Simon Ormestad Eid

Impact of whitefish invasion on Cladocera communities

A paleolimnological study

May 2019

Master's thesis

Master's thesis

2019

Simon Ormestad Eid

NTNU
Norwegian University of
Science and Technology
Faculty of Natural Sciences
Department of Biology

NTNU
Norwegian University of
Science and Technology

NTNU
Norwegian University of
Science and Technology

NTNU
Norwegian University of
Science and Technology

Impact of whitefish invasion on Cladocera communities

A paleolimnological study

Simon Ormestad Eid

Natural Resources Management
Submission date: May 2019
Supervisor: Sigurd Einum
Co-supervisor: Anders G. Finstad

Norwegian University of Science and Technology
Department of Biology

Acknowledgement

During my work at NTNU I owe many people my gratitude. First and foremost, I would like to thank my supervisors Sigurd Einum and Anders G. Finstad for their patience and feedback in the final stages of the thesis finalization. The help and guidance given by Hanna-Kaisa Lakka in the field and laboratory was invaluable during my work and she deserves all the praise she can get.

I would like to say my thanks to Thor Harald Ringsby's effort and dedication to Natural Resources Management and our study environment which have resulted in renewed interest for the issues concerning nature and humans interacting.

Finally, I would like to say thanks to all the great people I've meet here during my stay, they have made the experience of Trondheim a great place to live.

Simon

Abstract

Introduced species is shown to have effects upon the native populations both in experiments and in the study of ecosystems. Effort into understanding how anthropogenic translocations impacts and changes the freshwater communities is of great importance to be able to manage and conserve the ecosystem services and biodiversity. In order to understand the impacts of translocation of predators in freshwater systems, using paleolimnological methods have gained attention in order to study systems in an eco-evolutionary time frame. Whitefish (*Coregonus lavaretus*) is a specialized zooplanktivorous species which has been spread across Røros municipality during the settlement of the area during the initial mining industry. By comparing Cladocera abundance in lakes with whitefish presence and absence, we can gain understanding about the Cladocera zooplankton communities' response's to whitefish presence over a longer time frame. The finding in this study concludes that whitefish presence or absence does not explain the abundance for 12 out of 13 genera in the Cladocera community. For the one genus (*Alonella*) that experienced reduction in abundance due to whitefish presence, the directional change is contradictory to what the size efficiency hypothesis predicts. Previous short-term studies and experiments have revealed clear negative impacts on larger sized Cladocera. These finding give reason to believe that introduction of certain predators (whitefish) might not pose a direct threat to the prey communities abundance for the different genera found in Røros. Potential reasons to why this was the result is discussed. Further investigation into what affects the abundances of Cladocera's presence in invaded waters might reveal what constitutes successful responses to invasive effective zooplanktivorous species.

Abstrakt

Introduserte arter har blitt vist å ha effekter på lokal populasjoner både i eksperimenter og i studier av økosystemer. For å kunne ivareta biodiversitet og økosystemtjenester er økt forståelse av menneskelig påvirkning av ferkvann og de tilhørende økosystemene viktig. Paleolimnologiske metoder har fått økt oppmerksomhet med tanke på å kunne forstå effektene av invasive arter siden det tillater å studere systemene i et øko-evolusjonær tidsperspektiv. Sik er en spesialisert zooplanktivor art som har blitt spredt i Røros kommune etter at bosetninger ble etablert som et resultat av gruveindustrien. Ved å sammeligne Cladocera forekomster i innsjøer med sik fraværende og tilstedværende kan vi økte forståelsen av introduserte arters effekter på byttedyr sammfunn. Denne studien fant ingen effekt i forekomst for 12 av 13 analyserte slekter i ordenen Cladocera. En slekt (*Alonella*) viste en reduksjon som følge av sik, motsatt av hva størrelse effektivitet hypothesen predikerer. Tidligere studier og eksperimenter har vist at en reduksjon i større Cladocera arter forventes. Funnene presentert her gir grunn til å tro at sik ikke representerer en betraktlig trussel for forekomstene hos Cladocera. Potensielle forklaringer på hvorfor ingen betraktlige forskjeller blir observert til tross for sik tilstedeværesle eller fravær blir diskutert. Videre studier som kan forklare responsene hos Cladocera som følge av utsetting av sik annbefales.

Table of contents

Introduction

Freshwater ecosystems are important both directly and indirectly for human survival, but anthropogenic impacts may cause huge stress on these ecosystems. Exploitation of water, harvesting of fish, building of dams and anthropogenic translocation of species have all increased during the 20th century (Strayer and Dudgeon 2010). All these factors represent issues regarding maintaining biodiversity and continued existence of relatively undisturbed freshwater ecosystems. Human ability and will to spread species across ecosystem pose issues for the receiving ecosystems communities. Active translocation of predators could outcompete species with similar niche or result in negative impact on the abundance of the native prey communities or in local extinction. Whitefish (*Coregonus lavaretus*) is widespread across Europe, with native populations in southern- Norway and parts of northern- Norway. During the establishment of the mining community in Røros, whitefish was introduced to several water bodies (Korsen 2004). Whitefish preys actively on Cladocera, especially during late summer and early fall when they are most abundant, both in the littoral and pelagic zone (Tolonen 1997, Amundsen 2010, Sandlund et al. 2010). Cladocera are widespread and can be found in almost any freshwater habitat (Forró et al. 2008), most Cladocera are filter-feeders that feeds upon bacteria, algae, ciliates, rotifers and copepod nauplii (Korhola and Rautio 2001). A reduction in abundance of larger sized Cladocera is expected due to the presence of and effective visual predator due to selective feeding (Brooks and Dodson 1965), subsequently an increase in abundance of smaller sized Cladocera is expected due to the availability of resources that are not consumed by larger competitive Cladocera. The opposite is expected for lakes without an effective visual planktivorous predator. This outcome is in congruence with optimal foraging theory which predicts that a predator's feeding behavior will optimize net energy intake and therefore shape prey preference (Stephens 2008). The effect of optimal foraging theory and size selective hypothesis will therefore have effects upon the community level resulting in direct changes in abundance of certain Cladocera taxa favored by the predator. In experiments (days to years) and studies of lakes after introduction of whitefish, it is observed that it preys upon larger Cladocera speices (Hanazato et al. 1990, Berg et al. 1994). By studying the presence of whitefish and the effect on Cladocera communities, especially by investigating freshwater systems that have experienced invasion over a longer time period we would expect stronger effects, that being a strong negative effect in abundance of Cladocera taxa that are large sized relative to other Cladocera, it is also expected that certain genera will not be

associated with lakes where whitefish is present. Utilizing that Cladocera remains preserve well in the sediment allows for removing among and within year variation when collecting and comparing the community data. The method assumes that all remains preserve quantitively equally for all taxa, allowing comparison of the top sediment of lakes with whitefish present versus lakes with absence, revealing the effect of whitefish translocation and the effects upon the abundance of the different Cladocera taxa.

Materials and Methods

Study area

Sixteen lakes from Røros municipality, Norway were sampled and analyzed (figure 1). All lakes are located between 623 and 751 M.A.S.L and they cover an area between 0.037 km^2 and 15.7322 km^2 (table 1). Eight lakes are without whitefish, while the remaining eight have whitefish present, this is a result of lug flume that allowed connectivity between Håelva and Femunden, as well as translocation during the early 20th century (Korsen 2004). Additional detailed information about locations can be found in table 1.

Figure 1 Map showing all sampling locations marked with an x, map made with online map construction service provided by norges vassdrags- og energidirektorat.

Table 1, Fish data and abiotic information for all sampled lakes

Lakename	Fish presence		Abiotic information				
	Whitefish	Fish Community	Area(km^2)	WaterBodyID	Meters above sea level	Latitude	Longitude
Abbortjonna	No	Brown trout	0.0215	140171	665	62.426043	11.863968
Dalstjonna	Yes	Brown trout	0.1754	35396	629	62.530252	11.476555
Feragen	Yes	Pike, Eurasian minnow, Brown Trout, Artic charr	15.7322	127	654	62.553380	11.868751
Gjettjonna	No	*	0.1426	35369	623	62.566547	11.392367
Gubbtjonna	Yes	Burbot, Perch, Brown trout	0.051	35445	656	62.469494	11.793116
Harsjoen	Yes	Burbot, Brown trout, Artic charr	1.4298	247	751	62.573382	11.656854
Korssjoen	No	Pike, Burbot, Brown trout	8.1853	1359	759	62.452792	11.530222
Langen	Yes	Burbot, Eurasian minnow, Brown trout, Artic charr, Grayling	0.7734	35338	749	62.601313	11.707582
Langesjoen	No	Pike, Perch, Brown trout, grayling	0.056606	35516	688	62.427561	11.855158
Oksloken	No	Brown trout	0.0075	140001	658	62.460635	11.813552
Olaloken	No	Brown trout	0.0122	139978	657	62.467540	11.794377
Ormkastjonna	No	Pike	0.037	139979	655	62.466712	11.787776
Rismottjonna	Yes	Brown trout, Pike, Perch, Eurasian minnow	0.5951	35386	623	62.540510	11.451635
Roragen	Yes	Pike, Burbot, Perch, Eurasian minnow, Brown trout	1.3448	177	673	62.579607	11.811254
Storhittersjoen	Yes	Burbot, Eurasian minnow, Artic charr	1.1449	246	721	62.605379	11.637403
Storkrokattjonna	No	Perch	0.0776	35529	679	62.422567	11.875004

Lakenames are anglicized when needed, fish data are gathered from NINA and artsdatabanken, M.A.S.L, area and WaterBodyID are gathered from Norges Vassdrag- og Energi-direktorat. Latitude and longitude are given in WGS 84 format. For Olaloken no accurate measurement for M.A.S.L was obtainable, therefore it is an approximation listed in the table. * denotes rotenone treatment in 2017.

Field extraction of sediment

Sediment sampling was done in October 2017 and January 2018. October sampling was performed from a boat, whereas the January sampling was done through the ice. Sediment was extracted with a messenger operated gravity corer (kajak 13.030). For both sampling events attempts were made to locate the deepest part of the lake using an echosounder to ensure the most representative sample of the Cladocera communities. Remains from littoral species have been shown to integrate into the pelagic benthos sedimentation (Frey 1988). The corer was lowered into the lake and allowed to penetrate and sink into the benthos sediment before remote sealing ensured that the core could resurface. Resurfaced cores were sealed in the bottom and top with a rubber bung and transported and stored vertically. During January low temperatures would destroy the surface-water interface during transportation due to ice formation in the water column of the core. In accordance to Tomkins et al. (2008) water was removed from the core leaving 2-3 cm of water left to preserve water-sediment interface, sodium polyacrylate was added to the water, forming a gel allowing transportation and storage in below 0 Celsius conditions without ice formation.

In accordance with the law of superposition the top of the core should hold the most recent Cladocera remains. Core extraction followed the criteria's of Hvorslev (1949) : (1) no disturbance of structure, (2) no change in water content or void ratio, (3) no change in constituent or chemical composition. Two cores from each lake was extracted to ensure satisfaction of Hvorslev's criteria's if unforeseen events would happen. Cores was transported back to laboratory and stored in cooler (5 Celsius degrees) until segmentation.

Slide preparation in laboratory

To allow for analysis of the Cladocera remains in the sediment, vertical extruding and segmentation was performed with a piston rod and fraction tray as supplied by KC Denmark A/S. The core was segmented into 1 cm length cakes, except the first 0.5 cm. The 1 cm segments were stored in plastic bags and weighted. Two subsamples were taken from each lake at a depth of 0.5-1.5 cm, before extraction of the subsample's homogeneity was ensured by kneading of the sediment. This depth was chosen due to least amount of disturbance and lower water content compared to 0.0-0.5 cm depth, the sample depth of 0.5-1.5 cm represents the current assemblage of Cladocera's. Sediment subsamples for dry sediment analysis filled a 2.35 mL Eppendorf tube and the mass of the sediment was weighed. Covering the Eppendorf tube was plastic film perforated to allow water evaporation. Tubes were freeze-dried for 48 hours, then weight was measured again allowing for calculation of water content.

The second sample was prepared for microscope analysis. Following methods described in Atlas of Cladocera by Szeroczyfiska (2007), but with minor adjustments.

A 1 mL subsample was extracted with a 10 mL syringe and put in 250 mL beakers together with 125 mL of 10 % potassium hydroxide, The beaker was then kept at 55 Celsius degrees in a water bath for 25-30 minutes resulting in deflocculation of the sediment, but no reaction with the chitinous Cladocera remains. Stirring was done occasionally to ensure all the sediment got to react with KOH. Water (approximately 150 mL) was added to stop the reaction. The content was then sieved through a 51 microns sieve, the resulting sample put in a 15 mL centrifuge tube and centrifuged at 3100 revolutions per minute for 10 minutes. After centrifuging, water was removed and 0.6 mL 96% ethanol was added and mixed with the sediment to conserve remains during storage.

0.1 mL of the sediment-ethanol mixture was placed on microscope slides with two drops of heated liquid glycerol-safranin to allow for easier identification of Cladocera remains. Cover glass was added on top. 4 slides were prepared for each lake, however, due to lack of sediment after dehydration only 3 slides where prepared from the sample from Ormkastjonna.

Identification of Cladocera remains where done with a light microscope with 200x magnification, and morphological details where studied using 400x magnification. Remains were only counted once by following a pattern horizontally and moving the view one view distance for each move

vertically. All body parts were counted, the highest number of any body part of a genera or species was used to determine the total number of individuals in a slide. Remains where determined to lowest taxonomical levels possible in accordance to Szeroczyfiska (2007) and Korosi and Smol (2012). See appendix for examples of remains found.

Statistical analysis

Two types of statistically analysis was performed, indicator spices analysis (ISA) and generalized linear models. ISA was performed in order to see if any genera was associated with lakes with or without whitefish. Analysis was done at the genus level since not all remains was determined at speices level.

Data analysis and visualization utilized RStudio (version 1.0.153) with packages ggplot2 (Wickham 2016), nlme (Pinheiro J 2017) and dplyr (Wickham 2018).

Indicator species analysis

Indicator species analysis (Dufrêne and Legendre 1997) was performed identifying if there was a match between the occurrence of certain taxa and whitefish presence or absence. Analyses were performed with the R-package vegan (Oksanen 2019). A genus matrix was constructed with quantity given as average number of individuals per gram sediment (averaged across slides). The matrix was then multiplied with a vector containing 2 values denoting presence/absence of whitefish. Calculation of proportional abundance and proportional frequency, then multiplying these values giving an indicator value (IV). The highest IV for each genus is kept across groups, statistical significance is determined by Monte Carlo method where 999 permutations were performed. See table 2 for indicator values and associated p-values.

GLM mixed effect with offset

The response of each individual genera to whitefish presence or absence was analyzed using generalized linear models (GLM) including a mixed effect and offset. Seven genera were excluded from the analysis due to being only found in one lake. The global model (equation 1) included abundance (counts) of the focal genus of the sample offset by total abundance of Cladocera in the sample as dependent variable, and lake area and presence or absence of whitefish as predictor. Lake was used as random factor. Poisson distribution was assumed due to the nature of it being count data, therefore it is log linked.

$$\frac{Log(y)}{\frac{Log(Y)}{100}} = \beta_0 + X_1\beta_1 + X_2\beta_2 + \gamma + \varepsilon \qquad \text{(Equation 1)}$$

Here, log(y) denotes the number of individuals per gram dry sediment for a given genus, Log(Y)/100 is total number of individuals per gram sediment for all genera observed in one lake, divided by 100 to allow for easier interpretation of results. The offset allows adjusting for sampling effort for better comparison due to unequal sedimentation rates in the different lake bodies since catchment areas differ. β_0 denotes the intercept. $X_1\beta_1$ denotes the area of the lake in km^2, normalized to deviation from mean area of all lakes to ease interpretation. $X_2\beta_2$ denotes the effect of whitefish presence. ε are residuals from the model. γ is the random effect (intercept) of lake.

Results

Here, I present analysis from the indicator spices analysis (ISA) and generalized linear models with mixed effect and offset (GLM). ISA did not reveal any statically significant results; however, one genus is of interest biologically and is in accordance with earlier literature. GLM analysis resulted in null model for 7 genera due to having the lowest AIC values, resulting in reverting back to the null hypothesis, no effect of whitefish or area of lake. Five of the genera had best explanatory model with whitefish, area square km or area square km + whitefish, but due to ΔAIC value<5 when comparing best model and null model for 4 of the genera, it was determined to select null model due to parsimony. This is done in accordance with the recommendations by Burnham et al. (2011).
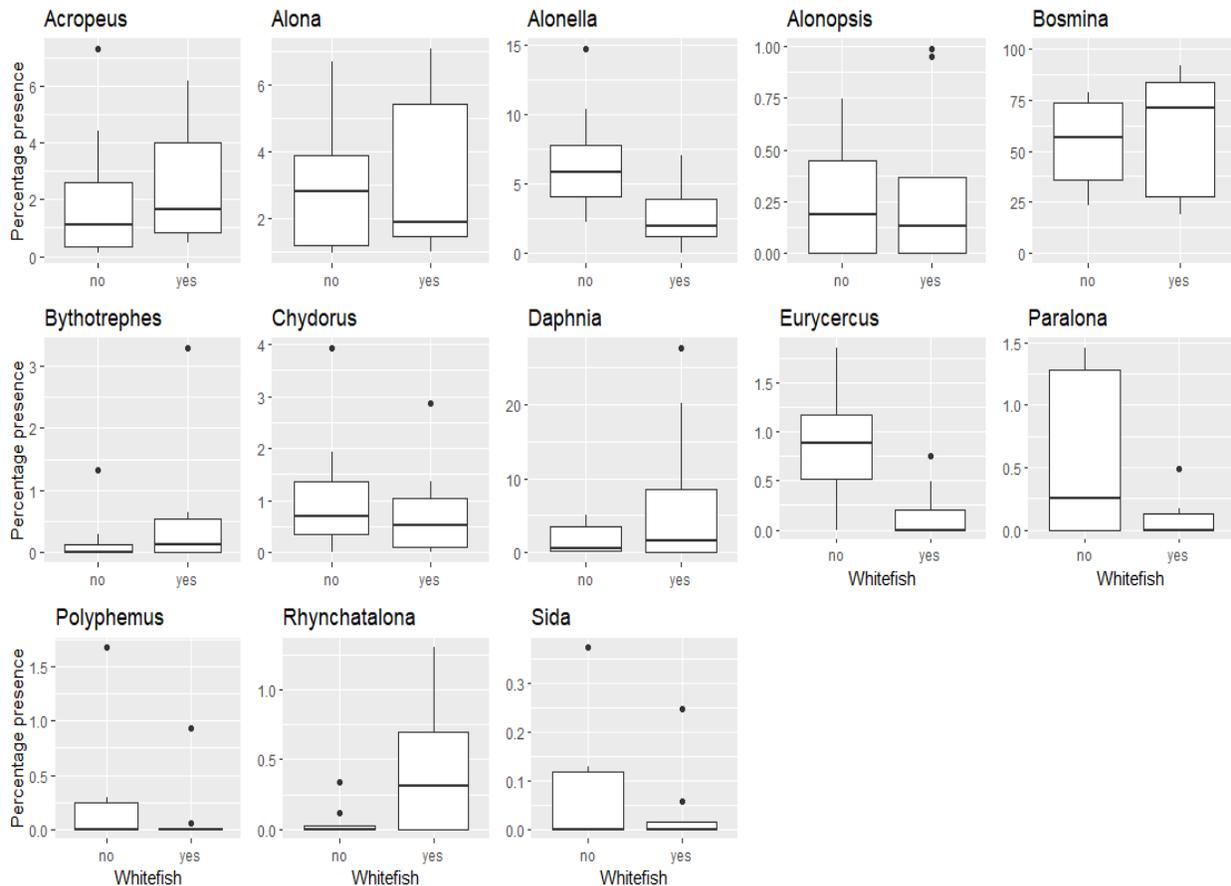

Figure 2, Percentage presence of 13 genera comparing lakes with and without whitefish, with mean, 95% confidence interval and outliers shown (dots). Y-axis for different genera have unequal scale.

Indicator Species Analysis results

There were no statistically significant results of the indicator species analysis, the low association values and high p-values for all taxa expect *Polyphemus* is attributed to the fact that they are only observed in one lake each (table 2). *Polyphemus* have an association value of 0.643 and p-value of 0.175, though not statistically significant, it gives indication that it is associated with lakes without whitefish. The strictness of the test will not give statistically significant p-values if the genus is found in lakes of different categories (presence/absence of whitefish), indicating that none of the genera observed are strictly connected to either whitefish absence or presence.

Table 2, Indicator species analysis table

Lakes without Whitefish		
Genus	Association	p-value
Polyphemus	0.643	0.175
Camptocercus	0.333	1
Diaphanosoma	0.333	1
Disparalona	0.333	1
Holopedium	0.333	1
Lakes with Whitefish		
Latona	0.378	0.412
Monospilus	0.378	0.412

Indicator species analysis at taxonomic level genus, association indicates how strongly linked a genus is to lakes with absence/presence of whitefish, a value of 1 denotes presence in all lakes.

GLM results

Out of the 20 genera, 13 genera were analyzed with GLM as described in methods. The area of the lake was determined to be the best model for 2 genera (*Paralona* and *Polyphemus*). For *Acropeus* and *Eurycercus* the best model was determined to be the model with only whitefish, however since ΔAIC value where <5 compared to the null model in all of the cases listed above, there is little support in keeping these models as the best explanation since they contains more explanatory variables. Therefore, the model with area or whitefish for the aforementioned models are discarded. Whitefish + area was the best explanatory model for *Alonella*, residuals were inspected by checking residuals for normal distribution and shown to be a good fit.

The number of individuals was predicted to be as following in lakes without whitefish for *Alonella* $=2.11(\pm0.21SE)-0.27LakeArea(\pm0.053SE$, z-value = 10.08, -5.04, p-value = <0.001, <0.001) for the average lake size it is expected 8.24≈8 individuals per 100 total individuals.

In lakes with whitefish number of individuals is expected to be =0.65(±0.30SE)-0.27LakeArea(±0.053SE, z-value = 4.67, -5.04, p-value = <0.001, <0.001), back transformed it is estimated to be 1.92 ≈2 individuals per 100 total individuals. This represents a 77% decrease in number of individuals for the average lake size when whitefish is present.

In conclusion only one genus showed a response to the presence of whitefish and area of lake, *Alonella* abundance was predicted to be reduced due to both predictors.

Table 3, Model selection table for 13 genera with tested models

Taxon	ΔAIC			
Genus	Area + Whitefish	Area	Whitefish	-1
Acropeus	2.2	1.0	0.9	**0.0**
Alona	4.0	2.0	2.0	**0.0**
Alonella	**0.0**	11.4	20.7	26.2
Alonopsis	2.0	0.1	2.0	**0.0**
Bosmina	2.3	0.6	2.0	**0.0**
Bythotrephes	1.9	2.1	0.0	**0.2**
Ceriodaphnia	4.0	2.0	2.0	**0.0**
Chydorus	3.1	1.8	1.5	**0.0**
Daphnia	2.9	1.0	1.9	**0.0**
Eurycercus	1.8	5.0	0.0	**3.7**
Paralona	0.8	1.0	0.0	**1.0**
Poly7phemus	1.9	0.0	3.0	**1.2**
Rhynchatalona	0.6	2.8	0.0	**0.8**

Comparison of models for each genus based on Akaike information criteria, values given relative to lowest AIC value. -1 is model with just intercept. Response for *Alonella* is in the text (See GLM results). Numbers in bold shows model selected based on AIC value and parsimony.

Discussion

Earlier findings show that presence of an invasive vertebrate predator have negative effects upon the larger sized zooplankton spices, this has been shown in lake experiments and mesocosm setups (Elser and Carpenter 1988, Hanazato and Yasuno 1989), and the effect of introducing whitefish have resulted in decrease of larger Cladocera spices (Hanazato et al. 1990, Berg et al. 1994). The findings in this study does not find lower abundance of larger Cladocera in lakes with whitefish compared to uninvaded lakes, the only taxa that had a response was *Alonella* which constitutes the smallest spices in the order Cladocera (Fryer 1968). This is contradictory to what is predicted due to predation by the size efficiency hypothesis, were larger prey spices are expected to decrease in abundance.

As seen in figure 3 there are large variation in abundance for most of the taxa found in the lakes, but *Bosmina* dominates. Nykänen et al. (2009) made a comparison of sediment and traditional zooplankton sampling counts that showed that certain species and genera conserved better in the sediment compared to others, *Bosmina* remains was shown to conserve well in contrast to *Daphnia*. Therefore, some bias due to how remains conserve are expected. In the study of how microfossils preserved in the sediment, Rautio (2000) concluded that caution should be exercised when looking at few genera or species. Since 13 genera was analysed in the GLM and all lakes is assumed to have equal preservation of remains for each genus, this allows for comparison and observing the predicted effect.

There are fewer studies concerning the effect upon the prey community due to a predator presence over a longer time period. Findings concerning *Brythotrephes longimanus* effect on zooplankton community found evidence for larger species diversity in lakes were its existence had occurred over a longer time period compared to newly invaded lakes (Kelly et al. 2013). These findings complicate the issue of a predator's immediate effect after invasion compared to long-term effects. Prey naiveté, lack of morphological and behavior adaption could explain strong reduction of abundance of certain taxa in the short term (Park 2004), but plasticity and evolutionary responses could allow for recovery in the long term. The results from this study indicates that the taxa observed and their abundance when comparing lakes did not show a trend in accordance to what the size efficiency hypothesis would predict.

Phenotypic plasticity allows for expression of different phenotypes in relationship to varying environmental pressures. This has been shown in *Daphnia galetea* in pond and experimental setups, where a spine-length to body ratio increased with *Chaoborus* presence (Fuji 2007). Due to predator presence, *Daphnia longispina* have been shown to swarm during the day as a way to minimize the chance of becoming prey to *Chaoborus* (Vetti Kvam and Kleiven 1995). Fewer studies concerning behavioral and morphological adaptations in Cladocera due to a vertebrate predator exists, but diel vertical migration due to kairomone concentration in experiments with *Daphnia* shows increased diel vertical migration with increased kairomone concentration from a vertebrate predator (Loose and Dawidowicz 1994). For daphniids, both morphological and behavioral adaptation help to reduce the chance of mortality, showing that different responses exist to increased predator pressure. The effect of introducing whitefish in Lake Pyhäjärvi in Finland showed a decrease in carapace length for *Bosmina coregoni* (Salo et al. 1989). Life history responses alteration due to predation is shown to take place, earlier maturation and increased investment in offspring could allow for compensation due to predator presence, these life history changes are often correlated with size selection. Weider and Pijanowska (1993) found for *Daphnia magna* that clone individuals were smaller at first reproduction with a vertebrate planktivorous present compared to control or invertebrate (*Chaoborus*) treatment as in accordance with the size selectivity hypothesis. Langeland and Nøst (1995) showed that stomach contents of Cladoceras for whitefish was significant larger compared to the environment, but it preys on both larger and small Cladocera species. This indicates that prey is selected based upon relative size, resulting in a shift towards smaller sized individuals for each species, but possibly not resulting in extinction locally but resulting in a shift towards smaller body size for all species over an eco-evolutionary time period. Predator-induced diapause has been shown to take place when kairomones were added to tanks of *Daphnia magna*, control tanks had only animals producing eggs parthenogenic (Slusarczyk 1995).

Even if extinction takes place after a predator is introduced, recolonization from other surrounding lakes could take place. Cladocera zooplankton has been shown to recolonize, disperse and settle in new waterbodies, even for newly created artificial lakes (Louette and De Meester 2005). The same has been observed in mesocosm experiments where empty tanks was settled by several Cladocera species due to translocation by wind (Cáceres and Soluk 2002). ISA showed for

Polyphemus that it was associated (0.643) with lakes where whitefish is absent, the only species belonging to this genus is the species *pediculus.* It inhabits mainly the littoral zone but is also found pelagic and is large sized (0.8-1.7 mm). It was found in four lakes without whitefish, while it was only found in one lake with whitefish. This gives some indication that it might not thrive under the predation pressure from whitefish, or that it is not an effective predator in competition with whitefish. The model selection for GLM resulted in the null model, therefore it was estimated no loss in the number of individuals due to the whitefish presence for *Polyphemus.* The GLM analysis showed that *Alonella* had a predicted reduction in number of individuals by 74% due to whitefish presence, from an estimated 8 individuals per 100 to 2 individuals per 100 for an average lake size area. *Alonella* is the smallest Cladocera genus found in Norway and they are littoral scrapers (Fryer 1968). Cyclopoid copepods and small-bodied Cladocera was shown to be an important part of larvae diet for *Coregonus clupeaformis* (Hoyle et al. 2011), less conclusive but similar results was observed by Hart (1931) indicating that whitefish in the larvae stage could change the abundance of *Alonella*.

In addition to whitefish larvae, Andersson (2015) showed that densely raked whitefish or small sized individuals had zooplankton stomach content that were smaller compared to less densely raked or larger whitefish, but there was no constraint in the maximum prey size for densely raked morphs, indicating that morphology of the predator is important when determining the effect upon the prey community.

Earlier experience with a predator could ensure that adaptation is already present in the prey community and they are less vulnerable to introduction of an effective zooplanktivorous. In four of the sampled lakes, whitefish was present with artic charr (*Salvelinus alpinus*). Cladocera make up a large part of diet composition for both whitefish and artic charr (Sandlund et al. 2010). This highlights that even if whitefish is introduced and outcompetes artic charr (Eloranta et al. 2011) anti-predator behavior and adapted life-history as earlier maturation might already be present in the Cladocera communities and therefore the effect of an invasive predator might not pose a great threat. Ricciardi and Atkinson (2004) meta-analysis revealed that "the magnitude of an aquatic invader's impact is related to the invader's taxonomic distinctiveness within the recipient community". This further emphasizes that if freshwater systems prey communities have

experience with predators that show similar behavior and prey utilization, they will more likely have adapted certain morphological or behavioral anti-predator responses dampening the effect of an invasive predator.

All the responses to an invasive predator discussed above could help preserve the Cladocera communities and help explain the rather large variation in abundance for the different taxa.

Conclusion

Only one genus was found to respond to whitefish presence or absence. *Alonella* constitutes the smallest genus of the Cladocera's, but it was found to decline due to whitefish presence. This is contradictory to what the size efficiency hypothesis predicts, and suggests that whitefish invasions not had negative impacts on larger sized Cladocera in Røros. The discussion highlighted the possible responses that might result in no difference in invaded lakes when compared to uninvaded lakes. Investigating the deeper parts of the sediment and comparing abundances of the different Cladocera taxa before and after whitefish introduction could reveal if the abundance has been stable. This will help understanding the idiosyncratic responses of each Cladocera lake community. In addition, studying the morphology of the whitefish in the different invaded lakes as well as their feeding preference during the larvae stage may shed further insights into the question of why *Alonella* was found to decline.

References

Amundsen, P., Knudsen, R., & Bryhni, H. T. 2010. Niche use and resource partitioning of arctic charr, european whitefish and grayling in a subarctic lake. Hydrobiologia **1**:3-14.

Andersson, E. 2015. Adaptive trait utility in the feeding apparatus of European whitefish (Coregonus lavaretus).

Berg, S., E. Jeppesen, M. Søndergaard, and E. Mortensen. 1994. Environmental effects of introducing whitefish, Coregonus lavaretus (L.), in Lake Ring. Pages 71-79 *in* E. Mortensen, E. Jeppesen, M. Søndergaard, and L. K. Nielsen, editors. Nutrient Dynamics and Biological Structure in Shallow Freshwater and Brackish Lakes, Dordrecht.

Brooks, J. L., and S. I. Dodson. 1965. Predation, Body Size, and Composition of Plankton. Science **150**:28-35.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology **65**:23-35.

Cáceres, C. E., and D. A. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia **131**:402-408.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species:the need for a flexible assymmetrical approach. Ecological Monographs **67**:345-366.

Eloranta, A. P., A. Siwertsson, R. Knudsen, and P.-A. Amundsen. 2011. Dietary plasticity of Arctic charr (Salvelinus alpinus) facilitates coexistence with competitively superior European whitefish (Coregonus lavaretus). Ecology of Freshwater Fish **20**:558-568.

Elser, J. J., and S. R. Carpenter. 1988. Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. Oecologia **76**:148-154.

Forró, L., N. M. Korovchinsky, A. A. Kotov, and A. Petrusek. 2008. Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. Hydrobiologia **595**:177-184.

Frey, D. G. 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. Journal of Paleolimnology **1**:179-191.

Fryer, G. 1968. Evolution and Adaptive Radiation in the Chydoridae (Crustacea: Cladocera): A Study in Comparative Functional Morphology and Ecology. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences **254**:221-385.

Fuji, K. H., T. Oda, S. 2007. Change in phenotypic plasticity of a morphological defence in Daphnia galeata (Crustacea: Cladocera) in a selection experiment. Journal of Limnology **66**.

Hanazato, T., T. Iwakuma, and H. Hayashi. 1990. Impact of whitefish on an enclosure ecosystem in a shallow eutrophic lake: selective feeding of fish and predation effects on the zooplankton communities. Hydrobiologia **200**:129-140.

Hanazato, T., and M. Yasuno. 1989. Zooplankton community structure driven by vertebrate and invertebrate predators. Oecologia **81**:450-458.

Hart, J. L. 1931. The spawning and early life history of the whitefish, Coregonus clupeaformis (Mitchill), in the bay og Quinte, Ontario. Contributions to Canadian Biology and Fisheries **6**:165-214.

Hoyle, J. A., O. E. Johannsson, and K. L. Bowen. 2011. Larval Lake Whitefish abundance, diet and growth and their zooplankton prey abundance during a period of ecosystem change on the Bay of Quinte, Lake Ontario. Aquatic Ecosystem Health & Management **14**:66-74.

Hvorslev, M. J. 1949. Subsurface exploration and sampling of soils for civil engineering purposes. American Society of Civil Engineers,:521.

Kelly, N. E., N. D. Yan, B. Walseng, and D. O. Hessen. 2013. Differential short- and long-term effects of an invertebrate predator on zooplankton communities in invaded and native lakes. Diversity and Distributions **19**:396-410.

Korhola, A., and M. Rautio. 2001. Cladocera and Other Branchiopod Crustaceans. Pages 5-41 *in* J. P. Smol, H. J. B. Birks, and W. M. Last, editors. Tracking Environmental Change Using Lake Sediments: Volume 4: Zoological Indicators. Springer Netherlands, Dordrecht.

Korosi, J. B., and J. P. Smol. 2012. An illustrated guide to the identification of cladoceran subfossils from lake sediments in northeastern North America: part 1—the Daphniidae, Leptodoridae, Bosminidae, Polyphemidae, Holopedidae, Sididae, and Macrothricidae. Journal of Paleolimnology **48**:571-586.

Korsen, I. 2004. Ferskvannsfisk - problemarter i Sør-Trøndelag. Fylkesmannen i Sør-Trøndelag.

Langeland, A., and T. Nøst. 1995. Gill raker structure and selective predation on zooplankton by particulate feeding fish. Journal of Fish Biology **47**:719-732.

Loose, C. J., and P. Dawidowicz. 1994. Trade-Offs in Diel Vertical Migration by Zooplankton: The Costs of Predator Avoidance. Ecology **75**:2255-2263.

Louette, G., and L. De Meester. 2005. High Dispersal Capacity of Cladoceran Zooplankton in Newly Founded Communities. Ecology **86**:353-359.

Nykänen, M., K. Vakkilainen, M. Liukkonen, and T. Kairesalo. 2009. Cladoceran remains in lake sediments: a comparison between plankton counts and sediment records. Journal of Paleolimnology **42**:551-570.

Oksanen, F. G., B. Friendly, M. Kindt, R. Legendre, D. Solymos, P. O'Hara, B. Simpson, G. Szoecs. . 2019. vegan: Community Ecology Package. R package version 2.5-4.

Park, K. 2004. Assessment and Management of Invasive Alien Predators. Ecology and Society **9**.

Pinheiro J, B. D., DebRoy S, Sarkar D. 2017. _nlme: Linear and Nonlinear Mixed Effects Models_.

Rautio, M. S., S. Korhola, A. 2000. Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. Journal of Limnology **59**:81-96.

Ricciardi, A., and S. K. Atkinson. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters **7**:781-784.

Salo, J., M. Walls, M. Rajasilta, J. Sarvala, M. Räsänen, and V.-P. Salonen. 1989. Fish predation and reduction in body size in a Cladoceran population: palaeoecological evidence. Freshwater Biology **21**:217-221.

Sandlund, O. T., J. Museth, T. F. Næsje, S. Rognerud, R. Saksgård, T. Hesthagen, and R. Borgstrøm. 2010. Habitat use and diet of sympatric Arctic charr (Salvelinus alpinus) and whitefish (Coregonus lavaretus) in five lakes in southern Norway: not only interspecific population dominance? Hydrobiologia **650**:27-41.

Slusarczyk, M. 1995. Predator-induced diapause in daphnia. Ecology **76**.

Stephens, D. W. 2008. Optimal Foraging Theory. Pages 2561-2566 *in* S. E. Jørgensen and B. D. Fath, editors. Encyclopedia of Ecology. Academic Press, Oxford.

Strayer, D. L., and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society **29**:344-358.

Szeroczyfiska, K. S., K, K. 2007. Atlas of Subfossil Cladocera from Central and Northern Europe.

Tolonen, A. 1997. Size-specific food selcetion and growth in benthic whitefish, *Coregonus lavaretus*(L.) in a subarctic lake. Boreal Environmental Research.

Tomkins, J. D., D. Antoniades, S. F. Lamoureux, and W. F. Vincent. 2008. A simple and effective method for preserving the sediment–water interface of sediment cores during transport. Journal of Paleolimnology **40**:577-582.

Vetti Kvam, O., and O. T. Kleiven. 1995. Diel horizontal migration and swarm formation in Daphnia in response to Chaoborus. Hydrobiologia **307**:177-184.

Weider, L. J., and J. Pijanowska. 1993. Plasticity of Daphnia Life Histories in Response to Chemical Cues from Predators. Oikos **67**:385-392.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis.

Wickham, H. F., R. Henry, L. Muller, K. 2018. dplyr: A Grammar of Data Manipulation.

Appendix

Remains in pictures are identified with Atlas of Cladocera by Szeroczyfiska (2007)
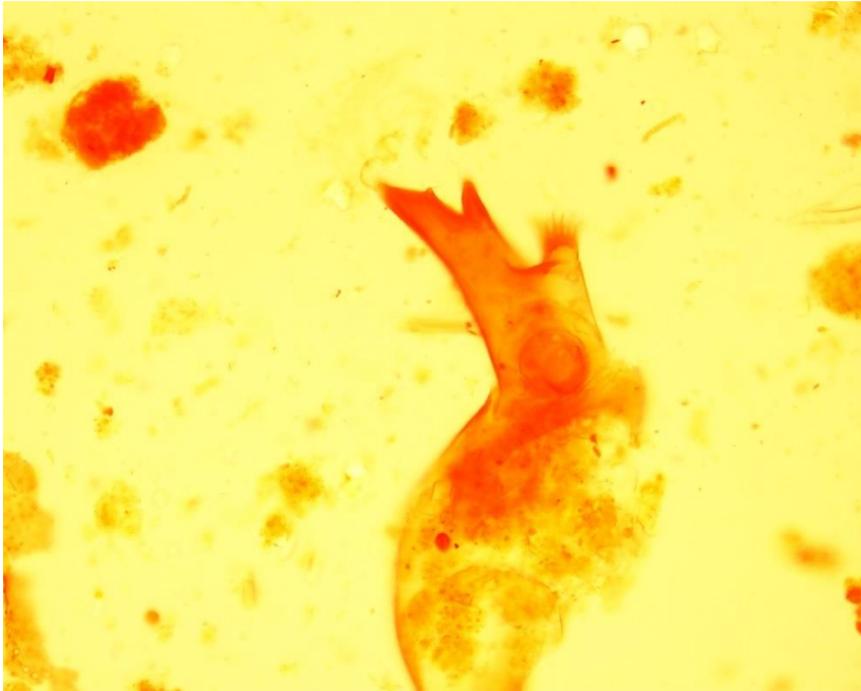
Figure A1, *Bythotrephes longimanus*, mandible, Rismottjonna.
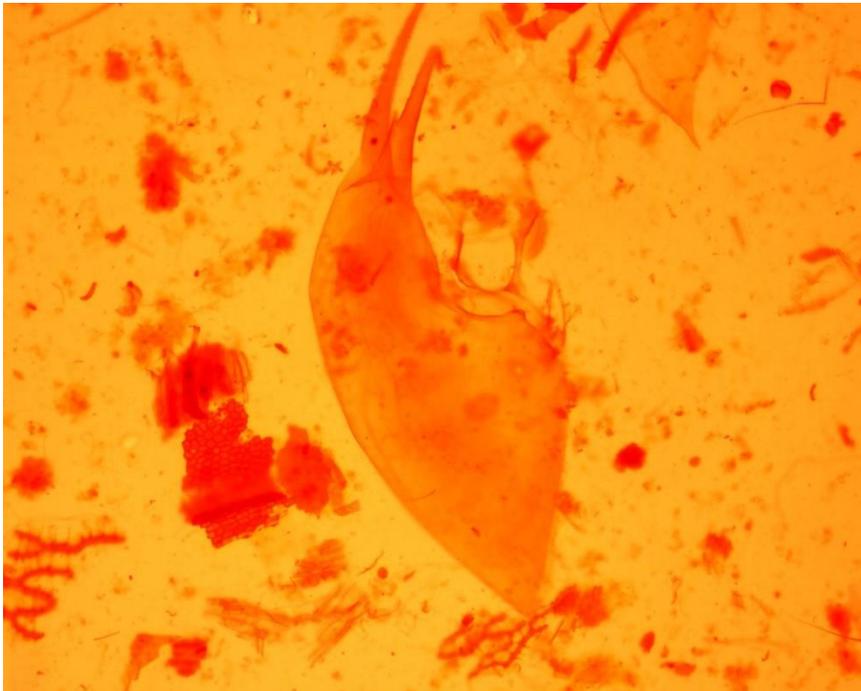
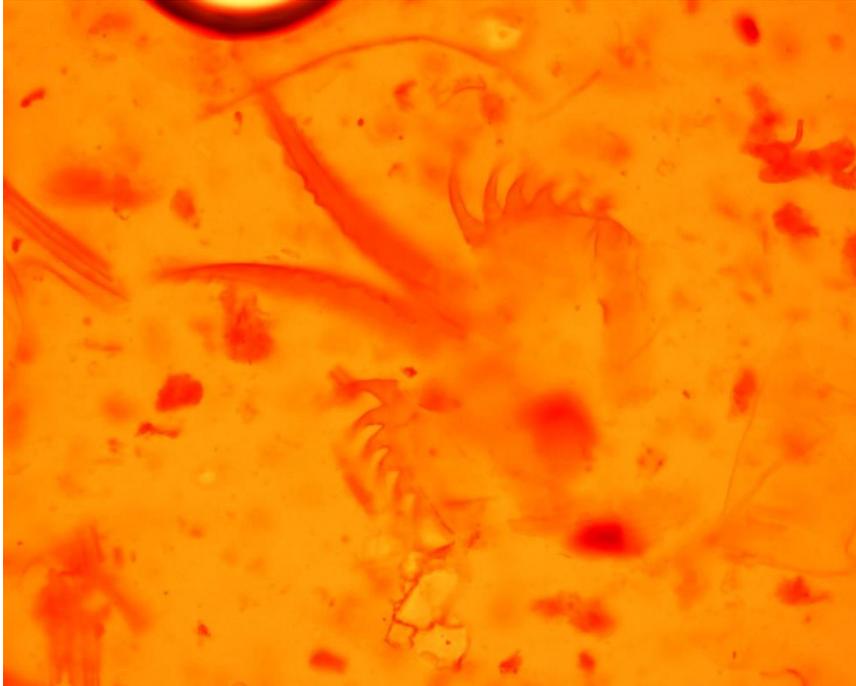Figure A2, *Bosmina longispina*, headshield, Oksloken.
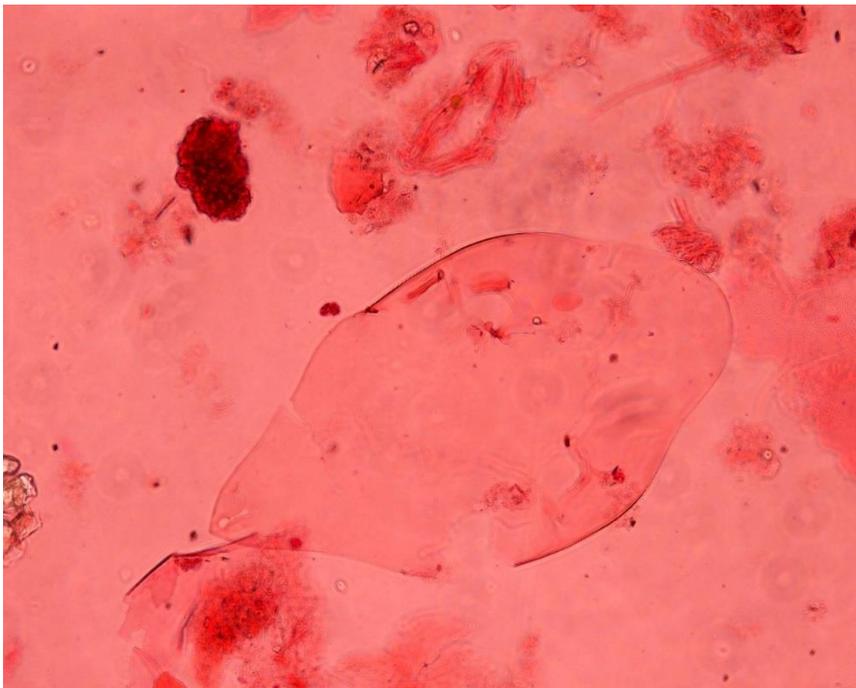
Figure A3, *Daphnia sp*, postabdominal claws, Oksloken.

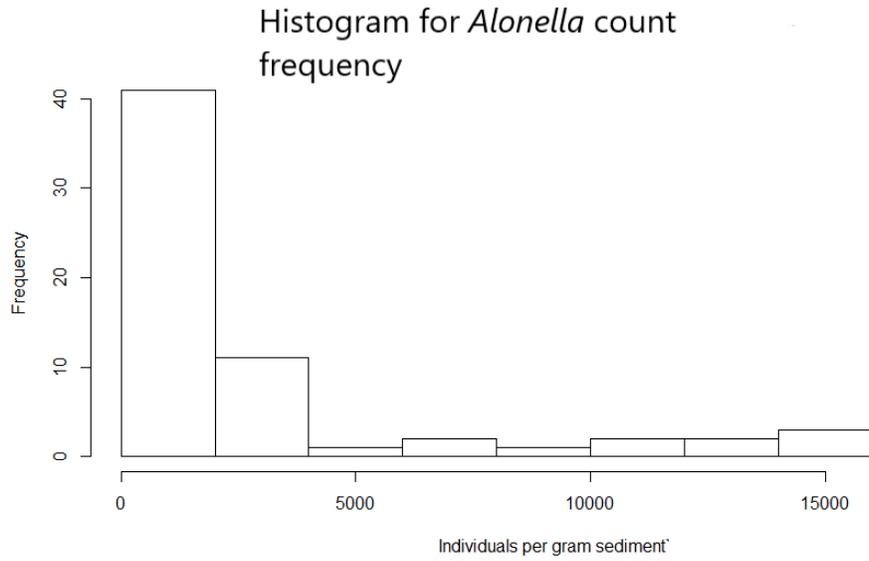

Figure A4, *Alona affinis*, headshield, Abbortjonna.
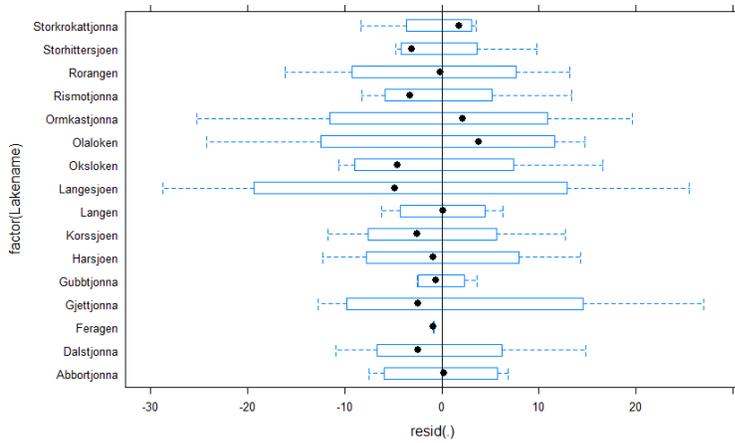
Figure A5, Histogram with count frequency for *Alonella*.

Figure A6, Residuals for *Alonella* model with whitefish + area.