# Linking light and productivity in lakes to zooplankton biodiversity, biomass and resource use efficiency

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# Abstract

**Introduction:** Lake productivity is determined by the amount of nutrients and light available. While phosphorus is the main limiting nutrient in freshwater systems light availability can be reduced by several factors, while the most important one in Scandinavian lakes is the amount of dissolved organic compounds (DOC). Primary productivity can affect zooplankton biomass and diversity by bottom-up driven mechanisms while zooplankton biomass and diversity can also be affected by fish via top-down control. The resource use efficiency of zooplankton gives an estimate about the realized amount of zooplankton biomass per available nutrients (total phosphorus). **Methods:** To investigate the effect of light and primary productivity in lakes on zooplankton diversity, biomass and resource use efficiency we sampled 75 lakes in southern Norway and Sweden during summer 2011. Total nutrients (total phosphorus and nitrogen), particulate nutrients (particulate organic carbon and particulate organic phosphorus), dissolved nutrients (dissolved organic compounds) were measured and estimates of gross primary productivity were used to determine the productivity of the lakes. Zooplankton samples were taken to determine zooplankton biomass (as dry weight) and zooplankton diversity (species richness). Additionally, existing data about fish diversity (species richness) were used. **Results:** Zooplankton biomass was positively affected by total phosphorus and negatively affected by total organic compounds (TOC). Additionally, a positive relationship between the estimated gross primary productivity (EPP) and zooplankton biomass was observed. Zooplankton diversity increased with longitude but decreased with latitude while resource use efficiency (RUE) of zooplankton showed the opposite relation and decreased with longitude and increased with latitude. Resource use efficiency of zooplankton also decreased with increasing zooplankton and fish diversity. **Discussion:** While the amount of nutrients had a positive effect on zooplankton biomass, increasing DOC concentrations reduced the amount of light and thus had a negative effect of zooplankton. There was no significant effect of zooplankton diversity or fish diversity on zooplankton biomass, while they both gave a negative contribution to zooplankton resource use efficiency. Fish diversity and zooplankton diversity showed an increase among the longitudinal gradient and a decrease with latitude.

# Preface

First I want to thank both my supervisors, Tom Andersen and Dag O. Hessen for their patience, encouraging comments, and for always being generous with time for valuable discussions.

Thank you to the COMSAT crew Tom Andersen, Dag O. Hessen, Marcia Kyle, Serena Rasconi, Marcus Lindholm and Robert Ptacnik for one of the greatest summers ever, when sampling data for the project.

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# Introduction

## Lake productivity and the P-limitation paradigm

There is a consensus that nutrient availability controls productivity in lake ecosystems (Schindler 1977; Smith 1979; Carpenter 2008; Sterner 2008; Elser et al. 2009), although there has been a long lasting debate on the role of various elements. In the early 70's there was claim that inorganic carbon (C) was the limiting nutrient for some lake ecosystems. This turned out to be partly propaganda spread by an industry with commercial interests (manufactures of household detergents) than the results of objective scientific work (Tom Andersen, pers. comm), but also scientific belief that at least highly productive lakes could have shortage of $CO^2$. To test the role of candidate elements much effort was devoted to bioassay experiments where inorganic C was added to phytoplankton cultures in (semi-) enclosed containers that restricted the influence of physical conditions (e.g. turbulence of the water and interaction with the overlying atmosphere) a lake would experience in an open environment. In the Experimental Lake Area (ELA) project, Schindler (1977) demonstrated at larger scale that in a natural environment there is sufficient exchange of carbon dioxide ($CO_2$) between the water body and the atmosphere through diffusion to maintain the proportionality of chlorophyll and C to phosphorus (P) concentration. He concluded that it was enough to add P and nitrogen (N) to stimulate algal growth, and that first and foremost the availability of P was the major regulating element for primary production in lakes. This was later supported by Smith (1979) and Fee (1979) among others.

The results from the ELA project laid the foundation for the P-limitation paradigm (Carpenter 2008; Kalff 2002). The supply of N by nitrogen-fixing cyanobacteria was shown to fairly balance the ratio of total nitrogen (TN) to total phosphorus (TP) in two lake experiments where fertilizers deficient in nitrogen were added. These findings in combination with the results of others now moved the focus over to P as the limiting nutrient. Since P was seen as the key element regulating primary production (Sterner, R. W. Elser 2002), it was also assumed that P should be essential also for pelagic production of consumers, however even though there seem to be a generally positive correlation between P, primary production and zooplankton production (or biomass), there is a wide scatter in zooplankton:P or zooplankton:phytoplankton, suggesting that other factors than P alone or bulk primary

production indeed play a role for secondary production and resource use efficiency (Hessen et al. 2006).

The flip side of this was that the focus on P blurred the importance of other factors as possible explanatory variables for primary or secondary productivity. Lake morphometry was reinforced as one of the "laws" of limnology by Fee (1979), and Elser (1990) could show us that it is not enough to manipulate P to affect primary productivity and algal biomass in oligotrophic lakes in the temperate zone, but that both N and P had to be provided in combination to get a strong increase in algal biomass. Not only does this emphasize the importance of the complementarity between N and P as limiting nutrients, but it also implies that addition of even small amounts of P often is enough to shift algal communities from P-limited to N-limited in lakes with initially high N:P ratios (Kalff 2002).

Also this "bottom-up" regulation of productivity hinge on other factors than nutrients alone. Light and nutrients are resources that regulate the quantity, the distribution, and the structure of phytoplankton communities (Huisman & Weissing 1995; Diehl et al. 2002; Hessen et al. 2002). Light is a crucial factor for primary production which constraints the extension of the euphotic zone in lakes. The decline of light with depth is determined by water molecules, by the concentration of dissolved matter, and by particles (such as phytoplankton). Thus one of the major determinants of light attenuation and spectral composition in lakes, especially in Scandinavia, are the concentrations of terrestrially derived, coloured dissolved organic carbon (DOC, mostly humic compounds). The levels of DOC may be instrumental for benthic productivity and propagate all the way up to fish yields (Karlsson et al. 2009) . Less is known however, about the combined role of nutrients and DOC on zooplankton production and composition.

In aquatic ecosystems the resource availability may determine the potential biomass a system can support. The extent to which that potential is realized will depend strongly on the species diversity and composition (Fox 2004). Phytoplankton biodiversity (species richness) is a good predictor of the phytoplankton resource use efficiency (RUE), the biomass produced per unit of nutrient. This was shown for field samples from Scandinavian lakes and the Baltic sea (Ptacnik et al. 2008) and laboratory and lake data (Maren Striebel et al. 2009). Thus, biodiversity of phytoplankton and biomass-specific carbon production are positively linked. An increasing biomass does, however, not necessarily imply an increase in nutrient uptake. Accordingly, primary producers often show flexible and relatively high carbon to nutrient

ratios while herbivores exhibits relatively constant and lower carbon to nutrient ratios. This can result in a mismatch between elemental ratios of resources and consumers (Sterner & Hessen 1994; Urabe & Sterner 1996) and such a mismatch in biomass C:P ratios between phytoplankton and zooplankton can affect the transfer efficiency of energy and matter within the pelagic food web by causing P-limitation in consumer and thus reduced C-use efficiency (Sterner & Hessen 1994).

## Species diversity and resource use efficiency

Tilman (1996) showed us that productivity and resource use efficiency in grassland ecosystems increased with increasing diversity. Empirical evidence supports increasingly the occurrence of increased productivity (overyielding) in species mixtures compared with monocultures (Tilman et al. 1996; A. Hector 1999; Loreau & a Hector 2001; Tilman et al. 2001). On the other hand, Jiang et al. (2008) argued that neutral or negative biodiversity and ecosystem functioning relationships may be just as likely and under certain circumstances probably more common. In a large empirical study including more than 3000 natural phytoplankton samples, Ptacnik et al.(2008) were able to show that phytoplankton diversity is the best predictor of phytoplankton resource use efficiency in freshwater and brackish environments. Specifically, the amount of algal carbon per unit total phosphorus was positively related to genus richness of the phytoplankton communities (Ptacnik et al. 2008). There is distinct evidence that a positive diversity-productivity relationship exists within pelagic communities (Maren Striebel et al. 2009).

Phytoplankton taxa do certainly differ in resource use attributes such as uptake rates and storage of nutrients, storage of carbon reserves, and light use efficiency. Thus, biomass and size structure of algae as well as light may affect trophic efficiency or *resource use efficiency* (RUE). In this context I will treat the biomass of zooplankton per amount of phytoplankton or P as a measure of RUE.

## Top down versus bottom up effects

The cascade effects between different trophic levels in lake ecosystems may not be as straight forward as it first seems. While Shapiro et al. (1975) and Carpenter et al. (1985) predicted a straight forward top-down cascade from the piscivorous predators, via planktivors and herbivores, to phytoplankton, McQueen et al. (1986) came up with a theory called the bottom-up : top-down model (BU:TD model). This model predicts that the maximum attainable phytoplankton biomass is controlled by nutrient availability, while a combination of both top-down and bottom-up effects control the realized phytoplankton biomass. It also predicts that impacts of changes in piscivore biomass in mesotrophic to eutrophic lakes will have strong effects on planktivore numbers, weaker but observable effects on zooplankton biomass, but little or no effect on phytoplankton biomass. This was also shown to hold true for Lake St. George, Ontario, Canada (McQueen & Johannes 1989). What was interesting with this experiment was that as planktivore numbers increased, zooplankton biomass decreased, and as planktivores decreased, both zooplankton biomass and individual size increased. This also affected the zooplankton community structure, where the daphnids, first dominated by small species, suddenly became dominated by larger and more effective filter feeder species. This is also consistent with the cascading trophic interaction theory (Carpenter et al. 1985). Size selection, species selection, and reduction of zooplankton biomass as a direct consequence of an increase in planktivore numbers has been reported on several occasions (Hall et al. 1976; Vijverberg & Richter 1982; Post & McQueen 1987; Carpenter et al. 1987; Rudstam et al. 1993). Selective fish predation on zooplankton community structure does not necessarily result in a reduction of macrozooplankton biomass though. An increase in the biomass of cyclopoid copepods has been modeled (Rudstam et al. 1993) to counteract the high rate of selective predation on daphnid species; results which are supported by empirical evidence (Horn & Horn 1995). This kind of compensatory effect on total biomass has also been shown to exist for phytoplankton, where high grazing pressure has led to increased water transparency, but where phytoplankton biomass has remained the same because of the association between grazing pressure and proliferation of inedible algal species with occasional blooms in spring and fall (McQueen & Johannes 1989).

Two main structuring factors in lakes are thus nutrients and DOC (and implicit light), and this study address zooplankton biomass, diversity and community composition along these

two axis, including a number of other relevant parameters. The main goal of this study and thesis is threefold:

1. To assess bulk zooplankton biomass related to DOC and nutrients (P and N): Will DOC and nutrients represent respectively negative and positive contributions to zooplankton biomass?
2. To assess the relationship between zooplankton species diversity and biomass: Will elevated diversity yield elevated biomass?
3. How will "top-down" effects via fish predation affect zooplankton biomass and diversity?
4. How does RUE in the zooplankton community reflect productivity, DOC and zooplankton community composition?

To address these issues, I used a large data set from 75 lakes across an east-west gradient, where relevant parameters were sampled to address these fundamental questions.

# Material and Methods

## Sampling

### Background

The fieldwork and sampling for this master thesis was part of a larger campaign in the project "*Biodiversity, community saturation and ecosystem function in lakes*" (COMSAT; NFR-Miljø2015 196336/S30, 2009-2012). This project primary focused on the role of biodiversity for productivity on different trophic levels, as well as for providing and sustaining ecosystem services. Thus, the lakes were selected based on their phytoplankton diversity, on productivity (total phosphorus (TP) level), and on total organic carbon (TOC) concentrations. The latter is an important parameter related to function, as it influences the light climate of lakes (Karlsson et al. 2009) and the degree of heterotrophy (Sobek et al. 2003).

### Selection of lakes for sampling

When selecting the lakes to sample of the intention was to have lakes in southern Norway and Sweden spanning out a gradient of TP concentrations, TOC concentrations and algal species richness. To separate the effects of TOC and P, the lakes were selected to obtain a maximum orthogonality, yet a perfect selection for this criterion was impossible (Figure 1). The selection of lakes was based on existing data on Norwegian and Swedish lakes from the "Rebecca" dataset (Solheim et al. 2008) and the "Nordic lake survey 1995" dataset (Henriksen et al. 1998). These datasets were subset to lakes with latitude 57 - 64 degrees N, < 600 meters above sea level, area > 1 $km^2$, pH > 5, TP < 30 µg $L^{-1}$, and TOC < 30 mg $L^{-1}$. The three main variables were split in two factor levels (high / low), giving 8 different combinations of the TP concentrations, TOC concentrations, and phytoplankton species richness. From each of the 8 combinations, 12 lakes were chosen randomly. This resulted in 96 lakes spread over a geographical gradient from western Norway to eastern Sweden. The actual number of sampled lakes was reduced to 75 due to unfavorable weather conditions during sampling (Figure 2).

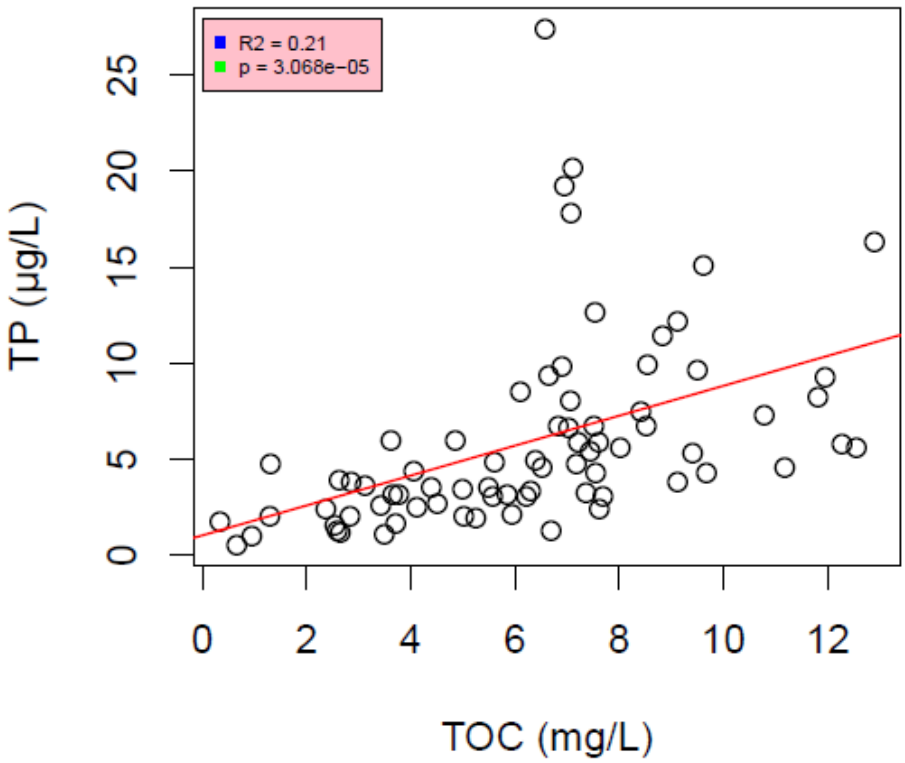


Figure 1: The gradient of TOC and TP for the chosen lakes.

## Sampling period

The sampling was conducted from a hydroplane in the period 20.07.2011 – 05.08.2011, and by car and boat between 08.08.2011 and 16.08.2011. Hydroplane was chosen to minimize the time spent on travelling between lakes. Additionally, it was important to minimize the temporal sampling window to ensure that both biotic (e.g. algal bloom conditions) and abiotic factors (e.g. water temperature) were as comparable as possible. Sampling was performed in the middle of the lake, away from inlets or outlets. If the landing point was too shallow (< 5 meter), if possible a deeper location was chosen. After sampling, filtrations and sample preparations were carried out in a portable laboratory.

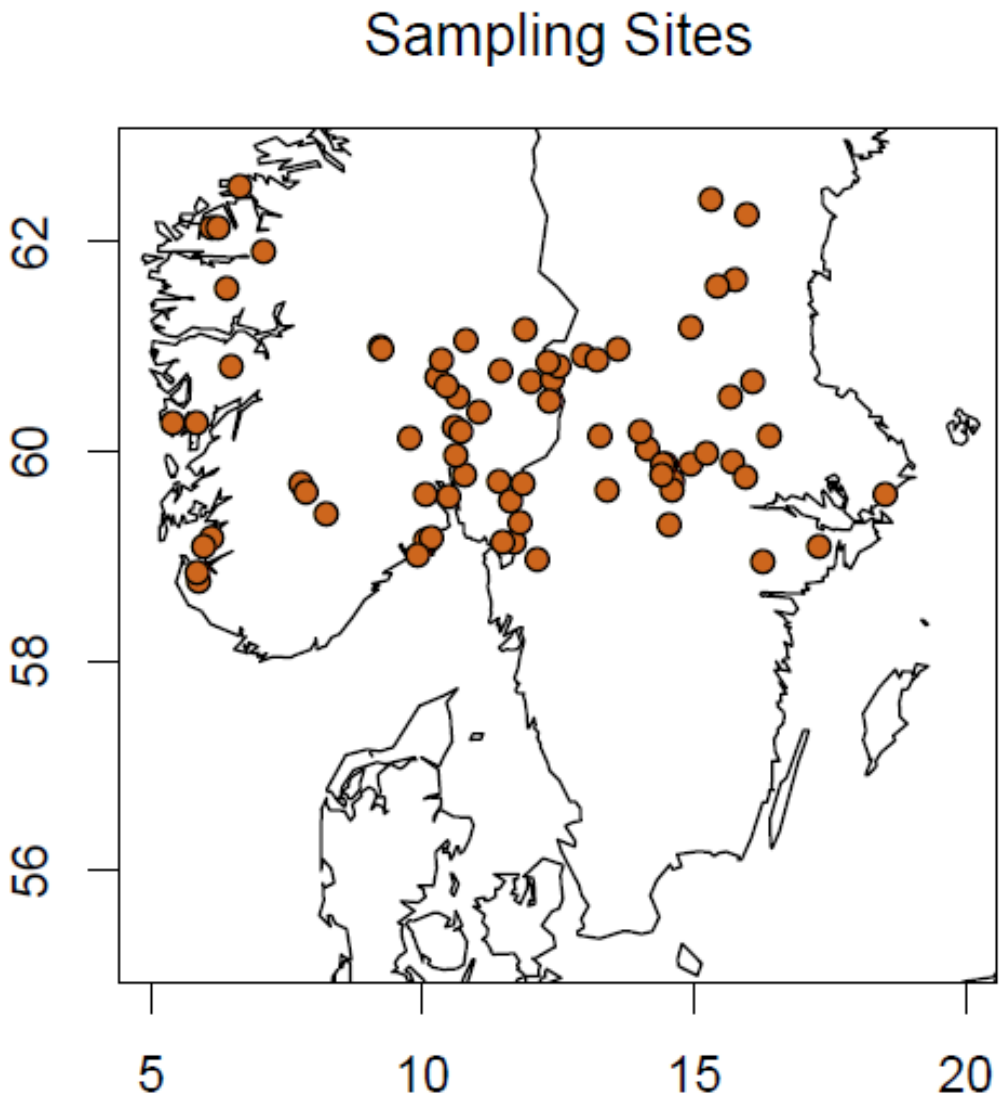


Figure 2: Map showing the 75 sampled lakes (colored dots). Axes show longitude and latitude (degrees). The lakes spanned out a geographical gradient from 5.40 to 18.52 degrees east, and 58.76 to 62.53 degrees north.

# Field sampling and in situ measurements

## Water samples

An integrating water sampler (IWS integrating water sampler, Hydro-BIOS, Germany) was used to collect water samples from 0 to 5 m. This type of water sampler samples from the surface and down, and has to be lowered at a certain speed. To ensure a steady inflow of water through the whole range of sampling depth, a built-in pressure sensor ceases intake of water by the piston if the lowering speed is violated (to high!). In 2 out of 75 lakes were the

depth did not exceed 5 m at the chosen location for the sampling, water samples were collected from the surface to just above the bottom. A total of three samples were distributed in three 5 L plastic bottles and brought back to the lab for further analysis.
Concentrations of total phosphorus and TOC were measured independently by the Norwegian institute for water research (NIVA) and the technical staff at the UiO according to standard protocols. The data used are the average of these two measurements. Total nitrogen (TN), particulate organic carbon (POC) and particulate organic phosphorus (POP) were measured at the UiO according to standard protocols. Seston C:P was calculated as the ratio between POC and POP and was used as a separate measure for food quality, since this is known to affect growth for zooplankton (Sterner & Hessen, 1994b) (for lake specific concentrations or ratios, see appendix table 1)

## Primary productivity estimates

Estimates of gross primary productivity (EPP in mg C $m^{-2}$ $day^{-1}$) were obtained using a bio-optical model. In summary, the bio-optical model was based on measurements of light absorption by the total phytoplankton community, light availability in the water column (obtained from incoming solar irradiance and total attenuation of down-welling irradiance), and measurements of phytoplankton photosynthetic efficiency using Pulse Amplitude Modulated (PAM) variable fluorescence techniques. EPP integrates the effects of nutrients and light-availability in the water column, and yields a maximum estimate of the amount of organic carbon that can be fixed under a surface of 1 $m^2$ per day. It should be noted that these also are a "snapshot" values, giving EPP at the time of sampling. For more details, see the master thesis by Thrane (2012) (for lake specific concentrations, see appendix table 1).

## Chlorophyll *a* in seston

For chlorophyll a determination in seston, water samples were filtered on 25 mm GF/C filters (Whatman) at the end of every sampling day. The filters were folded with the sample side facing inwards, put in 2 ml cryotubes (Nunc CryoTubes, Thermo Scientific, Roskilde, Denmark), snap-frozen in liquid N2 and stored at -80 º C until analysis. Samples were thawed just prior to measurement, then transferred to 1.5 ml Eppendorf tubes using a fine forceps. Subsequently, 1.2 ml of 96 % ethanol was added to each tube, and the pigments were extracted from the filters overnight (approximately 20 hours) in darkness, at room

temperature. After extraction, the seston samples were centrifuged at 15 000 rpm (Eppendorf centrifuge 5424, Eppendorf AG, Hamburg, Germany) for five minutes to remove filter debris. 750 µl of the supernatant from each sample was transferred to a 48 well plate together with the chlorophyll *a* standard dilutions. Fluorescence was measured in a plate reader equipped with a double monochromator (Synergy MX, BioTek instruments, Vermont, USA), with excitation at 425 nm and emission at 673 nm. The wavelengths of excitation and emission were chosen after measuring the fluorescence spectrum of the standard solution with different excitation and emission wavelengths. Concentration of chlorophyll *a* in the original water sample (µg $L^{-1}$) could then be calculated by dividing this number on the volume filtrated (in litre) and multiplying with 1000. Seston Clorophyll a concentrations were used as a proxy for phytoplankton biomass in regression analyzes (for lake specific concentrations, see appendix table 1).

## Chlorophyll *a* standard solutions

For calibration of the method, 1 mg of pure chlorophyll *a* (Sigma-Aldrich, product code 101139331) was dissolved in 100 ml 96 % ethanol resulting in the theoretical chlorophyll *a* concentration of 10 mg $L^{-1}$. This solution was then diluted to a stock solution of 5 mg $L^{-1}$. Concentration of the stock solution was verified by measuring the absorbance at the red maximum (λmax) in a spectrophotometer (Shimadzu UV-2550, Shimadzu Scientific Instruments, Maryland, USA) using a 1 cm cuvette. The specific absorbance coefficient of pure chlorophyll *a* in 95 % ethanol at λmax is 84.6 (liter $g^{-1}$ $cm^{-1}$) (Lichtenthaler and Buschmann 2001). This was used to calculate the concentration of the standard in mg $L^{-1}$ as $\lambda_{max}$

$$[chlorophyll\ a] = \frac{abs\ (\lambda\max)}{84.60}\ 1000$$

The concentration of the stock solution was slightly higher than expected (5.50 mg $L^{-1}$). A dilution series, ranging from 5.50 – 0.17 mg $L^{-1}$, was prepared by six sequential 1:2-dilutions of the stock solution.

## Corrections for chlorophyll on zooplankton filters

To correct for the potential contribution of algae on the zooplankton filters (some large algae were retained by the 90 µm mesh), a die tool with a diameter of 7.6 mm was used to punch out two subsamples from each zooplankton filter while still frozen. One sub sample was placed in a 1.5 ml Eppendorf tube using a fine forceps. The other subsample and its filter were then returned to the freezer before they got thawed. Subsequently, 1.1 ml of 96 % ethanol was added to each Eppendorf tube, and the pigments were extracted from the subsamples over night (ca. 20 hours) in darkness, at room temperature. After extraction, the subsamples were centrifuged at 20 000 rcf (Eppendorf centrifuge 5424, Eppendorf AG, Hamburg, Germany) for 10 minutes to remove filter debris. 250 µl of the supernatant from each sample was transferred to a 96 well plate together with the chlorophyll a standard dilutions. Fluorescence was measured in a plate reader equipped with a double monochromator (Synergy MX, BioTek instruments, Vermont, USA), with excitation at 425 nm and emission at 673 nm. The wavelengths of excitation and emission were chosen after measuring the fluorescence spectrum of the standard solution with different excitation and emission wavelengths. A standard curve relating chlorophyll *a* concentrations of the standards to measured fluorescence was calculated using polynomial regression ($p < 0.0001$, $R^2 = 0.99$). The unknown concentrations of chlorophyll *a* in the extract were found by predicting the model using the sample fluorescence as input data. Amount of chlorophyll *a* (µg) on the filter was found first by multiplying the concentration of the extract (µg $ml^{-1)}$ by the volume of the extract (ml), second by multiplying this product with the quotient of the area of the filter and the area of the punched out subsample.

## Zooplankton samples

Vertical zooplankton net hauls were taken from just above the bottom to the surface using a standard zooplankton net with 90 µm mesh size and a diameter of 40 cm. Two samples were collected in brown glass bottles. One of the samples was conserved with rectified ethanol, were the ethanol constituted a minimum of 70 % of the liquid, and the other with acid Lugol. These two bottles were kept in dark and cool until species determination (crustaceans) and thus diversity data. This analysis was performed by Bjørn Walseng at NINA. Another sample was collected in a 0.5 L steel container with pure water to keep the animals alive. These samples were filtered on pre weighted 40 mm GF/C filters (Whatman) immediately after our

return to the camp in the evening. The filters were placed in labelled petridishes before frozen at - 20 ° C for later analyses.

## Zooplankton dry-weight and resource use efficiency

Zooplankton from an integrating ne-haul was filtered of pre-weighted GFF-filters before freezing (- 20 °C). Before analysis the frozen zooplankton filters was thawed and dried at 60 °C over for ca 24 h, or until there was no further weight loss. The dry-weight of the subsample used for correction of algal mass (based on Chl a) was added to obtain total mass of the sample, and the weight of the filter *per se* was subtracted to get total zooplankton dry-weight ($DW_{tot}$).

The non-zooplankton matter ($DW_{corr}$) was estimated; first by dividing seston C with seston chlorophyll a, second by multiplying this quotient with the measured chlorophyll a on the filter, third by multiplying this product with 0.45, which is the converting factor for DW to C (Andersen, T. Hessen 1991).

The dry weight of zooplankton on the filter ($DW_{zoo}$) was found by the equation;

$$DW_{zoo} = DW_{tot} - DW_{corr}.$$

The dry weight of zooplankton in the sample (µg $L^{-1}$) from each location ($Z_{DW}$) was found by the equation;

$$Z_{DW} = DW_{zoo} / (Vf),$$

where V is the volume (L) of the net haul, and $f$ is the share of total sample on this filter (see appendix table 1 for lake specific zooplankton dry weight)

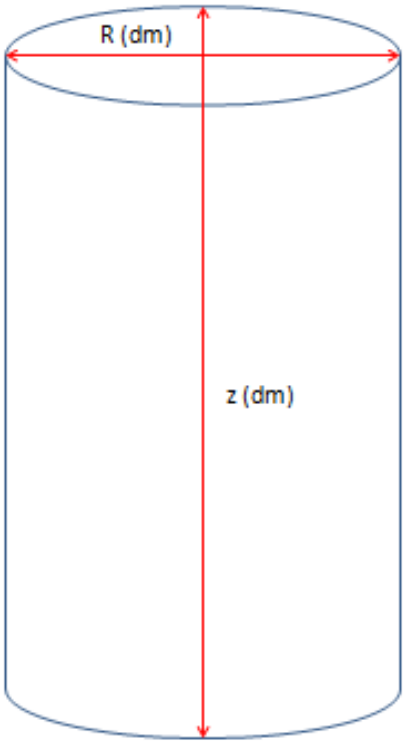


Figure 3: The volume of the net haul was calculated using the equation $V = \pi (R/2)^2 z$; V is the volume while R is the diameter of the net (dm) and z is the length of the net haul (dm).

## The zooplankton resource use efficiensy

As a measure of the resource use efficiency (RUE) of zooplankton, which could vary along the gradients of TOC and P, the ratio of zooplankton biomass versus its basal resource was used. Total P was chosen rather that algal mass or chlorophyll *a* first of all because it generally correlated well with phytoplankton mass, but also because it is more conservative than algal mass, and also because it may be important for production of bacteria and micro-zooplankton, which also may be an important resource for zooplanktonThe zooplankton resource use efficiency was calculated as the natural logarithm of the ratio between zooplankton dry weight and TP;

$$\log(ZDW/TP)$$

## Zooplankton diversity and community composition

The zooplankton diversity and composition were analyzed at the Norwegian Institute for Nature Research (NINA) in accordance with standard protocols. In general subsamples were examined until at least 200 organisms were counted. The remaining fraction was analyzed to ensure that all species in the sample were recorded. Cladoceran species were identified in accordance with Flössner (2000), whereas copepods were identified after Kiefer (1978). The zooplankton species data were scored as presence-absence.

## Fish diversity

The fish community composition and diversity was assessed by Markus Lindholm at Norwegian Institute for Water Research (NIVA). Several databases (see appendix table 2) were used for this purpose, but this may not necessarily have given a true representation of all species present. Complementary information to existing species lists was collected by making phone calls and sending emails to the local fish organization and up to several local men of resource. It should be noted that this does not include information about relative abundance.

# Results

## Background – general parameters

The samples lakes represented strong gradients in the key parameters total organic carbon (TOC), total phosphorus (TP), estimated primary production (EPP) as well as zooplankton biomass (Fig. 4). While concentrations of TOC were low at the western sites, TOC concentrations peak along the Norwegian-Swedish border and remain high in the Swedish sites. A similar pattern was observed for TP concentrations, meaning that a complete orthogonality between these two parameters was not achieved (see also Fig. 1). Although EPP differed strongly between lakes, the east-west pattern was less pronounced, and the same holds for zooplankton biomass.

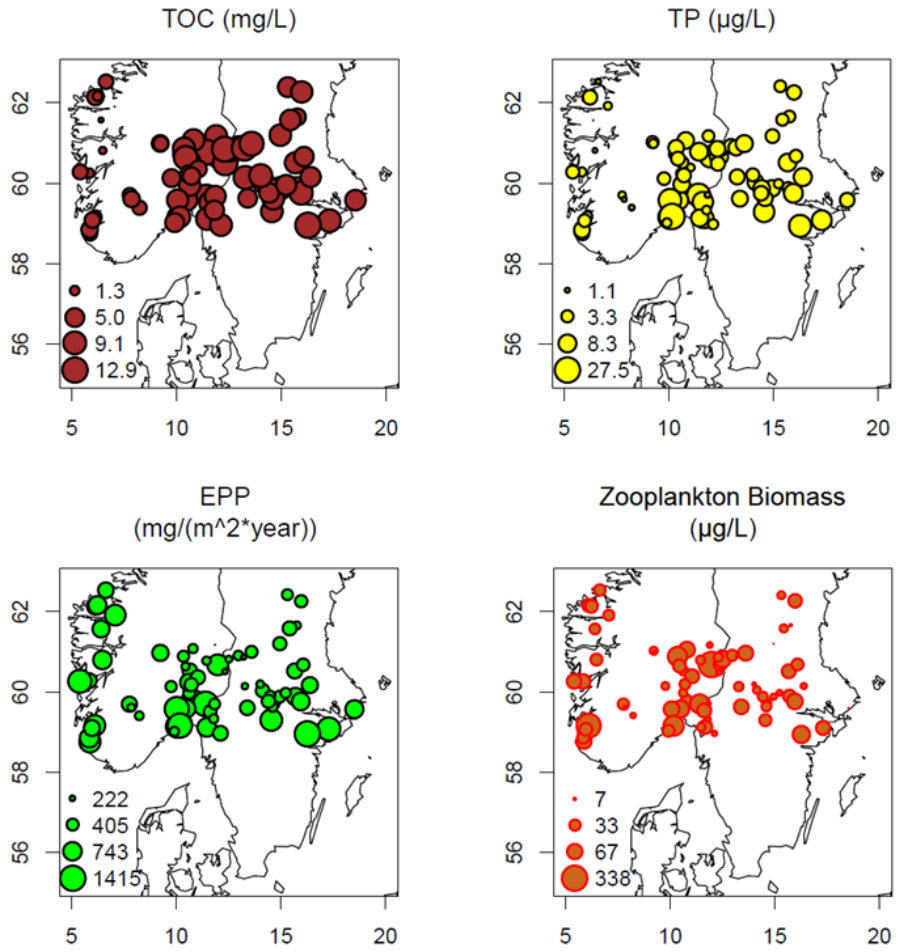


Figure 4: The lakes are plotted as points proportional to the natural logarithm of each variable, while numbers in legends links the approximately true values of each variable to respective point size.

The longitudinal gradient was significant for both TOC concentrations ($R^2 = 0.37$, $p < 0.0001$) and TP concentrations ($R^2 = 0.15$, $p = 0.0007$), when assessed by simple linear regression. There was a weak longitudinal response in zooplankton biomass ($R^2 = 0.07$, $p = 0.02$), while no significant relation between EPP and longitude existed. There was a weaker, but significant latitudinal gradient in TP concentrations ($R^2 = 0.10$, $p < 0.006$) and EPP ($R^2 = 0.09$, $p < 0.01$), both parameters decreasing from south to north. No significant relation between zooplankton biomass and latitude existed.

# Zooplankton Biomass

The relationship between zooplankton biomass (zooplankton dry weight, ZDW) was tested against four potential drivers, TP, TOC, sestonic C:P-ratio and EPP. ZDW was positively related (testing this with linear regressions) to TP ($p<0.001$; slope = $0.44 \pm 0.12$(SE)) and EPP ($p<0.001$; slope = $0.87 \pm 0.18$ (SE)), while not with TOC ($p=0.91$) or seston C:P ($p=0.92$) (Fig. 5). TOC showed no effect using a linear regression but showed a significant negative effect on ZDW when TP and TOC were included as additive variables (Table 1).

The proportion of variance in ZDW explained for the simple linear regression of EPP was 26 %, which is close to the total variance explained in the multiple regression analysis (29 %), reflecting that EPP primarily depend on TP (positive) and TOC (negative due to light absorbance). This suggests that we can use the outcome from the simple regression model instead of the multiple regression model when analyzing and interpreting variance in ZDW (see discussion).

No significant relation existed between ZDW and zooplankton species richness, or between ZDW and fish species richness (testing this with linear regressions) (figure 6).

**Table 1.** Multiple Regression Model: ln(ZDW)= ln(TP) + ln(TOC)

Coefficients:

| | Estimates | SE | t-value | p-value |
|---|---|---|---|---|
| intercept | 3.28 | 0.23 | 14.2 | < 2e-16 |
| ln(TP) | 0.76 | 0.14 | 5.4 | 8.94e-07 |
| ln(TOC) | -0.58 | 0.16 | -3.5 | < 0.001 |

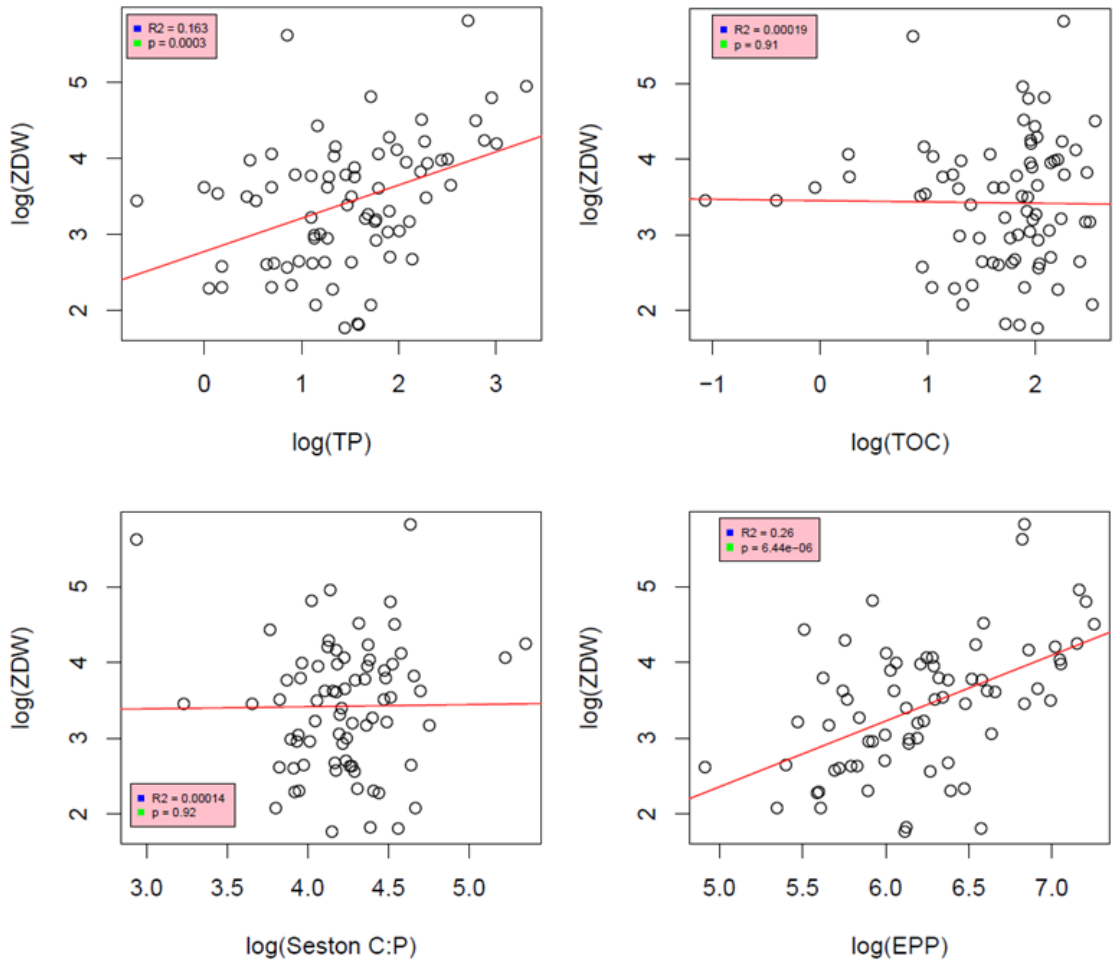


Figure 5: The relationship between ZDW and two of the most important lake chemistry parameters; TP and TOC (upper graphs), and the relationship between ZDW, seston C:P, and EPP (lower graphs).

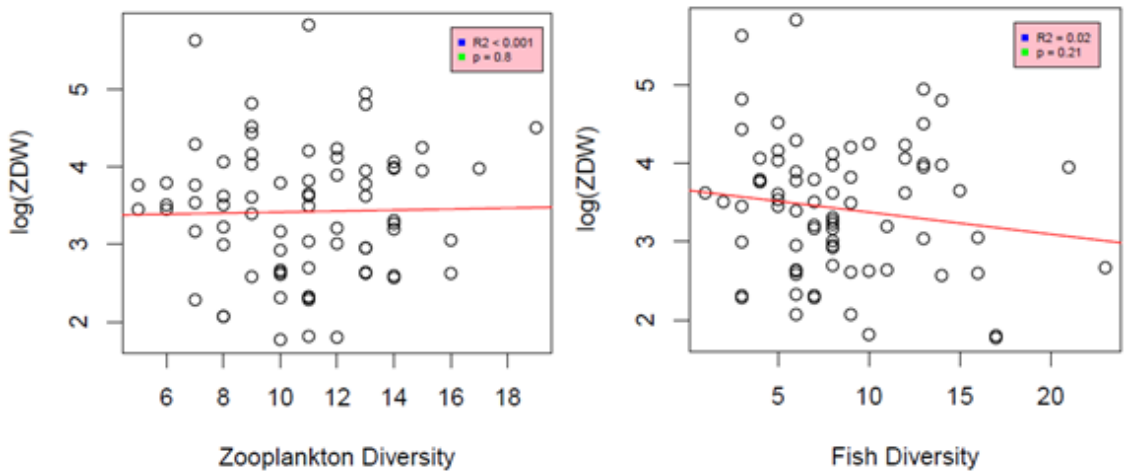


Figure 6: The relationship between ZDW and zooplankton diversity expressed as species richness (right), and the relationship between ZDW and fish expressed as species richness.

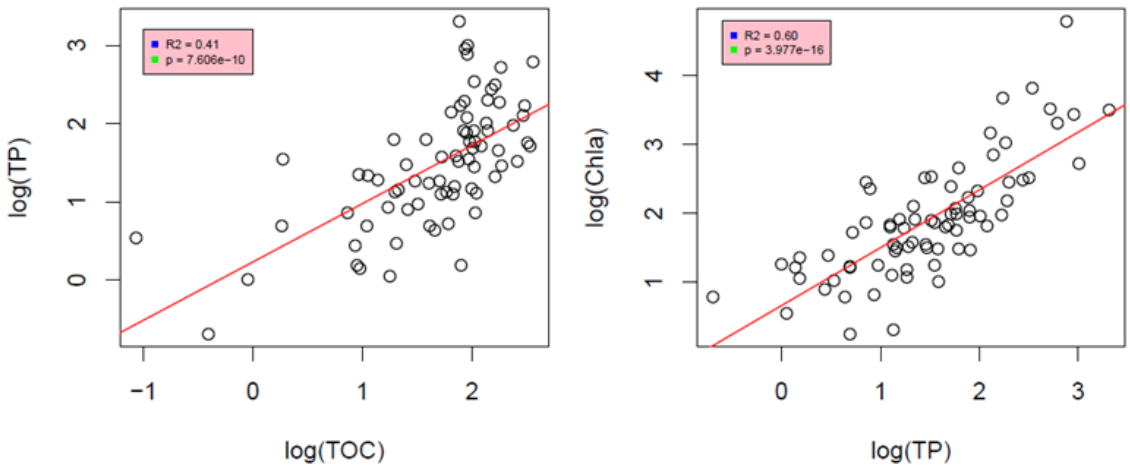


Figure 7: The relationship between TP concentrations and two important lake trophy indicators. Left: TP concentrations as a function of TOC concentrations, right: Chl a concentrations as a function of TP concentrations.

# Zooplankton diversity and fish diversity

There were two strong geographical gradients in zooplankton and fish species richness, both increased from the west to the east and from the north to the south (Fig. 8).

While longitude explained about 37% of zooplankton species richness, latitude explained about 20% of zooplankton species richness (using linear regression models for each parameter separately). A similar pattern existed for fish species richness, here 36% could be explained by longitude while only 10% of fish species richness was explained by latitude (Fig. 9).

While zooplankton species richness increased with 0.54 (SE=0.08) species per degree longitude, zooplankton species richness decrease with 1.42 (SE=0.33) species per degree latitude. Fish species richness increased with 0.80 (SE = 0.13) species per degree longitude and decreased with 1.51 (SE = 0.54) species per degree latitude.

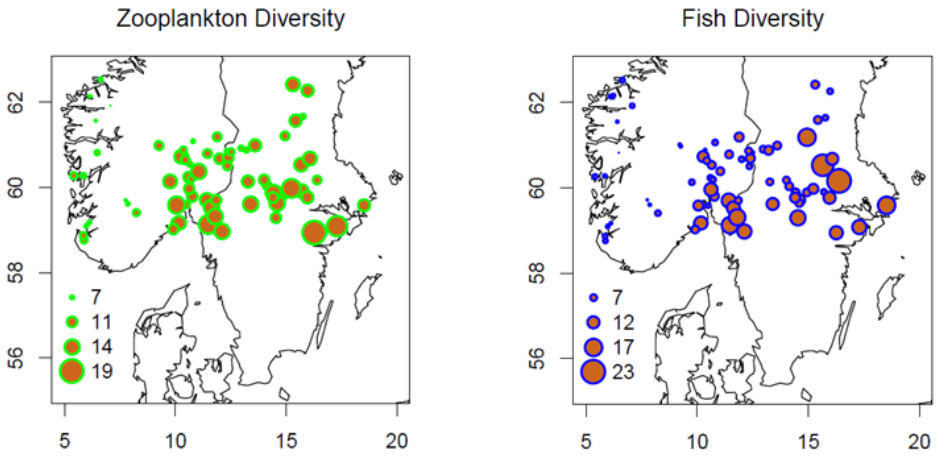


Figure 8: The sampled lakes with symbol size proportional to the number of recorded species of zooplankton (left) and fish (right).

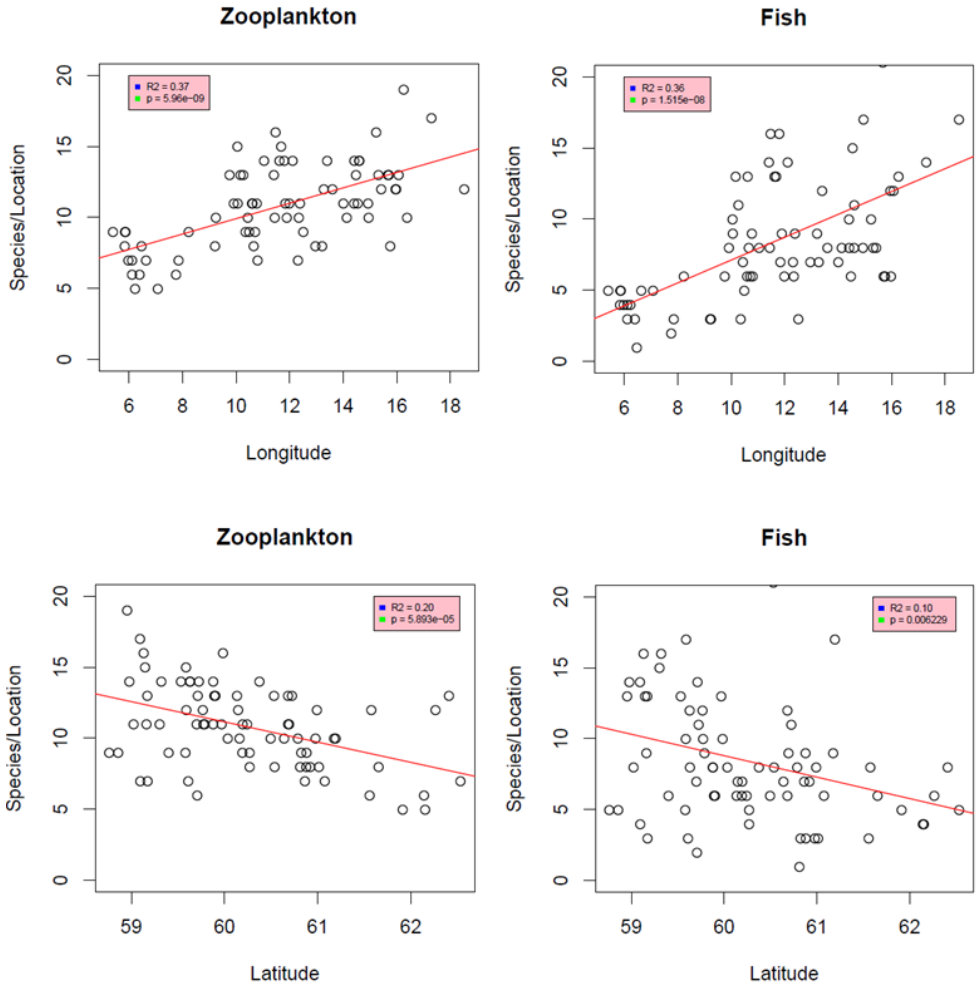


Figure 9: Number of species per location plotted as a function of longitude (upper graphs) and latitude (lower graphs). Left: Zooplankton. Right: Fish

**Zooplankton and fish species composition**

There were major shifts not only in diversity, but also in species composition of both zooplankton and fish from west to east.

The crustacean zooplankton diversity, with a total of 37 species recorded, ranged from 5 to 18 species per location, with a mean of 11 species per location. *Bosmina longispina* is by far the most usual species, found in 69 localities. 19 of the species are found in more than 10 localities, where 18 species has to be considered rare (Fig. 10).

The fish diversity, with a total of 31 species, varies with over an order of magnitude, from 1 to 23 species per locality, with a mean of 8.4. Trout, pike, perch and roach are the most frequent species, where we found 21 of the species in more than 10 localities, and where 10 of the species has to be considered pretty rare (figure 10).

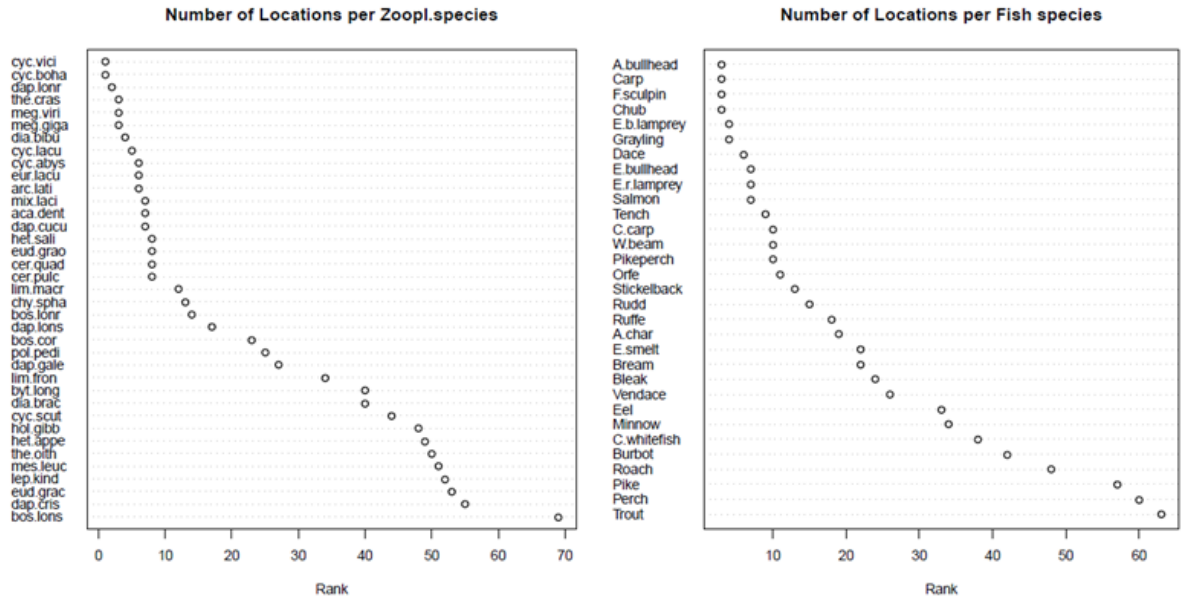


Figure 10: Number of localities (rank) for each species of zooplankton (left, see appendix table 3 for unabridged species names) and fish (right, see appendix table 4 for complete names and Latin names) in falling order.

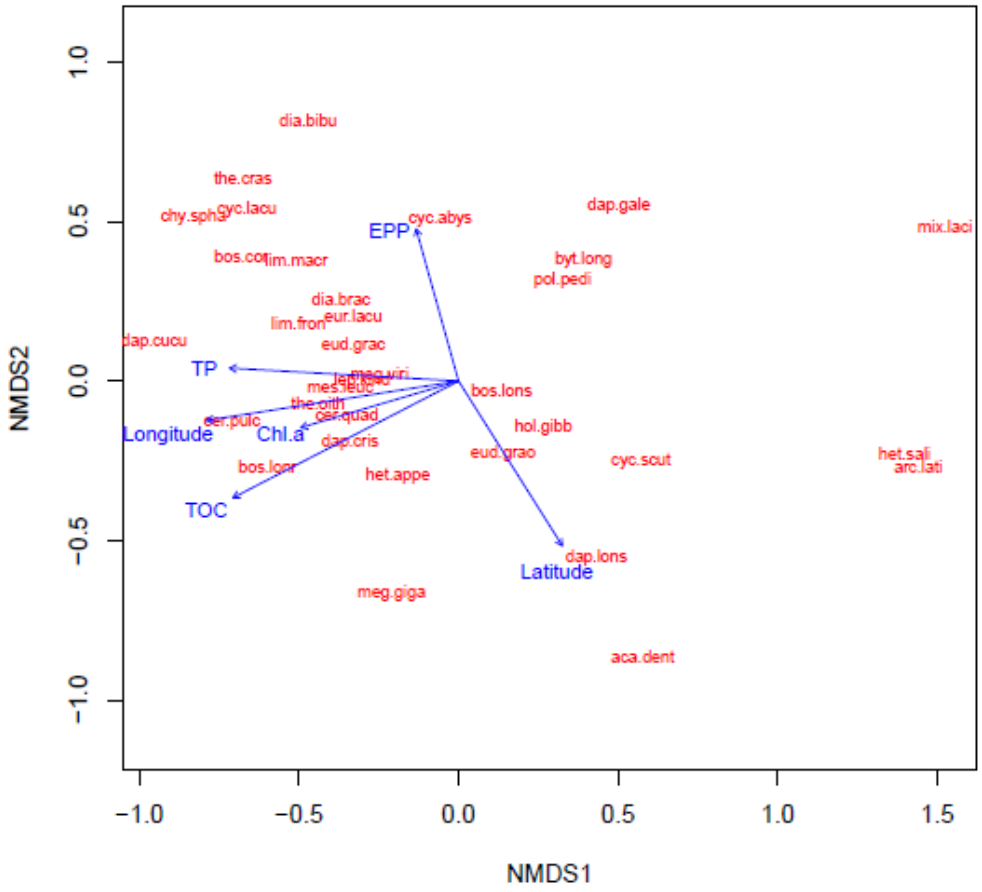


Figure 11: A metaMDS ordination of zooplankton species with superimposed environmental variables.

The distribution of crustacean zooplankton species was assessed by making an ordination with the use of a non-metric multidimensional scaling technique called metaMDS (with default monoMDS). The lowest stress was obtained when the number of dimensions was set to 3 (stress = 0.12), and two convergent solutions were found after 101 tries. The species are placed in a 3-dimensional space (figure 11) with respect to the dissimilarities (index = Bray-Curtis) between the species. We can see that the first axis seems to reflect the east-west gradient in TOC and TP, while the second axis is more a north-south gradient with a contribution from EPP. Axis 1 indicates big calanoid copepodes in the west and small cladocerans in the east. The dispersal of species is shown on axis 2 and there are large species on both sides.

# Resource use efficiency of zooplankton (RUE)

As a proxy of resource use efficiency in zooplankton, i.e. the efficiency by which organisms utilize and convert available resources, I used the ratio of zooplankton dry weight over total P (ZDW:TP). This is because TP is the key driver of primary production, but also because zooplankton directly depends on P and TP is a more accurate and a less dynamic parameter than e.g. Chl *a* (although the two is rather substitutable in this context, se figure 6 right panel). RUE showed exactly the opposite trend with longitude and latitude compared to zooplankton and fish diversity (figure 8 and 12). RUE was negatively related to longitude ($p<0.001$; slope = – 0.16 ± 0.03(SE)) (figure 12), meaning that there was an increase in the resource use efficiency from east to west, while the increase of RUE with latitude was no significant.

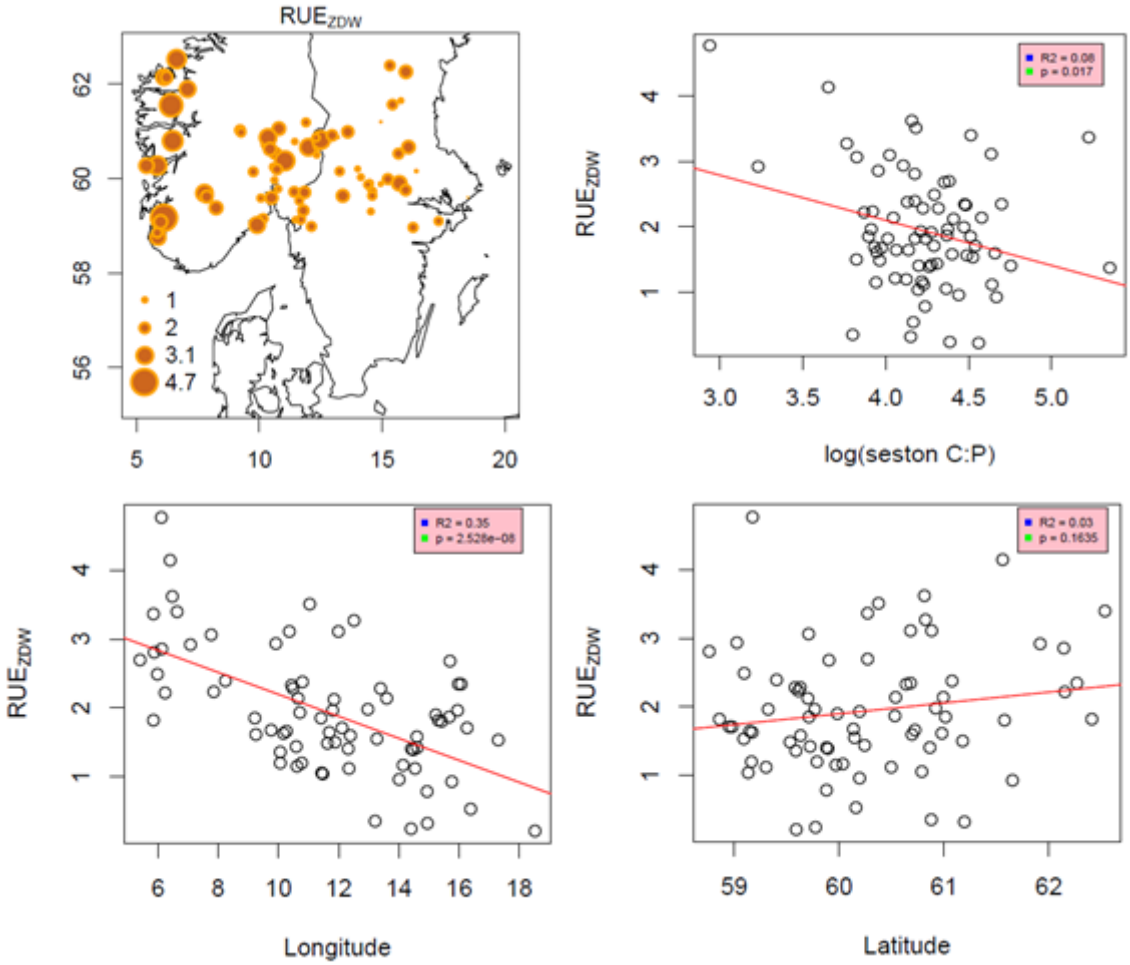


Figure 12: Upper graphs: The sampled lakes are plotted as points proportional to the natural logarithm of the ratio between ZDW and TP, called the recourse use efficiency (RUE) (right). RUE plotted as function of seston C:P (left). Lower graph: RUE plotted as a function of longitude (left) and latitude (right).

Zooplankton RUE was negatively related to TOC concentrations ($p<0.001$; slope = - 0.76 ± 0.13(SE)), to seston C:P ratio ($p < 0.017$; slope = - 0.7 ± 0.28 (SE)), while no significant relation between zooplankton RUE and EPP existed. Zooplankton RUE was negatively related to zooplankton ($p<0.01$; slope = - 0.11 ± 0.03(SE)) and fish species richness ($p<0.001$; slope = - 0.11 ± 0.02(SE)).

TOC concentrations explained about 33% of zooplankton RUE, seston C:P ratio explained only 8 % of zooplankton RUE, zooplankton diversity explained only 13 % of zooplankton RUE, while fish diversity explained 32 % of zooplankton RUE. All these parameters were obtained using separate linear regression (figure 12).

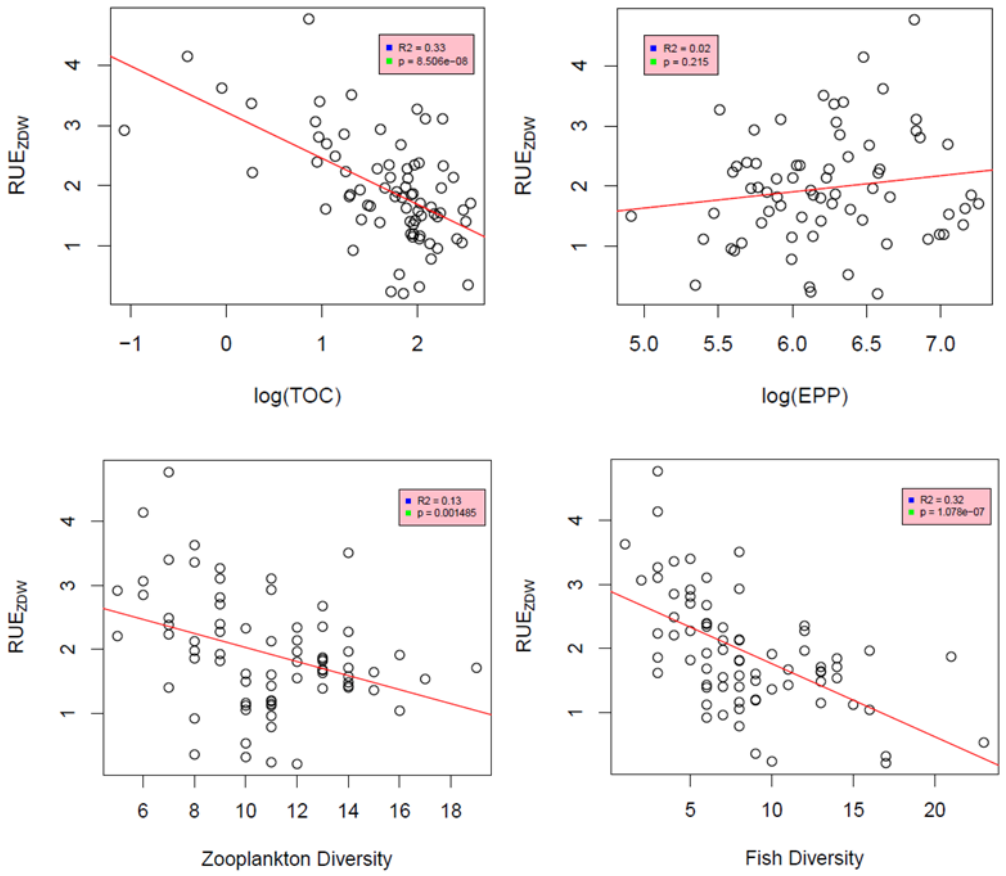


Figure 12: Zooplankton RUE plotted as a function of TOC, EPP (upper graphs), zooplankton and fish species richness (lower graphs).

# Discussion

## The effects DOC (light), nutrients and diversity on zooplankton biomass

All the sampled lakes had a molar N:P molar above 7 (min = 17.37, mean = 104, max = 570.6), meaning that they can be considered to be limited by phosphorus. Based on this strong phosphorus limitation in the sampled lakes and the strong positive correlation between TP and Chl *a* (figure 6), TP were chosen as a proxy for primary productivity. Additionally TP concentrations are known to be less dynamic than Chl *a* concentrations (as pigments can vary not only due to nutrient, but also light conditions) in lake ecosystems (Tom, pers. comment), and thus considered to be a good proxy for productivity in the lakes. Investigating potential drivers for zooplankton biomass concentrations at the different locations (in different lakes), TP concentrations were positively correlated with zooplankton biomass, but explained only ca 16 % of the variance, while TOC concentrations were not significantly related with zooplankton biomass. Taken these parameters together in a multiple regression, TP and TOC concentrations explained about 29 % of the zooplankton biomass, with a negative contribution from TOC and a positive contribution from TP (see table 1).

Even though TP concentrations are considered to be a good proxy for primary productivity, one has to keep in mind that only a certain amount of the TP is bio-available. This means that using TP concentration as a proxy for the potential maximum gross primary production might over estimate the maximum production, and thus also overestimate the potential food available for the zooplankton. Estimated primary production (EPP) (Thrane 2012), on the other hand, might be a better predictor for zooplankton biomass since directly represents the algal mass that can be produced from a given amount of nutrients and light (PAR) that are available in the water column. Comparing the explanatory power of TP and TOC concentrations with EPP for zooplankton biomass shows however that both proxies explain almost the same amount of variance in zooplankton biomass ($R^2 = 0.29$ and $R^2 = 0.26$ respectively). This means that, TP and TOC concentrations as predictors for zooplankton biomass can be substituted with EPP estimates.

Terrestrially derived organic matter could potentially have a positive effect on zooplankton biomass through the microbial loop (Christoffersen et al. 1990). In addition, it would also reduce transparency and could thus imply lower predation pressure from visual predators (Wissel et al. 2003). On the other hand, reduced transparency would also mean reduced photosynthesis in deeper layers (Houser et al. 2003). The analysis gave a strong positive relation between estimated primary productivity (EPP) and zooplankton biomass, and since EPP takes into account both positive effects of TP and the negative (via light limitation) of TOC concentrations, it should therefore integrate these contrasting effects.

There was a lot of variance in zooplankton biomass left to explain though, and I therefore regressed the variance in zooplankton biomass to both zooplankton and fish diversity. Fish predation would likely affect both community composition and zooplankton biomass (e.g. Carpenter et al. 1987). The fact that fish communities with higher diversity, which also have a higher probability of planktivorous fish species, had no significant effect on zooplankton biomass, suggest that while fish may affect size and community composition of zooplankton, it may not necessarily affect biomass. I.e. few and large zooplankton species may simply be replaced by smaller but more zooplankton species or individuals with increased fish predation pressure. It has been demonstrated that a decrease in the contribution from daphnid species on zooplankton biomass due to high predation pressure can be compensated by an increase in the contribution from cyclopoid copepod biomass (Rudstam et al. 1993; Horn & Horn 1995). It has also been reported that there can be a compositional turnover from a few large to several small cladoceran species when predation pressure is high, and that this can have a compensatory effect on total zooplankton biomass (McQueen & Johannes 1989). High predation pressure might also induce phenotypic plasticity within cladoceran species, where the mean size and the reproductive age decreases (Stibor & Lüning 1994). This might result in fewer eggs released per individual (Pijanowska et al. 2006), although also the opposite has been reported (Boersma et al. 1999), where the individuals produce more but smaller eggs. The reproduction rate can have stabilizing effects on, or even increase zooplankton biomass in both cases though (Boersma et al. 1999; Pijanowska et al. 2006). These compensatory effects might also explain why there was no positive relationship between zooplankton diversity and zooplankton biomass.

Fish communities with high diversity also have a higher probability to contain piscivores, and this might decrease the predation pressure from planktivores on zooplankton (Carpenter et al. 1987).

# Geographical patterns in zooplankton and fish diversity

There was a strong geographical gradient in zooplankton and fish species richness, both increased from the west to the east and from the north to the south. To which extent this reflects migration constraints, immigration history or confounding factors related to water properties is not settled. Zooplankton composition has been reported to be closely related to patterns of glaciations (Carter 1980; Stemberger 1995), and the distribution pattern for crustacean zooplankton- and fish species in the area of the sampled lakes has been reported to reflect the immigration pattern since the last period of glaciations (Refseth et al. 1998; Hewitt 2000; Hobæk 2002). A time span of approximately 8000 years since the last period of glaciations, in combination with the fact that zooplankton have moderate to good colonization abilities, should nevertheless be enough to experience a different distribution pattern for crustacean zooplankton- and fish species in the area of current interest (Hessen et al. 2006). The ability of dispersal for both crustacean zooplankton and fish might be restricted for several reasons though. Here, two physical migration constraints; connectivity between lakes, and a high mountain range in the west, are probably important when describing the restricted distribution pattern, both for zooplankton and fish, that we now can observe (figure 8). Many crustacean zooplankton species are globally distributed and may passively disperse by animal vectors or aerially (Cohen & Shurin 2003), however, the distance between lakes and pounds at a local scale, as well as to what extent the regional species pool is saturated or not, seems to be more important when describing dispersal patterns for crustacean zooplankton at larger spatial scales (Jenkins & Underwood 1998; Jenkins & Jr 1998; Cohen & Shurin 2003; Hessen et al. 2006). It has also been suggested that different taxonomical groups (i.e. crustaceans vs. copepods) have different colonization abilities due to large differences in features such as body and resting egg size, generation time and sexual versus asexual reproduction. Comparison across taxa done by Cohen et al. (2003) could not show any consistent differences between these groups though, instead species of both cladocerans and copepods ranged from highly effective to slow dispersers.

An alternative explanation for the distribution pattern that we observe for these lakes (figure 8) could be that lakes with high fish diversity brings with it selective predation pressure on larger and/or competitive superior crustacean zooplankton species, and that this in turn reduce competition and thus promotes species coexistence. To what extent predation may promote zooplankton diversity is still under debate (Mittelbach et al. 2004; D. O. Hessen, Faafeng, V. H. Smith, et al. 2006).

A previous study from 336 Norwegian lakes (Hessen et al. 2006) concluded that there were different dispersal abilities among zooplankton, and that this might reflect their current distribution, but also that some species more than others where regulated by intrinsic factors like production, predation, or competition. In my study, *Cyclops bohater*, *Cyclops vicinus*, and *Daphnia longiremis*, were found in less than three lakes (see figure 10), and are therefore considered to be geographically restricted. Whether they are geographically restricted due to low dispersal abilities, climatic constraints, or competitive exclusion is open for debate, however. Some of the small cladocerans and the large cladocerans and calanoid copepods found along the predation pressure gradient (axis 1, the east-west gradient in the ordination plot, see figure 11) may to a larger extent reflect productivity and predation patterns. Small cladocerans are known to appear in lakes with high predation pressure due to their competitive advantage through their small body size (e.g. *Bosmina longirotstris*, *Daphnia cucullata*, *Chydorus sphaericus*,), and the large cladocera and calanoid species are known to be found in lakes with low predation preassure (e.g. *Daphnia longispina*, *D. galeata*, *Heterocope saliens*, *Mixodiaptomus laciniatus*, *Arctodiaptomus laticeps*, etc).

The COMSAT study is based on a single sample (July) only. This means that the probability to encounter rare species, or species adapted to different seasons is limited, and thus the species encountered should not be regarded as a complete species list for the surveyed localities, but still being quite representative of the community composition.

# Resource use efficiency (RUE) of zooplankton

Zooplankton resource use efficiency is negative related to TOC concentration, which could be interpreted as if you have lower light you also have lower zooplankton resource use efficiency. This is probably an artefact of the longitudinal gradient though, where you have a strong correlation between longitude and TOC concentrations (see figure 4). This is supported by a slight negative effect from seston C:P on the zooplankton resource use efficiency. High TOC concentrations might have a negative effect on phytoplankton primary production due to its strong impact on light absorption and light attenuation (Carpenter et al. 1998; Karlsson et al. 2009), but lower light intensity should also decrease the C:P ratio in phytoplankton, and thus increase food quality for plankitvorous zooplankton (D. Hessen et al. 2002), and this in turn should have a positive effect on zooplankton resource use efficiency.

Zooplankton resource use efficiency is negatively related to both zooplankton and fish species richness, as well as to longitude. At first, this might look like a contradiction to the positive effect diversity has on primary production and recourse use efficiency reported, not only for phytoplankton, but also for higher organisms (Tilman et al. 1996; Ptacnik et al. 2008; Gamfeldt et al. 2013). This positive effect might not be directly transferable to the next trophical level though. E.g. increased phytoplankton diversity induced by light competition has been shown to also increase pigment diversity, thus the total amount of light that can be harvested for photosynthesis, and thereby enhance primary production and resource use efficiency (Maren Striebel et al. 2009). This has in turn been shown to increase the C:P ratio in the phytoplankton in accordance with the nutrient-light hypothesis (Urabe & Sterner 1996), and thereby decrease the quality of the food for the crustacean zooplankton (Andersen et al. 2004; Striebel et al. 2009). I therefore suspect there is daphnia dominance in the most western lakes in Norway, that this results in high RUE, and thus can explain why RUE is inverse correlated with species richness. The reason for this is three fold;

1) Larger daphnid species are typically to be found in lakes with low predation pressure (Dag pers. comment).

2) Phytoplankton community shifts to more edible species as lake productivity decreases (Lampert 1977; Watson and Kalff 1981; Hessen et al. 2006b).

3) Large species of daphnia are known to be the most effective filter feeders (McCauley and Kalff 1981).

This is also supported by the NMDS of zooplankton species richness (figure 11) where axis 1 indicates big calanoid copepodes in the west and small cladocerans in the east, a picture that typically reflects a gradient in predation pressure from fish. We can also see that larger species of both copepods and cladocerans are spread in both directions on axis 2. This pattern might indicate that this is a low-predation and low-production axis, and this fits well with the most western lakes in Norway.

These interpretations have to be taken with some precautions though! First, there is obviously some correlation between latitude, EPP and axis 2 that might contradict this interpretation. Environmental variables that correlate with each other should be identified, and be excluded according to their relevance such there are no correlating variables left, before superimposing the environmental variables on the NMDS plot. This can be done by running a PCA on the environmental variables. Second, a NMDS on fish species richness that makes it possible to correlate the NMDS axes from the zooplankton ordination with the NMDS axes from the fish ordination would have made the interpretation more robust. It would also be interesting to separate the cladoceran species, the calanoid copepods and the cyclopoid copepods from each other before simple linear regression analyses to see how they affect zooplankton biomass and zooplankton resource use efficiency separately. There was no time for this now, but this has to be considered in my further investigations.

# Conclusion

Zooplankton biomass seems to be driven by bottom-up effects, where TOC, and thus light, contributes negative. There was no obvious effect of zooplankton diversity or fish diversity on zooplankton biomass. There was a strong geographical gradient in zooplankton and fish species richness, both increased from the west to the east and from the north to the south. To which extent this reflects migration constraints, immigration history or confounding factors related to water properties is not settled. There was an inverse relationship between RUE and zooplankton species richness. One possible explanation to that can be that there is a hih dominance in the most western lakes by large daphnid species, and also by small edible phytoplankton species, and that this in combination with low seston C:P ratio consequently results in a high resource use efficiency.

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# Appendix

**Appendix table 1**: Surveyed lakes with related parameters.

| ID | Lake Name | Latitude | Longitude | ZDW (µg/L) | TOC (mg/L) | TN (mg/L) | TP (µg/L) |
|---|---|---|---|---|---|---|---|
| 170 | Gjersjøen | 59,790 | 10,775 | 32,73 | 6,898 | 1,28 | 9,8 |
| 180 | Øgderen | 59,714 | 11,413 | 121,58 | 6,944 | 0,3335 | 19,2 |
| 189 | Krøderen | 60,135 | 9,759 | 19,16 | 4,395 | 0,2501 | 3,55 |
| 191 | Rødbyvatnet | 59,582 | 10,487 | 91,32 | 6,652 | 0,9699 | 9,35 |
| 214 | Harasjøen | 60,682 | 11,992 | 338,62 | 9,613 | 0,3851 | 15,1 |
| 233 | Osensjøen | 61,176 | 11,888 | 13,72 | 7,6885 | 0,2842 | 3,05 |
| 236 | Rokossjøen | 60,787 | 11,441 | 23,81 | 11,81 | 0,3288 | 8,25 |
| 242 | Sør Mesna | 61,076 | 10,800 | 72,56 | 7,514 | 0,2543 | 6,7 |
| 252 | Vermundsjøen | 60,695 | 12,387 | 45,9 | 11,945 | 0,3595 | 9,25 |
| 258 | Gjønvatnet | 60,270 | 5,841 | 57,85 | 1,3 | 0,24 | 2 |
| 261 | Kalandsvatnet | 60,271 | 5,402 | 56,6 | 2,854 | 0,3494 | 3,8 |
| 264 | Myrkdalsvatnet | 60,812 | 6,471 | 37,62 | 0,954 | 0,08657 | 1 |
| 277 | Engsetdalsvatnet | 62,533 | 6,633 | 34,48 | 2,6555 | 0,2017 | 1,15 |
| 285 | Rotevatnet | 62,141 | 6,118 | 44,48 | 3,427 | 0,1704 | 2,55 |
| 288 | Vatnevatnet | 62,153 | 6,229 | 42,93 | 1,3135 | 0,1668 | 4,7 |
| 326 | Einavatnet | 60,538 | 10,653 | 25,31 | 5,5715 | 1,089 | 3 |
| 328 | Randsfjorden | 60,723 | 10,268 | 14,07 | 4,514 | 0,376 | 2,65 |
| 339 | Ringsjøen | 60,882 | 10,355 | 123,78 | 8,0215 | 0,5569 | 5,55 |
| 340 | Sæbuvatnet | 61,013 | 9,215 | 19,9 | 3,6585 | 0,3563 | 3,1 |
| 344 | Strondavatnet | 60,978 | 9,249 | 10,04 | 2,8325 | 0,3505 | 2 |
| 345 | Trevatna | 60,639 | 10,435 | 44,36 | 9,6795 | 0,3506 | 4,3 |
| 349 | Bogstadvannet | 59,971 | 10,618 | 20,85 | 7,026 | 0,3869 | 6,6 |
| 353 | Aspern | 59,147 | 11,684 | 51,68 | 8,539 | 0,8267 | 9,95 |
| 361 | Rødnessjøen | 59,532 | 11,626 | 54,11 | 9,1145 | 0,9793 | 12,2 |
| 363 | Rømsjøen | 59,701 | 11,844 | 10,04 | 6,6945 | 0,3952 | 1,2 |
| 374 | Edlandsvatnet | 58,763 | 5,871 | 64,21 | 2,6305 | 0,7918 | 3,85 |
| 378 | Hetlandsvatn | 59,175 | 6,109 | 277,11 | 2,3695 | 1,012 | 2,35 |
| 380 | Lutsivatn | 58,860 | 5,848 | 37,01 | 3,6215 | 0,9617 | 6 |
| 395 | Vostervatnet | 59,096 | 5,975 | 43,29 | 3,122 | 0,6077 | 3,6 |
| 404 | Jølstravatnet | 61,558 | 6,400 | 31,42 | 0,6647 | 0,2853 | 0,5 |
| 405 | Strynevatnet | 61,915 | 7,077 | 31,55 | 0,3441 | 0,1142 | 1,7 |
| 433 | Bandak | 59,402 | 8,230 | 13,17 | 2,588 | 0,1948 | 1,2 |
| 436 | Grungevatnet | 59,707 | 7,759 | 33,26 | 2,542 | 0,152 | 1,55 |
| 453 | Vinjevatn | 59,612 | 7,852 | 9,84 | 3,49 | 0,1655 | 1,05 |
| 481 | Åsrumvatnet | 59,163 | 10,058 | 66,72 | 7,1105 | 1,118 | 20,2 |
| 482 | Bergsvannet | 59,588 | 10,053 | 69,87 | 7,0695 | 0,3692 | 17,85 |
| 486 | Goksjø | 59,173 | 10,165 | 141,24 | 6,576 | 1,526 | 27,45 |
| 487 | Hallevatnet | 59,025 | 9,909 | 37,67 | 5,0125 | 0,7408 | 2 |
| 498 | Dagarn | 59,904 | 15,703 | 43,79 | 6,2165 | 0,2535 | 3 |
| 519 | Tærnan | 59,591 | 18,521 | 6,08 | 6,3915 | 0,3459 | 4,9 |
| 2252 | Rotnessjøen | 60,497 | 12,341 | 14,01 | 11,175 | 0,2817 | 4,55 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 2268 | Mylla | 60,244 | 10,591 | 10,27 | 4,114 | 0,2119 | 2,45 |
| 2312 | Femsjøen | 59,133 | 11,471 | 21,16 | 8,42 | 0,8249 | 7,45 |
| 2374 | Frøsjøn | 59,092 | 17,298 | 53,23 | 8,8315 | 0,4285 | 11,45 |
| 2678 | Torrsjøn | 58,978 | 12,114 | 12,99 | 7,619 | 0,3663 | 2,35 |
| 2870 | Visten | 59,630 | 13,397 | 58,5 | 4,859 | 0,2454 | 6 |
| 2872 | Stora Le | 59,322 | 11,794 | 13,52 | 5,253 | 0,5139 | 1,9 |
| 2875 | Næsræmmen | 60,034 | 14,137 | 18,73 | 7,6015 | 0,222 | 5,85 |
| 2878 | Rangsjøen | 60,824 | 12,508 | 84,02 | 7,365 | 0,2159 | 3,2 |
| 2887 | Tisjøn | 60,919 | 12,966 | 33,22 | 6,525 | 0,2106 | 4,55 |
| 2888 | Halsjøn | 60,864 | 12,311 | 23,7 | 12,275 | 0,2693 | 5,8 |
| 2899 | Jangen | 60,146 | 13,272 | 24,93 | 9,409 | 0,2441 | 5,25 |
| 3017 | Sør-Ælgen | 59,724 | 14,607 | 24,36 | 7,2185 | 0,2929 | 5,85 |
| 3019 | Møckeln | 59,304 | 14,538 | 38,49 | 7,5375 | 0,4738 | 12,6 |
| 3020 | Ljusnaren | 59,879 | 14,934 | 14,86 | 8,522 | 0,298 | 6,75 |
| 3025 | Halvarsnoren | 59,632 | 14,596 | 26,14 | 7,441 | 0,2895 | 5,4 |
| 3027 | Nætsjøn | 59,891 | 14,481 | 13,88 | 4,9925 | 0,1929 | 3,45 |
| 3029 | Ørlingen | 59,879 | 14,420 | 27,26 | 6,836 | 0,1894 | 6,7 |
| 3031 | Saxen | 59,774 | 14,410 | 6,18 | 5,6115 | 0,2528 | 4,85 |
| 3106 | Långbjørken | 59,768 | 15,952 | 68,94 | 9,503 | 0,3102 | 9,65 |
| 3160 | Skattungen | 61,194 | 14,945 | 5,85 | 7,5525 | 0,2328 | 4,25 |
| 3165 | Bæsingen | 60,161 | 16,389 | 14,53 | 6,107 | 0,2578 | 8,5 |
| 3167 | Runn | 60,531 | 15,673 | 51,88 | 7,063 | 0,4761 | 8 |
| 3185 | Stor Almsjøn | 60,878 | 13,208 | 7,93 | 12,545 | 0,2718 | 5,55 |
| 3189 | Dragsjøn | 60,993 | 13,599 | 61,39 | 10,78 | 0,2341 | 7,25 |
| 3201 | Milsjøn | 60,195 | 14,009 | 9,79 | 9,1175 | 0,2517 | 3,75 |
| 3220 | Norra Bredsjøn | 59,983 | 15,230 | 13,83 | 5,9425 | 0,2413 | 2,05 |
| 3384 | Hinsen | 60,682 | 16,074 | 37,26 | 5,492 | 0,2198 | 3,55 |
| 3397 | Storsjøn | 61,654 | 15,759 | 7,93 | 3,7675 | 0,1671 | 3,15 |
| 3399 | Grycken | 61,576 | 15,424 | 20,21 | 6,2985 | 0,2035 | 3,3 |
| 3516 | Holmsjøn | 62,410 | 15,313 | 19,21 | 5,8555 | 0,2022 | 3,1 |
| 3541 | Stornaggen | 62,267 | 15,971 | 48,87 | 7,1735 | 0,2127 | 4,7 |
| 5000 | Forssjøn | 58,954 | 16,264 | 90,2 | 12,895 | 0,9127 | 16,3 |
| 10000 | Hurdalsjøen | 60,376 | 11,041 | 53,39 | 3,7105 | 0,4097 | 1,6 |
| 10001 | Harestuvatnet | 60,193 | 10,712 | 29,86 | 4,06 | 0,3745 | 4,35 |

| ID | POC (µg/L) | POP (µg/L) | Chl a (µg/L) | EPP (MgC/m2/day) | Seston C:P |
|---|---|---|---|---|---|
| 170 | 381 | 6,6 | 8,82 | 1089 | 57,7 |
| 180 | 1093 | 12 | 31,12 | 1347,48 | 91,1 |
| 189 | 148 | 2,9 | 2,94 | 373 | 51,0 |
| 191 | 607 | 8,1 | 39,1 | 727 | 74,9 |
| 214 | 1218 | 11,8 | 33,65 | 930 | 103,2 |
| 233 | 151 | 3,3 | 3 | 136,16 | 45,8 |
| 236 | 683 | 8,7 | 23,67 | 287 | 78,5 |
| 242 | 348 | 5,6 | 6,93 | 316 | 62,1 |
| 252 | 569 | 5,4 | 7,25 | NA | 105,4 |
| 258 | 353 | 1,9 | 1,28 | 534 | 185,8 |
| 261 | 344 | 4,3 | 8,16 | 1151,31 | 80,0 |
| 264 | 198 | 3,1 | 3,54 | 743 | 63,9 |
| 277 | 228 | 2,5 | 3,34 | 569 | 91,2 |
| 285 | 120 | 2,3 | 2,26 | 555,25 | 52,2 |
| 288 | 139 | 2,9 | 3,46 | 719 | 47,9 |
| 326 | 217 | 3,8 | 6,06 | 507,72 | 57,1 |
| 328 | 149 | 2,8 | 3,46 | NA | 53,2 |
| 339 | 201 | 3,6 | 7,35 | 373 | 55,8 |
| 340 | 118 | 2,4 | 1,36 | 465 | 49,2 |
| 344 | 155 | 3 | 3,36 | 597 | 51,7 |
| 345 | 363 | 4,1 | 4,7 | 277 | 88,5 |
| 349 | 278 | 5,4 | 9,32 | 401,69 | 51,5 |
| 353 | 314 | 5,4 | 11,63 | NA | 58,1 |
| 361 | 374 | 7,1 | 12,33 | 430 | 52,7 |
| 363 | 197 | 2,4 | 2,87 | 362,62 | 82,1 |
| 374 | 332 | 5,1 | 6,72 | 955 | 65,1 |
| 378 | 68 | 3,6 | 6,42 | 917 | 18,9 |
| 380 | 430 | 6,6 | 14,33 | 779 | 65,2 |
| 395 | 337 | 4,6 | 4,52 | 588 | 73,3 |
| 404 | 85 | 2,2 | 2,2 | 652 | 38,6 |
| 405 | 91 | 3,6 | 2,8 | 929 | 25,3 |
| 433 | 156 | 2,4 | 3,88 | 297 | 65,0 |
| 436 | 133 | 2,9 | 2,46 | 543 | 45,9 |
| 453 | 126 | 2,5 | 1,74 | 270 | 50,4 |
| 481 | 612 | 9,9 | 15,07 | 1120 | 61,8 |
| 482 | 3371 | 16 | 120 | 1277 | 210,7 |
| 486 | 940 | 15 | 32,83 | 1292,98 | 62,7 |
| 487 | 170 | 2,8 | 3,44 | 312 | 60,7 |
| 498 | 342 | 4,4 | 6,27 | 678 | 77,7 |
| 519 | 363 | 3,8 | 2,72 | 716 | 95,5 |
| 2252 | 477 | 4,6 | 6,7 | 221,5 | 103,7 |
| 2268 | 349 | 4,7 | 10,5 | 647 | 74,3 |
| 2312 | 305 | 4,6 | 7,05 | 763 | 66,3 |
| 2374 | 655 | 7,1 | 11,97 | 1158 | 92,3 |
| 2678 | 292 | 4 | 11,63 | 527 | 73,0 |
| 2870 | 335 | 4,9 | 4,42 | 516 | 68,4 |

| | | | | | |
|---|---|---|---|---|---|
| 2872 | 110 | 2,2 | 2,2 | 305 | 50,0 |
| 2875 | 278 | 4,1 | 7,31 | 464 | 67,8 |
| 2878 | 203 | 4,7 | 4,48 | 247,26 | 43,2 |
| 2887 | 411 | 4,7 | 12,52 | 320 | 87,4 |
| 2888 | 569 | 4,9 | 7,95 | NA | 116,1 |
| 2899 | 365 | 4,1 | 6,06 | 237,71 | 89,0 |
| 3017 | 223 | 3,1 | 5,74 | 489 | 71,9 |
| 3019 | 652 | 9,5 | 45,04 | 1005,78 | 68,6 |
| 3020 | 256 | 3,7 | 4,37 | 401 | 69,2 |
| 3025 | 228 | 2,8 | 6,27 | 344 | 81,4 |
| 3027 | 241 | 3,4 | 5,93 | 328 | 70,9 |
| 3029 | 300 | 4,5 | 7,72 | NA | 66,7 |
| 3031 | 217 | 2,7 | 4,4 | 457 | 80,4 |
| 3106 | 571 | 7,2 | 20,48 | 694 | 79,3 |
| 3160 | 298 | 4,7 | 12,4 | 453 | 63,4 |
| 3165 | 503 | 7,8 | 17,16 | 587,93 | 64,5 |
| 3167 | 379 | 4,8 | 6,1 | 539 | 79,0 |
| 3185 | 246 | 5,5 | 10,9 | 210 | 44,7 |
| 3189 | 574 | 5,9 | 10,16 | 404,95 | 97,3 |
| 3201 | 246 | 2,9 | 4,83 | 267 | 84,8 |
| 3220 | 316 | 4,4 | 5,57 | 340 | 71,8 |
| 3384 | 340 | 3,1 | 3,24 | 424 | 109,7 |
| 3397 | 298 | 2,8 | 4,3 | 273 | 106,4 |
| 3399 | 250 | 3,6 | 6,73 | 488 | 69,4 |
| 3516 | 188 | 3,4 | 4,67 | 364 | 55,3 |
| 3541 | 316 | 3,6 | 6,4 | 415,03 | 87,8 |
| 5000 | 955 | 10,2 | 27,32 | 1414,54 | 93,6 |
| 10000 | 190 | 2,9 | 4,03 | 498 | 65,5 |
| 10001 | 276 | 4,1 | 4,5 | 457 | 67,3 |

**Appendix table 2**: Data bases for collected fish data:

Sweden

https://www.havochvatten.se/

http://www.viss.lst.se/

https://www.havochvatten.se/4.64f5b3211343cffddb280006920.html

Norway

http://www.artsdatabanken.no/frontpageAlt.aspx?m=2

**Appendix table 3**: Abbreviated and unabridged species names for zooplankton.

| Abr. | Species |
|---|---|
| dia.brac | *Diaphanosoma brachyurum* (Liév.)T |
| lim.fron | *Limnosida frontosa* Sars |
| hol.gibb | *Holopedium gibberum* Zaddach |
| cer.pulc | *Ceriodaphnia pulchella* Sars |
| cer.quad | *Ceriodaphnia quadrangula* (O.F.M.) |
| dap.cris | *Daphnia cristata Sars* |
| dap.cucu | *Daphnia cucullata* Sars |
| dap.gale | *Daphnia galeata* Sars |
| dap.lonr | *Daphnia longiremis* Sars |
| dap.lons | *Daphnia longispina* (O.F.M.) |
| bos.cor | *Bosmina coregoni* (Baird) |
| bos.lonr | *Bosmina longirostris* (O.F.M.) |
| bos.lons | *Bosmina longispina* Leydig |
| chy.spha | *Chydorus sphaericus* (O.F.M.) |
| pol.pedi | *Polyphemus pediculus* (Leuck.) |
| byt.long | *Bythoptrephes longimanus* Leydig |
| lep.kind | *Leptodora kindti* Focke |
| lim.macr | *Limnocalanus macrurus* Sars |
| aca.dent | *Acanthodiaptomus denticornis* (Wierz.) |
| eud.grac | *Eudiaptomus gracilis* Sars |
| eud.grao | *Eudiaptomus graciloides* (Lillj.) |
| arc.lati | *Arctodiaptomus laticeps* (Sars) |
| mix.laci | *Mixodiaptomus laciniatus* (Lillj.) |
| eur.lacu | *Eurytemora lacustris* (POPPE) |
| het.appe | *Heterocope appendiculata* Sars |
| het.sali | *Heterocope saliens* (Lillj.) |
| cyc.abys | *Cyclops abyssorum* |
| cyc.boha | *Cyclops bohater* |
| cyc.lacu | *Cyclops lacustris* |
| cyc.scut | *Cyclops scutifer* Sars |
| cyc.vici | *Cyclops vicinus* Uljanin |
| meg.giga | *Megacyclops gigas* (Claus) |
| meg.viri | *Megacyclops viridis* (Jur.) |
| dia.bibu | *Diacyclops bicuspidatus* (Sars) |
| mes.leuc | *Mesocyclops leuckarti* (Claus) |
| the.cras | *Thermocyclops crassus* (Fisch.) |
| the.oith | *Thermocyclops oithonoides* (Sars) |

**Appendix table 4**: Complete names for fish.

| **English** | **Latin** |
|---|---|
| Trout | *Salmo trutta* |
| Salmon | *Salmo salar* |
| Arctic char | *Salvelinus alpinus* |
| Common whitefish | *Coregonus lavaretus* |
| Grayling | *Thymallus thymallus* |
| Pike | *Esox lucius* |
| Perch | *Perca fluviatilis* |
| Ruffe | *Gymnocephalus cernuus* |
| Pikeperch | *Sander lucioperca* |
| Minnow | *Phoxinus phoxinus* |
| Stickelback | *Gasterosteidae* |
| European Eel | *Anguilla anguilla* |
| Burbot | *Lota lota* |
| Bleak | *Alburnus alburnus* |
| Roach | *Rutilus rutilus* |
| Orfe | *Leuciscus idus* |
| Dace | *Leuciscus leuciscus* |
| Bream | *Abramis brama* |
| Chub | *Leuciscus cephalus* |
| White beam | *Blicca bjoerkna* |
| Rudd | *Scardinius erythrophthalmus* |
| European smelt | *Osmerus eperlanus* |
| Vendace | *Coregonus albula* |
| Fourhorn sculpin | *Myoxocephalus quadricornis* |
| Tench | *Tinca tinca* |
| Carp | *Cyprinus carpio* |
| Crusian carp | *Carassius carassius* |
| European river lamprey | *Lampetra fluviatilis* |
| Eurpean brook lamprey | *Lampetra planeri* |
| European bullhead | *Cottus gobio* |
| Alpine bullhead | *Cottus poecilopus* |