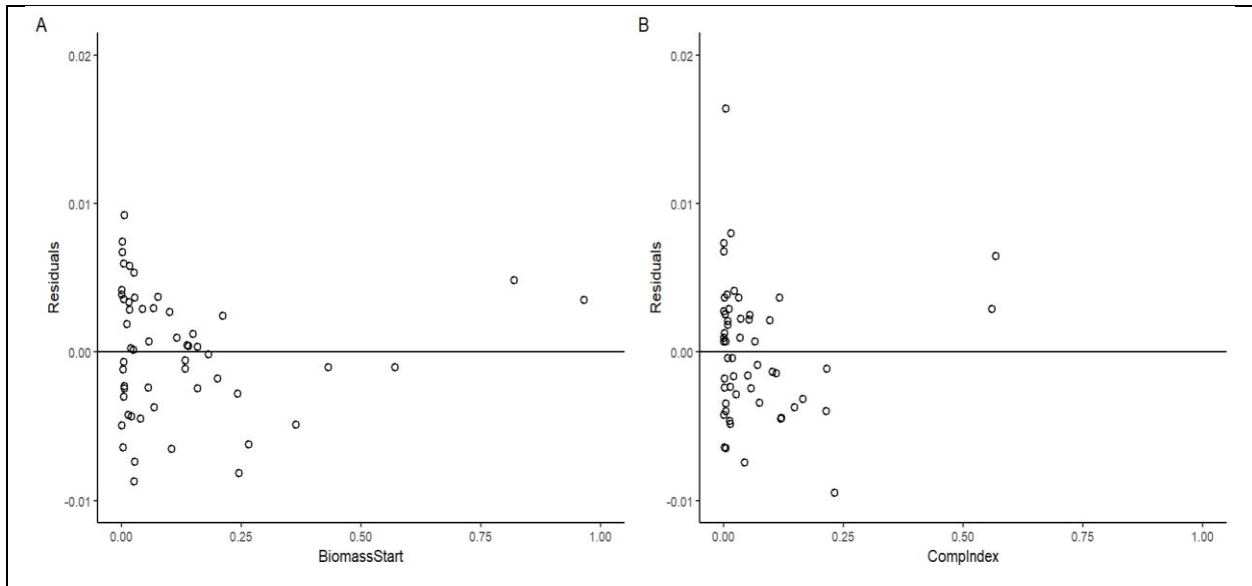


Figure A2: Residuals for **A)** best BioGR-model against TBM of *Daphnia spp.* at the start of a period and random effect of lake category, and **B)** best NumGR-model against Competition Index and random effect of lake category.

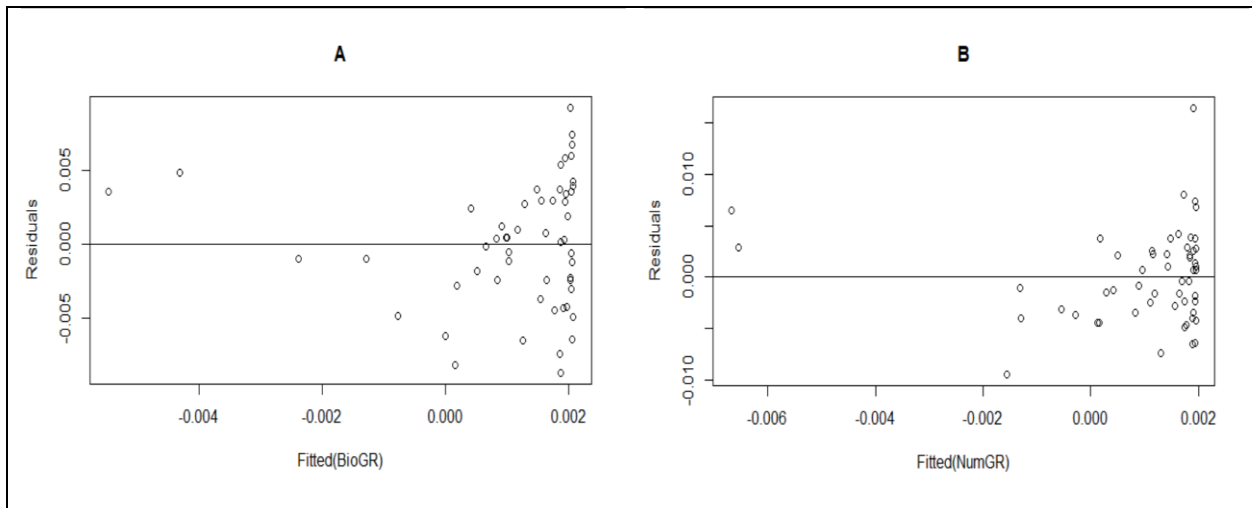


Figure A3: Residuals vs. fitted values of **A)** model for BioGR with TBM of *Daphnia spp.* at the start of a period as explanatory variable and random effect of lake category, and **B)** model for NumGR with Competition Index as explanatory variable and random effect of lake category.

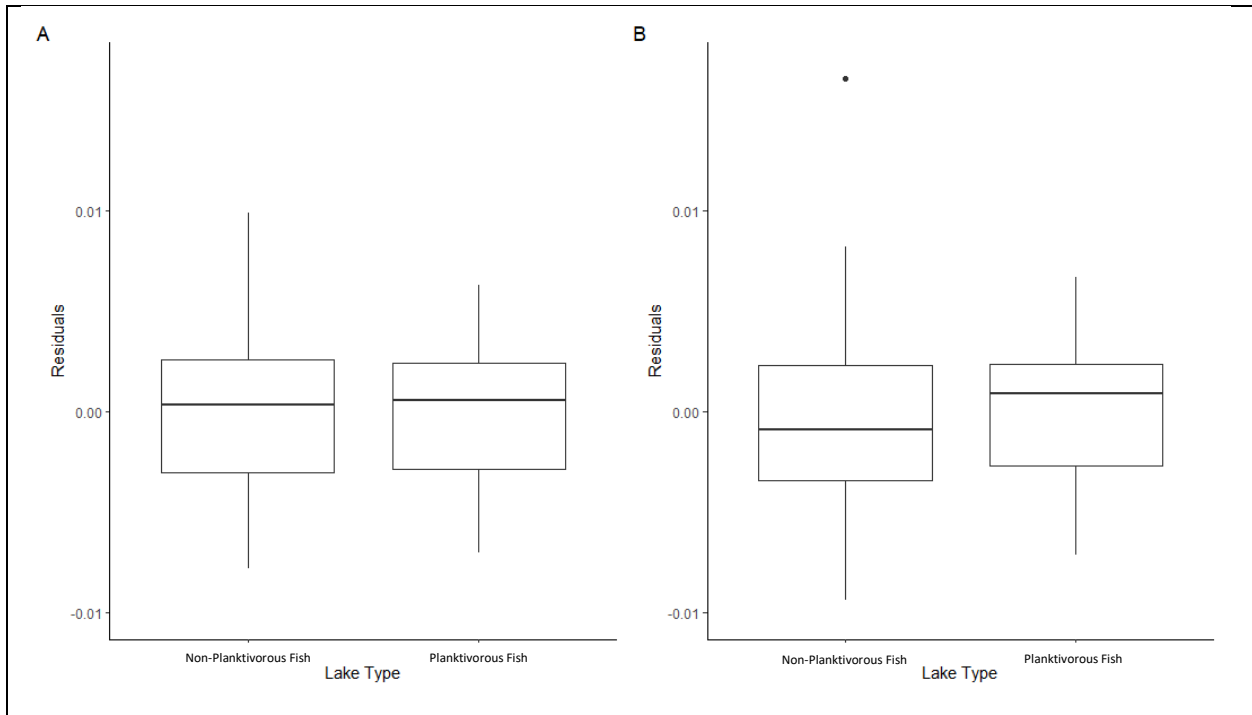


Figure A4: Residuals for lake type of **A)** model for BioGR with TBM of *Daphnia spp.* at the start of a period as explanatory variable and random effect of lake category, and **B)** model for NumGR with Competition Index as explanatory variable and random effect of lake category.

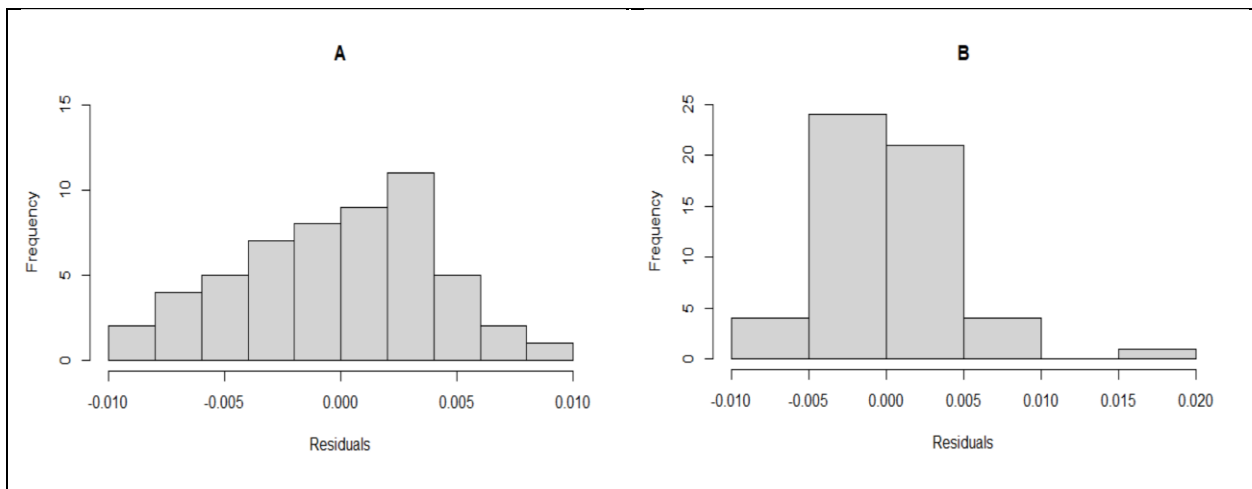


Figure A5: Histograms for residuals of **A)** model for BioGR with TBM of *Daphnia spp.* at the start of a period as explanatory variable and random effect of lake category, and **B)** model for NumGR with Competition Index as explanatory variable and random effect of lake category.

Seasonal dynamics of body size in *Daphnia spp.*

Table A5: Parameter estimates for the best model describing the variation observed in individual size in the *Daphnia spp.* as with sampling event and lake type as explanatory variables, and the random effect of Lake ID.

	Estimate	SE
<i>Fixed effects</i>		
Intercept	0.00599	0.00121
Round 2	- 0.00136	0.00037
Round 3	0.00665	0.00046
Round 4	0.00185	0.00057
Round 5	0.00141	0.00044
Round 6	0.00108	0.00058
Lake type (Planktivorous fish)	- 0.00365	0.00165
Round 2 : Lake type (Planktivorous fish)	0.00203	0.00047
Round 3 : Lake type (Planktivorous fish)	-0.00453	0.00055
Round 4 : Lake type (Planktivorous fish)	0.00047	0.00065
Round 5 : Lake type (Planktivorous fish)	0.00081	0.00054
Round 6 : Lake type (Planktivorous fish)	0.00088	0.00066
<i>Random effects (SD)</i>		
Lake ID	0.00268	
Residual	0.00449	

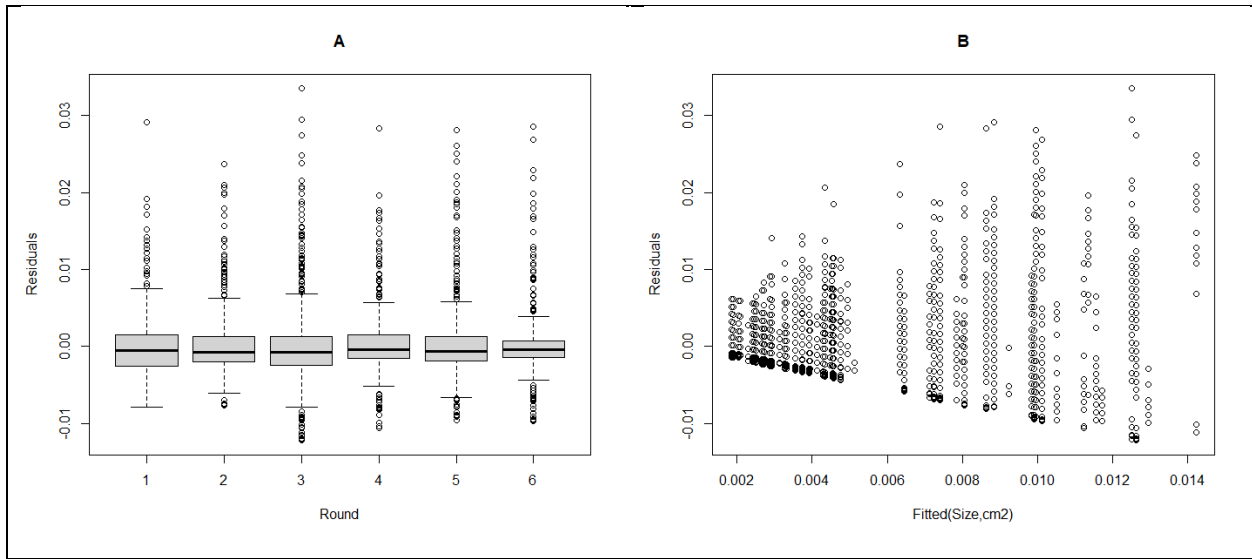


Figure A6: Model residuals for individual size of *Daphnia spp.* with interaction between round and lake type, and random effect of Lake ID plotted against **A)** Round (Sampling event), and **B)** Fitted values of model

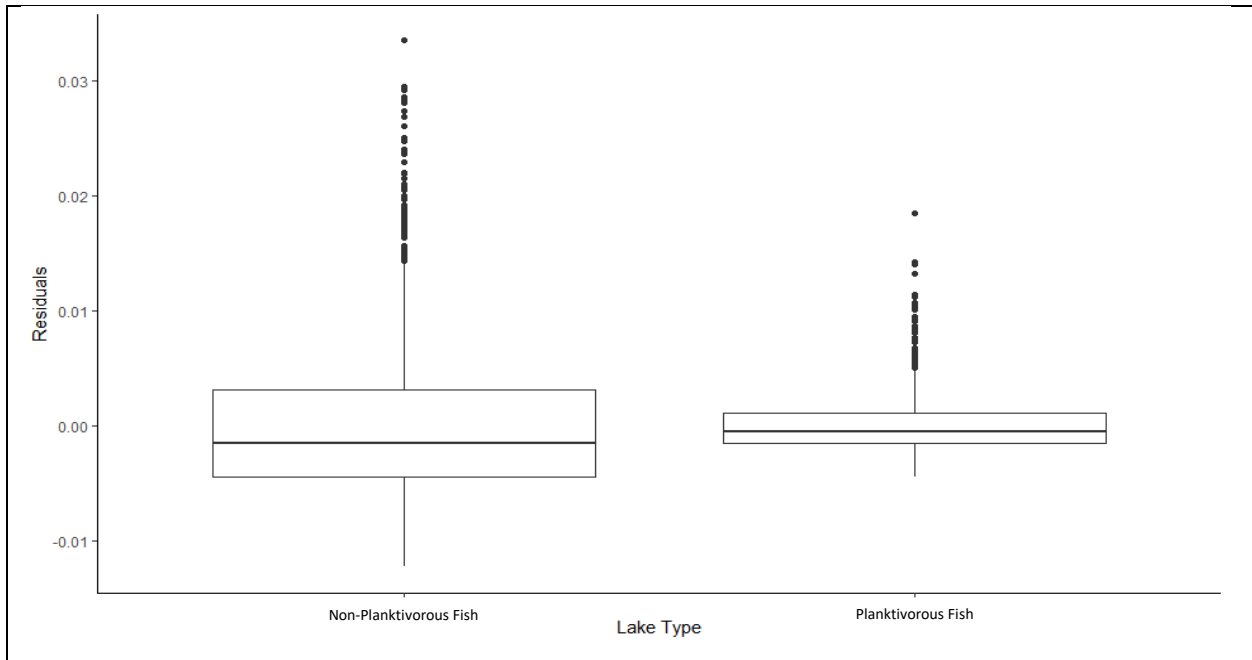


Figure A7: Model residuals for individual size in *Daphnia spp.* with interaction between round and lake type, and random effect of Lake ID plotted against lake type.

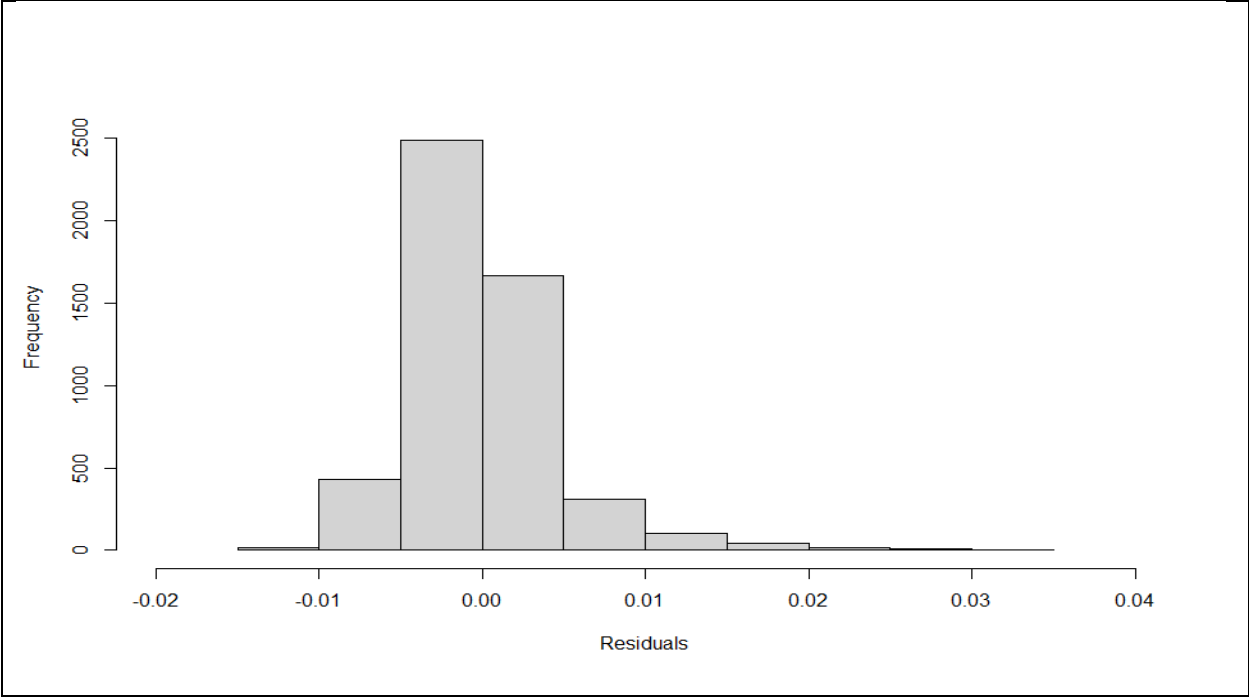


Figure A8: Histograms of model residuals for individual size in *Daphnia spp.* with interaction between round and lake type, and random effect of Lake ID.

Zooplankton community composition

Between lake type differences

Table A6: Parameter estimates (fit with REML) for the best model describing the variation observed in dissimilarity in community composition of samples with the interaction between sampling time and contrast type, and the random effect of lake pairings

	Estimate	SE
<i>Fixed effects</i>		
Intercept	0.23269	0.02187
Round 2	0.22483	0.01361
Round 3	0.39136	0.01361
Round 4	0.42756	0.01361
Round 5	0.38337	0.01361
Round 6	0.28829	0.01440
Contrast type (Same Lake type)	-0.00509	0.03245
Round 2 : Lake type (Same Lake type)	- 0.00171	0.02019
Round 3 : Lake type (Same Lake type)	- 0.01084	0.02019
Round 4 : Lake type (Same Lake type)	- 0.07450	0.02019
Round 5 : Lake type (Same Lake type)	- 0.17331	0.02019
Round 6 : Lake type (Same Lake type)	- 0.13060	0.02136
<i>Random effects (SD)</i>		
Lake pairings	0.11786	
Residual	0.17326	

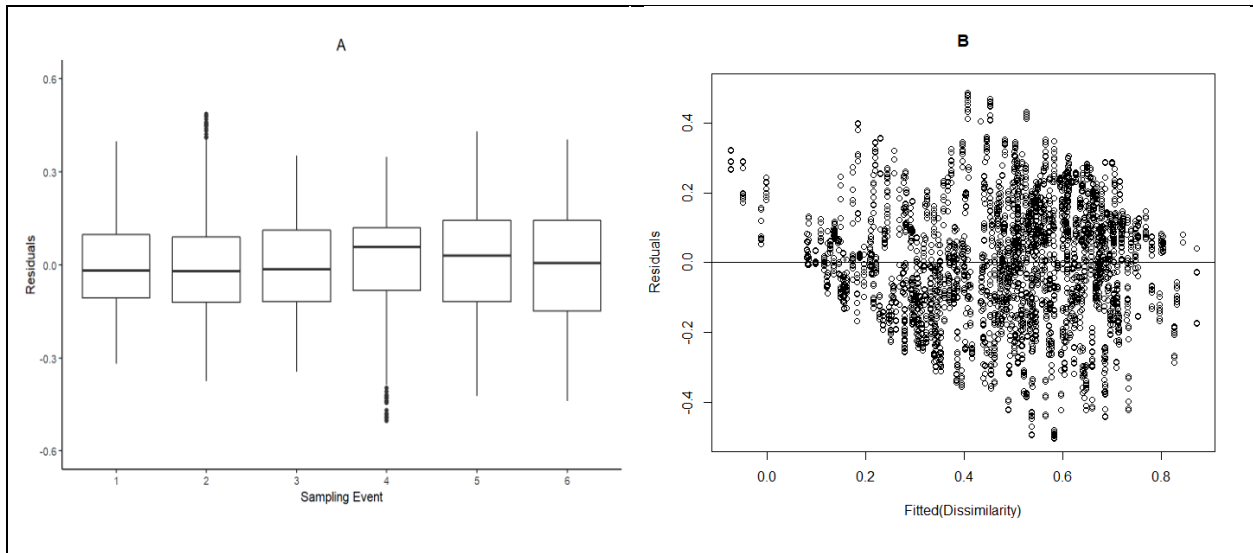


Figure A9: Model residuals for dissimilarity in community composition between samples with interaction between sampling time and contrast type, and the random effect of lake pairings plotted against **A)** Sampling event, and **B)** fitted values of the model.

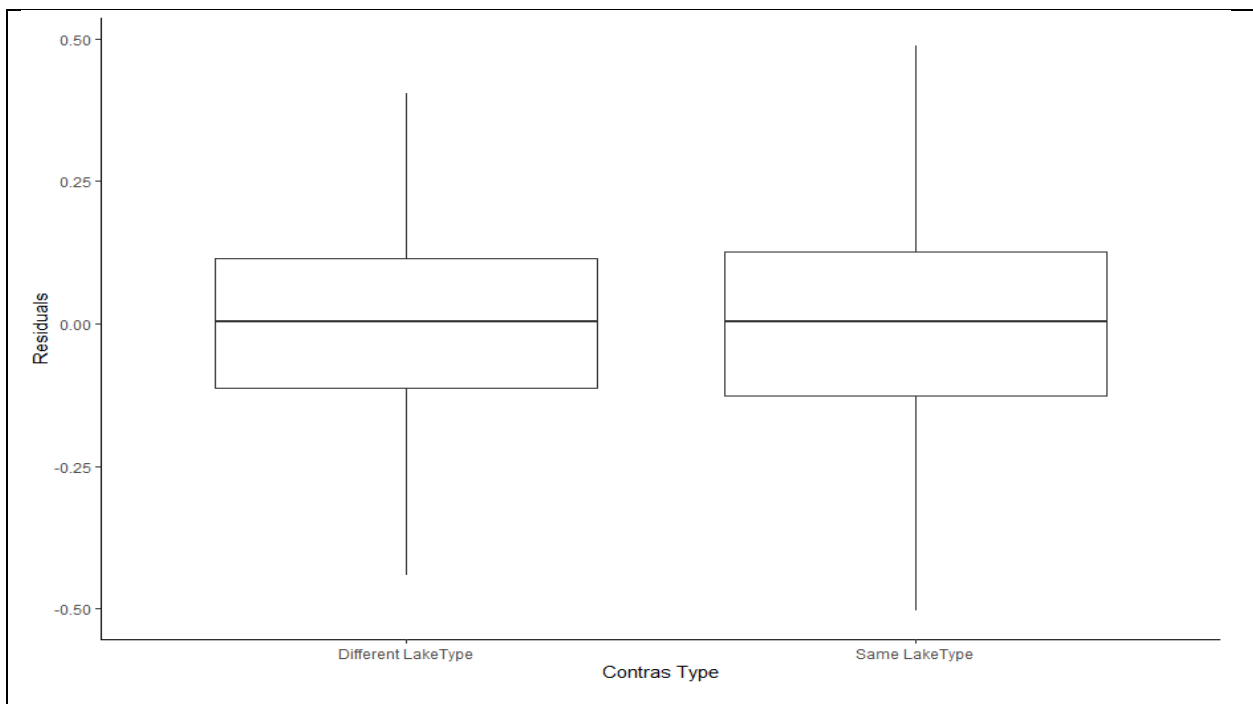


Figure A10: Model residuals for dissimilarity in community composition between samples with interaction between sampling time and contrast type, and the random effect of lake pairings plotted against Contrast type (is the samples compared have the same of different lake type).

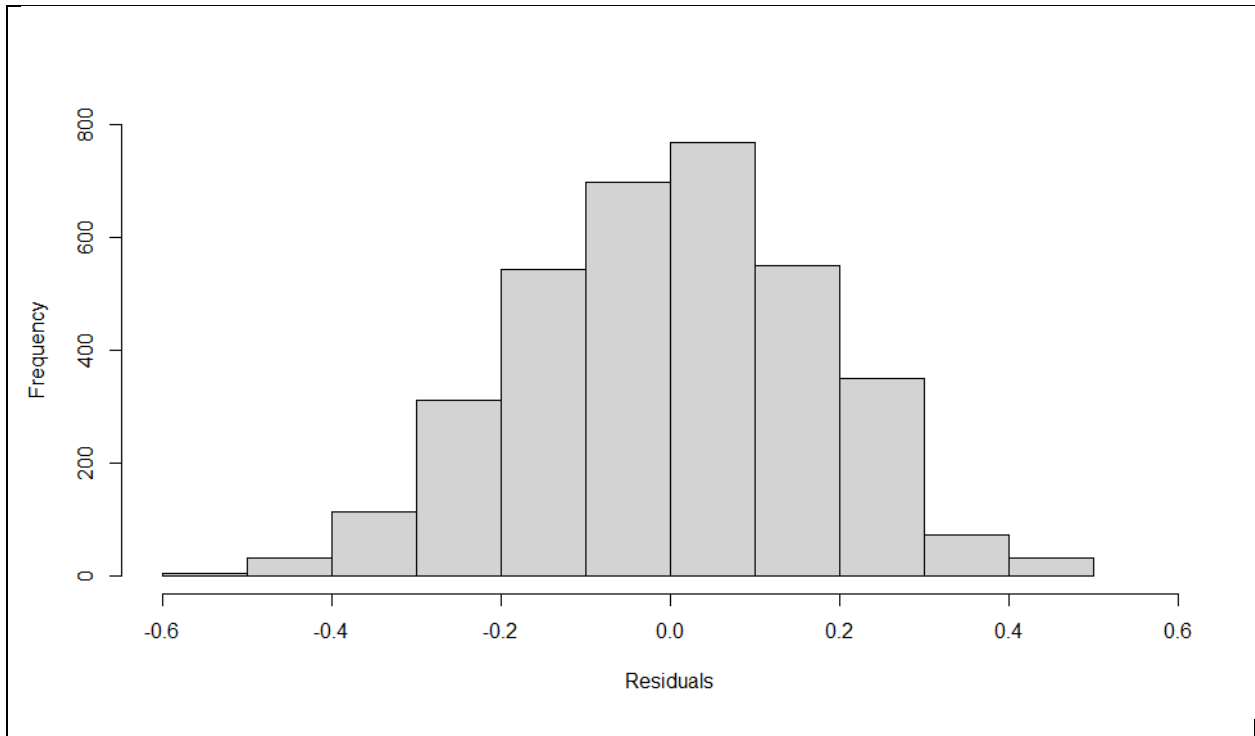


Figure A11: Histograms of model residuals dissimilarity in community composition between samples with interaction between sampling time and contrast type, and the random effect of lake pairings.

Within lake type differences

Table A7: Parameter estimates (fit with REML) for the best model describing the variation observed in dissimilarity in community composition of samples with the interaction between time interval between samplings and lake type, and the random effect of Lake ID.

	Estimate	SE
<i>Fixed effects</i>		
Intercept	0.28506	0.05228
Time interval 2-3	- 0.01679	0.03138
Time interval 3-4	0.05183	0.03138
Time interval 4-5	0.02494	0.03138
Time interval 5-6	- 0.17570	0.03327
Lake type (Planktivorous fish)	0.10477	0.07393
Lake type (Planktivorous fish) : Time interval 2-3	0.01690	0.04438
Lake type (Planktivorous fish) : Time interval 2-3	-0.11125	0.04438
Lake type (Planktivorous fish) : Time interval 2-3	- 0.13570	0.04438
Lake type (Planktivorous fish) : Time interval 2-3	0.00086	0.04573
<i>Random effects (SD)</i>		
Lake ID	0.11595	
Residual	0.16307	

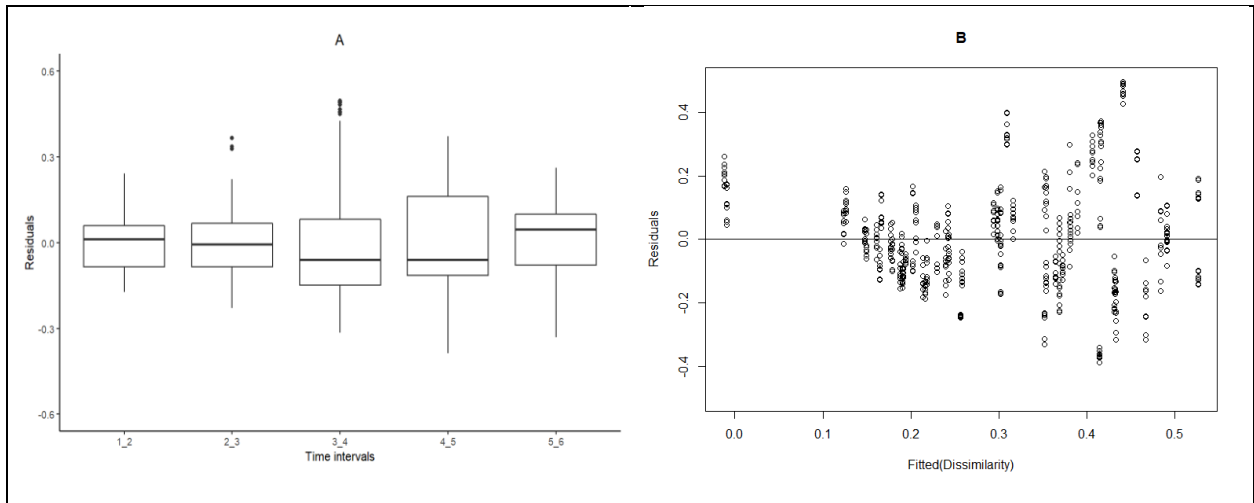


Figure A12: Model residuals for dissimilarity in community composition of samples with interaction between time interval and lake type, and the random effect of Lake ID plotted against **A)** Sampling event, and **B)** fitted values of the model.

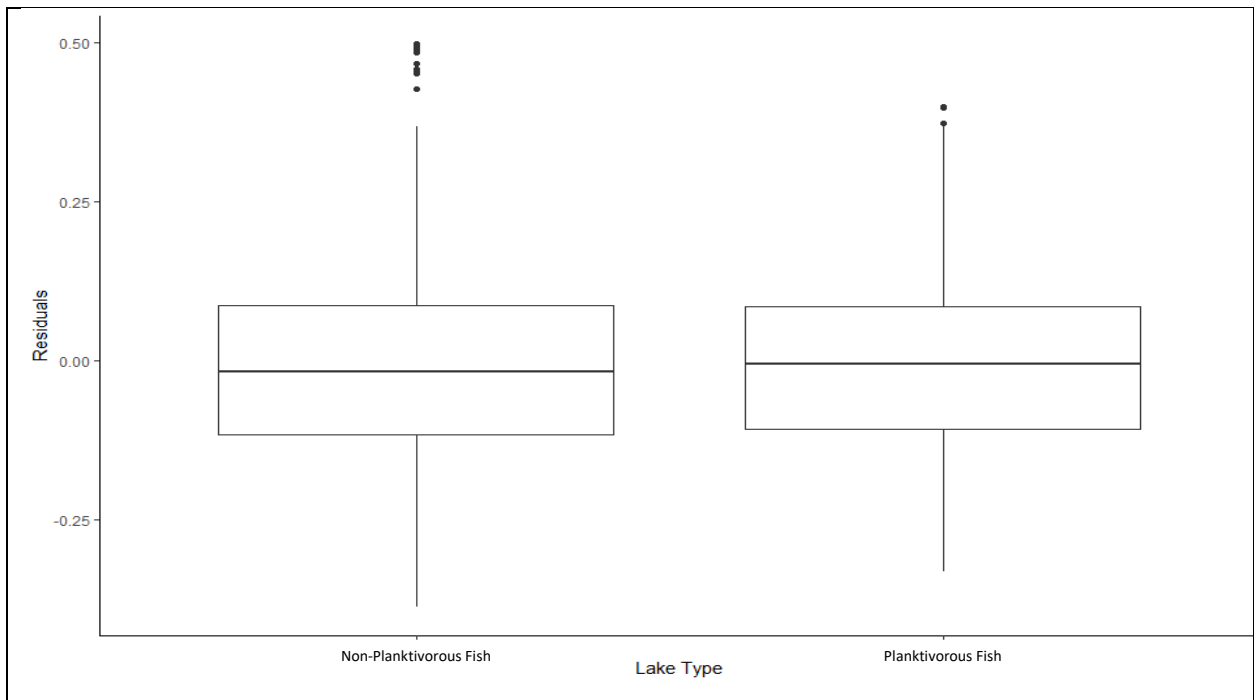


Figure A13: Model residuals for dissimilarity in community composition of samples with interaction between time interval and lake type, and the random effect of Lake ID plotted against lake type.

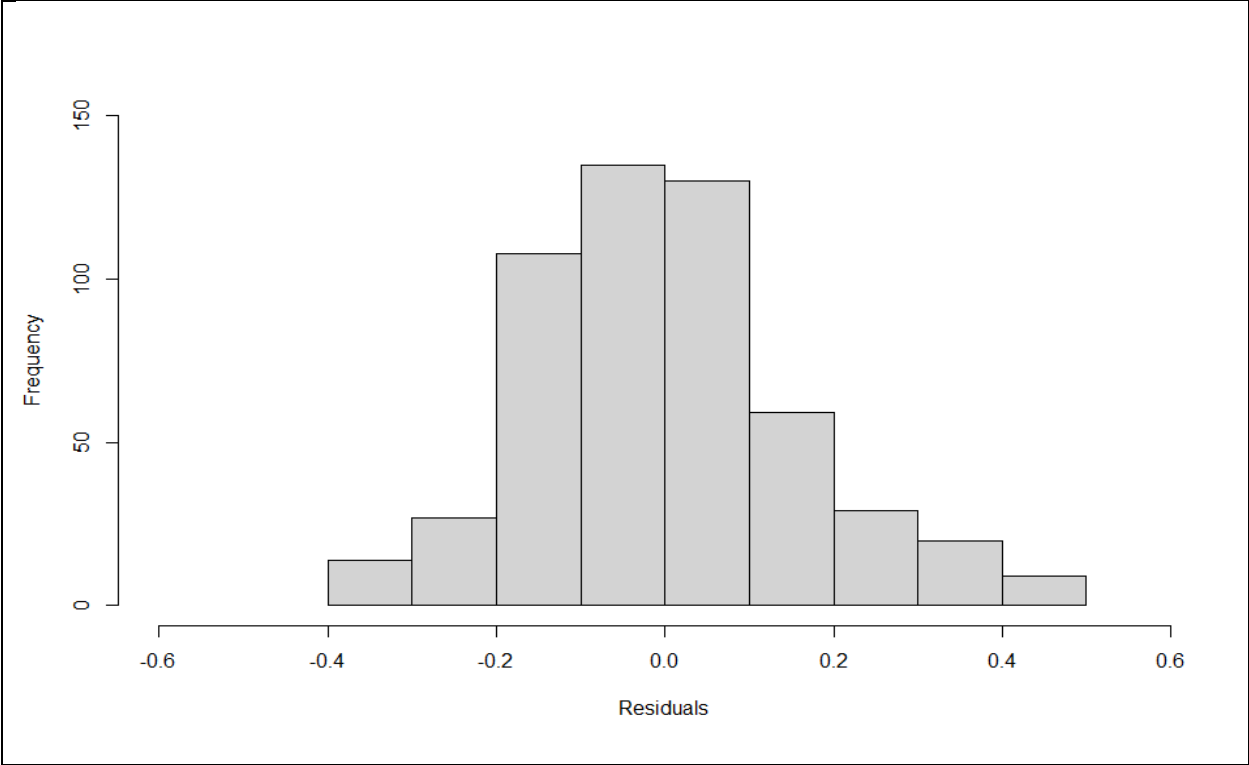


Figure A14: Histograms of model residuals for dissimilarity in community composition between samples with interaction between time intervals and lake type, and the random effect of Lake ID.

