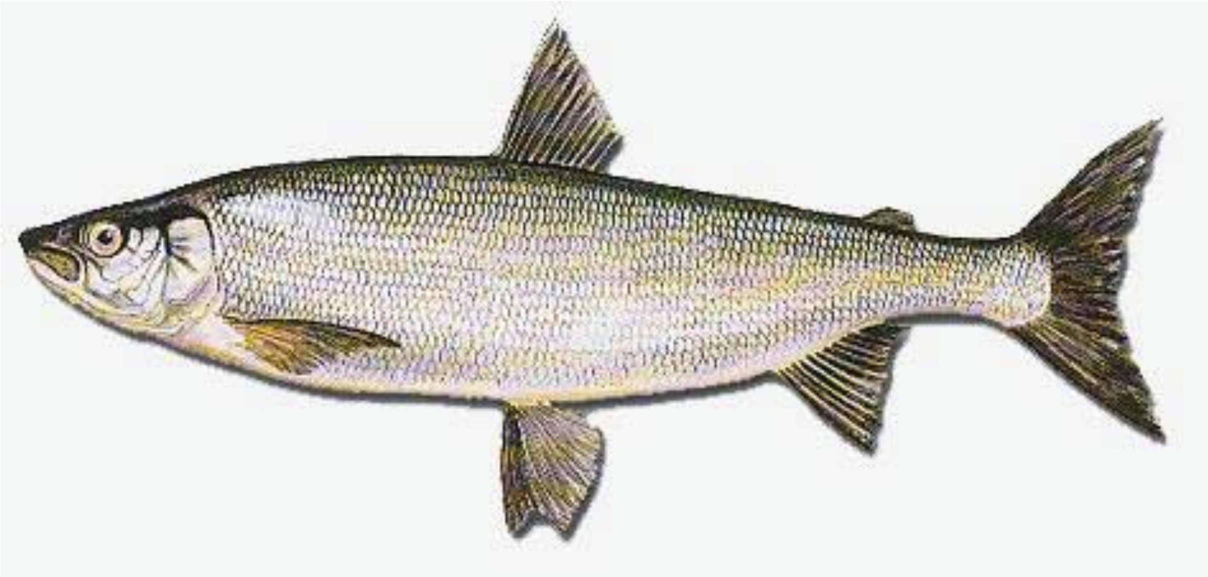
Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology and Natural Resource Management

Master Thesis 2015
60 credits

Effects of culling on the pelagic whitefish population in Lake Randsfjorden aiming at establishing a commercial fishery

Lars Erik Høitomt

Effects of culling on the pelagic whitefish population in Lake Randsfjorden aiming at establishing a commercial fishery



Lars Erik Høitomt

Master thesis in Nature Resource Management

Department of Ecology and Natural Resource Management

Norwegian University of Life Sciences

Ås 2015

Acknowledgements

This thesis was carried out at the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences (NMBU), and is a study of the probabilities for commercial exploitation of whitefish in Lake Randsfjorden after several years with intensive culling. First, I want to thank Oppland County Council and Randsfjorden Vannområde for funding my project.

I would especially like to thank my supervisor professor Thrond O. Haugen (NMBU) for outstanding supervising during the whole process, especially for teaching and helping me with the statistics. I will also thank Haugen for helping me conducting the fieldwork and laboratory work. For help with the hydroacoustic survey, analysis of the collected data and for teaching me valuable working routines, I would like to thank PhD-student Atle Rustadbakken.

I would also like to thank Tom Hammerstad for providing extra whitefish and Jarl Eivind Løvik for analyzing the zooplankton samples. Finally, I want to thank my family and fellow students for all help during the fieldwork.

Ås, May 2015

Lars Erik Høitomt

Abstract

The fishery in Lake Randsfjorden has long traditions, and especially the European whitefish *Coregonus lavaretus* has earlier played an important role as additional food supply for local communities in the area. After a rapid decrease in the exploitation of whitefish in the late 1980s, the population became overcrowded and stunted. The high infection intensity of the tapeworm *Triaenophorus crassus* became a particular problem as this parasite encyst in the whitefish flesh and makes the fish less attractive for human consumption. In 2007, hydroacoustic-, gillnet- and zooplankton surveys were conducted in Randsfjorden examining the conditions of the whitefish stock and opportunities for establishing a commercial fishery. The conclusions were that the whitefish stock was overcrowded, strongly infected by *T. crassus* and needed considerable improvements before a commercial fishery could be established. Based on information from this survey, an intensive culling programme using trap nets and shore seines was initiated the same year aiming at increasing the quality of the whitefish stock.

In 2014, after seven years of intensive culling, a new survey using same methods as the 2007-survey was conducted with purpose of examining the effects of the culling programme and providing recommendations for further actions in the lake.

Due to low gillnet catches and hydroacoustic surveys less suitable for comparison, it became difficult to arrive at a reliable conclusion concerning changes in whitefish density between 2007 (4.6 kg/ha, daytime survey) and 2014 (13.3 kg/ha, night survey). However, a hydroacoustics time series from Randsfjorden indicated a long term decline in biomass density since early 1990s up to present. The age composition of whitefish in the lake had gone through significant juvenilisation compared to 2007. However, the whitefish showed few improvements in growth as annual growth rates and stagnation lengths were the same as found in 2007. The infection intensity of *T. crassus* had slightly improved since 2007 with an overall reduction in number of parasites pr. fish. However, the parasite was still a major problem in Randsfjorden as 90 % of the whitefish were found to be infected. The composition of the zooplankton community did not corresponded with the high infection of *T. crassus* as the first intermediate host *Cyclops scutifer* occurred in a very low number in the zooplankton samples.

The intensive culling programme needs extensive improvement and new strategies in order to increase whitefish growth. New and more efficient fishing gears should be developed for a more efficient removal of whitefish. The density of smelt *Osmerus eperlanus* and roach

Rutilus rutilus had significantly increased since 2007, and their possible interactions with whitefish need further attention. A more comprehensive sampling of the zooplankton community is required in order to attain more knowledge about the transmission of *T. crassus* between pike *Esox lucius*, *C. scutifer* and whitefish in Randsfjorden. This knowledge may be valuable when developing new strategies in order to handle the parasite. In other lakes, removal of pike has shown positive results in reducing infection intensity of *T. crassus* in whitefish. Extensive pike removal should therefore also be considered for Randsfjorden. The whitefish stock in Randsfjorden needs further improvements before a commercial fishery can be established.

Sammendrag

Fisket i Randsfjorden har lange tradisjoner og tidligere har fiske etter sik *Coregonus lavaretus* spilt en viktig rolle for lokalbefolkning. Mot slutten av 1980-årene falt imidlertid interessen for fisket, og innsatsen gikk betydelig ned, noe som raskt førte til en overbefolkning og forkrøpling av sikbestanden. I 2007 ble det gjennomført en undersøkelse av siken i Randsfjorden for å kartlegge mulighetene for et næringsfiske i innsjøen. Konklusjonen var at siken var småvokst og av så dårlig kvalitet at den ikke kunne omsettes som menneskemat. Siken var i stor grad infisert av grovhaket gjeddemark *Triaenophorus crassus* som ødelegger kjøttkvaliteten og gjør fisken uappetittlig. Med bakgrunn og råd fra denne undersøkelsen ble det samme år iverksatt et tynningsfiske med not og storruser for å øke veksten og kvaliteten på siken.

I 2014 ble det på nytt gjennomført en undersøkelse av siken i Randsfjorden for å kartlegge om syv år med tynningsfiske hadde ført til forbedringer i sikbestanden. Undersøkelsen ble gjennomført ved å bruke de samme metodene som ble brukt under kartleggingen i 2007.

På grunn av lave garnfangster fra prøvefisket og lite sammenlignbare ekkoloddundersøkelser fra 2007 (4.6 kg/ha, dagkjøring) og 2014 (13.3 kg/ha, nattkjøring), var det vanskelig å komme med klare konklusjoner angående endringer i bestandstetthet hos sik. Allikevel viser en tidsserie over ekkoloddundersøkelser fra 1990 og fram til i dag at det har vært en nedgang i biomassetettheten i innsjøen. Tettheten av krøkle *Osmerus eperlanus* og mort *Rutilus rutilus* hadde økt siden 2007 og bestandsutviklingen til disse næringskonkurrentene burde overvåkes da de kan ha en negativ påvirkning på siken. Det har vært en klar forynging i sikbestanden siden 2007, da andelen gammel fisk har blitt sterkt redusert. Det er lite som tyder på at siken har fått forbedret veks gjennom denne perioden da den gjennomsnittlige årlige vekstraten og stagnasjonslengden var lite endret siden 2007. Infeksjonsgraden av grovhaket gjeddemark viste små forbedringer med en gjennomsnittlig nedgang i antall parasitter per fisk, men gjeddemarken var fortsatt et stort problem da 90 % av sikbestanden så ut til å være infisert av parasitten. Den antatte mellomverten for gjeddemark i Randsfjorden, hoppekrepsen *Cyclops scutifer*, ble kun funnet i små mengder i zooplanktonprøvene. Den lave forekomsten av denne arten i prøvene forsvarer ikke den store infeksjonsgraden av gjeddemark i siken.

En ytterligere økning i beskatningen ser ut til å være en forutsetning for økt vekst hos siken. Dette kan gjøres ved å ta i bruk flere storruser, men også nye redskap som ringnot, trål eller andre effektive fangstredskaper burde vurderes. Nye rutiner for innsamling av zooplankton i Randsfjorden må utvikles for å få bedre kunnskap om smitteoverføringen av parasitten

mellom gjedde *Esox lucius*, *C. scutifer* og sik. Denne kunnskapen kan vise seg å bli nyttig i utviklingen av nye metoder for reduksjon av parasitten i fisken. Utfisking av gjedde kan være et viktig tiltak for redusere gjeddemark i siken. Både norske og canadiske forsøk har tidligere vist at omfattende fjerning av gjedde kan spille en nøkkelrolle i reduksjonen av parasitten. I 2014 var kvaliteten på siken fortsatt for dårlig til å kunne omsettes som menneskemat, og bestanden trenger omfattende restaurering før et kommersielt sikfiske kan igangsettes.

Table of contents

1. Introduction

Overharvesting of sea living fish is a well known problem with many examples were populations have been driven close to extinction due to poor regulations. A good example is the overharvesting and poor regulations which resulted in a collapse of Atlantic cod *Gadus morhua* in the Vest Atlantic ocean in beginning of the 1990s (Sumich & Morrissey 2004).

In contrast, overcrowded and stunted fish populations are a common situation in many Nordic freshwater lakes (Klemetsen & Amundsen 2000; Taugbøl et al. 2004). Compared to many terrestrial animal populations, several fish species are able to sustain large and dense populations without facing the same collapses that regularly occur in dense populations of animals such as lemming *Lemmus lemmus* and willow ptarmigan *Lagupus lagopus* (Lekang 1988). High annual recruitment, low predation pressure, introduction of superior non-native competitors and low human exploitation are some of the elements that may cause high population densities in freshwater fish communities (Lekang 1988; Hegge et al. 1990; Borgstrøm & Hansen 2000; Museth et al. 2007). This thesis will focus on how intensive exploitation may be crucial in order to adequately recover an overcrowded and stunted population of European whitefish *Coregonus lavaretus* for human interests.

Overcrowded fish populations must not be described as a problem in an ecological view as overcrowding may be a result of natural processes and not just human activities (Lekang 1988). In a human context, overcrowding is regarded as a problem when fish size and quality are reduced. In a dense population, the fish will have to use much energy in competition for food and less for growth, which may result in more small grown fish with low condition (Lekang 1988). Several studies have shown that overcrowding in whitefish populations may be linked to low human exploitation, and extensive culling is often necessary to restore a stunted population of old, small and slow-growing fish, to a population of younger fast-growing fish of better quality (Amundsen 1988; Taugbøl et al. 2004; Museth et al. 2007). A study in Lake Sølensjøen, southeastern Norway, has shown that a strong reduction in exploitation of whitefish resulted in an overcrowded population with reduced fish size and fish quality (Museth et al. 2007). In addition, the introduced whitefish was a superior competitor to the native species arctic char *Salvelinus alpinus* which almost disappeared when the whitefish become dominant in the lake. An intensive culling programme was initiated in order to improve the fish quality. This action gave positive results as the whitefish increased in size and quality. The population of arctic char also recovered as the competition from whitefish was reduced (Museth et al. 2007). Similar results were found by Amundsen (1988) in Lake Stuorajavri, northern Norway, where an intensive culling programme improved the size and quality of whitefish living in benthic areas. The infection intensity of the tapeworm *Triaenophorus crassus* was a major concern in this lake as the plerocercoids of this cestoda encyst in the whitefish flesh and aesthetically reduce its market value (Miller 1952; Amundsen & Kristoffersen 1990). The parasite has a life cycle which involves three hosts (Miller 1952) (Figure 1). Copepods serve as the first intermediate host, whitefish and other ciscoes are second intermediate hosts, while pike *Esox lucius* is the final host (Miller 1952). The parasite is a well known problem in many Canadian lakes, and several experiments have been conducted in order to control the parasite (Miller 1952). Killing the eggs (embryos)

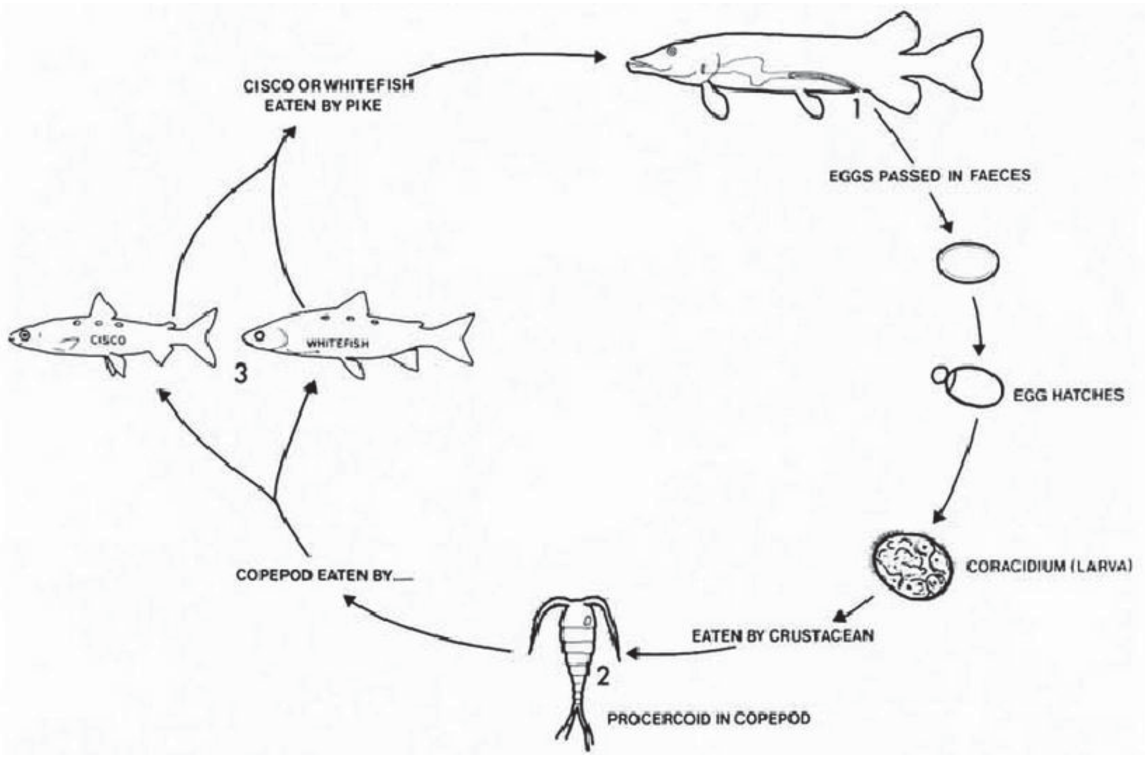


Figure 1: The life cycle of *T. crassus* (Dick & Watson 1977).

using chemicals and electricity have failed, and controlling the copepods is regarded as impractical as they are too widespread in the lake (Miller 1952). Amundsen and Kristoffersen (1990) found that the most efficient way to reduce the infection was to remove the pike and hence reduce the parasite reservoir. However, pike removal has to be extensive as one mature parasite living the intestine of a pike can produce more than 1100 000 eggs (Miller 1952). Amundsen and Kristoffersen (1990) also claimed that a comprehensive reduction of planktivorous fish might increase the population of larger uninfected zooplankton species as selective predation on these are reduced. Hence, the infection intensity of *T. crassus* in whitefish may by be reduced if the fish change its diet from the infected copepods to larger and more preferred species such as cladocerans (Amundsen & Kristoffersen 1990). However, other zooplankton consumers in the lake may also contribute with high feeding pressure on the zooplankton fauna, and removing whitefish alone may not be enough to increase the proportion of large cladocerans in the system. Miller (1952) also recorded that removal of coregonid fishes in some Canadian lakes had a positive effect on the infection intensity as the overall reduction in the parasite reservoir reduced the transmission rates. However, there is still no general blueprint method available to deal with the parasite and different methods give various results in different lakes.

In Lake Randsfjorden, the planktivorous whitefish population became stunted as the exploitation from local fishermen decreased rapidly at the end of the 1980s after many generations with continuous fishing (Hegge et al. 1990). Between 1989 and 1995, the mean condition factor had decreased from 1 to 0.63-0.83, and the mean weight declined from more than 300 g in 1980 to only 161 g in 1995 (Lindås et al. 1996). People still fishing had to use gillnets with smaller mesh sizes in order to catch the fish (Torgersen & Gregersen 2009). Further studies have also shown that most of the whitefish were strongly infected by *T. crassus* and therefore unsuitable for human consumption (Lindås et al. 1996; Rustadbakken et al. 2010). At the end of the 1990s, commercial interests for inland fisheries had again increased and several culling projects were initiated in order to restore stunted fish populations to earlier harvestable conditions (Taugbøl et al. 2004). The Ministry of Agriculture and Food announced in 2006 a new action plan which focuses on commercial inland fisheries and fishing tourism in order to create new jobs and increase welfare in the districts (Rustadbakken et al. 2010). Based on the new action plan, the ongoing project "Høstfisk" was initiated in 2007 with focus on the possibilities for commercial fishing in the two lakes Randsfjorden in Oppland County and Engeren in Hedmark County (Rustadbakken et al. 2010). Experiments in the two lakes is thought be crucial for further development of commercial inland fisheries in Norway. The licensees in Randsfjorden organized independent business development projects to do research related to fish quality and density, market options and product development (Rustadbakken et al. 2010). The Norwegian Institute for Water Research (NIVA), the Oppland County Governor, representatives of the Ministry of Agriculture and Food, Randsfjordforbundet, Norsk Innlandsfiskelag, Innlandsfisk AS and Hadeland produkter have been participating in the project with knowledge and financial support (Høitomt 2013). In 2007, NIVA conducted a full scale fishing survey in order to examine the whitefish population in Randsfjorden. They came to the very much the same conclusions as Lindås et al. (1996) that the population needed comprehensive cultivation before the whitefish commercially could be utilized for human consumption (Rustadbakken et al. 2010).

Lindås et al. (1996) claimed that the whitefish population needed to be culled by at least 30 tons annually to restore a population of good quality whitefish. NIVA announced that the culling should be performed by primarily using trap nets, seines and gillnets, and that the annual catches should be at least 50 tons in order to restore the population (Høitomt 2013). The use of trap nets has shown positive results in many though smaller lakes. They are often more efficient and require less labor than gillnetting (Taugbøl et al. 2004) (Appendix 1). However, it is uncertain how effective the trap nets will be in larger systems such as Randsfjorden.

In 2007, local landowner organizations started to cull the whitefish population in Randsfjorden after clear guidelines from NIVA (Høitomt 2013). According to Høitomt (2013) and Randsfjorden Grunneierforening (2014) the total catches of whitefish between 2007 and 2014 were at 208 342 tons with an annual average catch of 26 tons. This is lower than the recommendation from NIVA, and Høitomt (2013) announced that new and more effective trap nets should be tested and eventually included in the culling programme. It is claimed that the culling already shows some positive results as the whitefish seem to have increased in size and condition (Høitomt 2013).

The objective of this thesis is to examine effects of the culling that have taken place in Randsfjorden since 2007 and provide advices for further developments in this project. By repeating the same fish- and hydroacoustic surveys ran by Rustadbakken et al. (2010) in 2007, and comparing the results, I aim at quantifying changes in growth, quality, quantity and parasitic load of the whitefish. I further assess eventual changes that have taken place between 2007 and 2014 in the entire fish community composition as well as in the zooplankton community.

2. Material and methods

2.1. Study species

The European whitefish or common whitefish is a slender fish with a silvered compresses body that belongs to the family Salmonidae. Some scientists and taxonomists claim that this classification is incorrect and that the European whitefish is only one of more than 50 species that should be separated and placed in an independent family, Coregonidae (Kottelat & Freyhof 2007). The discussion whether the coregonids are different species or just subspecies with different morphology and biology has been going on for half a century (Enge 1956), and the complexity of the systematics is described as a nightmare (Kottelat & Freyhof 2007). In this thesis, the traditional classification of the *Coregonus lavaretus* as one polymorph species is followed (Enge 1956; Sandlund & Næsje 2000). The European whitefish is primarily a freshwater fish, but tolerates low salt concentrations and may form anadromous populations (Sandlund & Næsje 2000; Kottelat & Freyhof 2007). The whitefish normally feed on bottom living invertebrates or zooplankton, but may also consume insects from the surface or fish fry (Sandlund & Næsje 2000). The whitefish is a polymorph species and can form sympatric morphs with different biology and morphology in the same lake (Enge 1956; Sandlund & Næsje 2000). They often utilize different habitats and food recourses and may also have significant differences in spawning time and location, such as lake and river spawning morphs. The whitefish commonly occur as 1 or 2 morphs in a lake, but in larger systems such as Randsfjorden, 4 morphs have been described (Enge 1956; Sandlund & Næsje 2000).

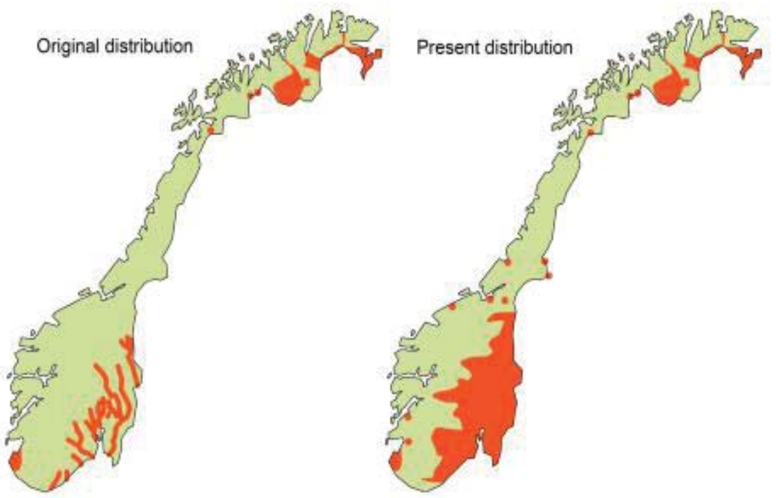


Figure 2: Maps showing the original distribution (left, based on Huitfeldt-Kaas (1918)) and present distribution (right, data from NINA database) of whitefish (orange areas) in Norway (Sandlund et al. 2011).

The whitefish has its natural distribution in Northern Europe, but is also common in Asia and North America (Kottelat & Freyhof 2007). In Norway, the whitefish naturally occur in eastern parts of the country, from Buskerud County to the south of Nord-Trøndelag County in th north, and in Finnmark County. A few populations also occur naturally in Agder and Rogaland counties (Sandlund & Næsje 2000) (Figure 2). The distribution of the species is now far beyond the natural distribution due to comprehensive human introductions to new lake systems (Sandlund et al. 2011). The massive introductions of the whitefish can be explained by its high productivity. The whitefish is reported to be the freshwater fish with the highest production pr. ha in Norway (Lekang 1988). The whitefish was also very easy to catch with various fishing gears throughout the year (Sandlund et al. 2011). However, these introductions were not without problems as many lakes suffered from collapses in brown trout *Salmo trutta* and arctic char populations due to superior competition from the whitefish (Huitfeldt-Kaas 1918; Svärdson 1976; Sandlund et al. 2011).

2.2. Study system

Randsfjorden is located in the lower parts of Oppland County, 134 m above sea level. The lake is the fourth largest in Norway, and stretches 75 km through Nordre Land, Søndre Land, Gran and Jevnaker municipalities. The total area of the lake is 134 km^2 with a maximum depth of 120.5 m (Nielsen et al. 1985). The drainage basin is estimated to 3 663 km^2, and the main tributaries are Dokka-Etna, Lomsdalselva and Vigga. The only distributary is Randselva at Jevnaker. The fish community is mainly dominated by whitefish and smelt *Osmerus eperlanus*, but also perch *Perca fluviatilis*, pike, brown trout, European minnow *Phoxinus phoxinus*, river lamprey *Lampetra fluviatilis* arctic char, ninespine stickleback *Pungitus pungitius* and common roach *Rutilus rutilus* are abundant species in the lake (Rustadbakken et al. 2010). Randsfjorden was first dammed in 1912 with a maximum regulation level of 2.40 m, but the level was increased to 3.00 m in 1951 (Nielsen et al. 1985). One of the main tributaries, Dokkaelva, was dammed in 1989 (Lindås et al. 1996).

Figure 3: Traditional fishing with shore seine in Dokka-Etna (Photo: Geir Høitomt).

The fishery in Randsfjorden has long traditions (Eknæs 1979), and especially the whitefish has been intensively exploited by the locals (Styrvold et al. 1981; Hegge et al. 1990; Lindås et al. 1996) (Figure 3). In earlier times, the whitefish played an important role as an additional food supply for people struggling to fulfill the needs of their household (Eknæs 1979). The fish were caught by using a wide range of fishing gears. In Dokka-Etna, whitefish were usually caught using benthic gillnets, purse seines, shore seines and landing nets during the spawning migration from September-October, and the annual yield varied from 6 to 15 tons (Lindås et al. 1996). The catches were even higher during July and August when fishermen used pelagic gillnets to catch whitefish feeding on zooplankton in the lake. The annual yield used to be between 20 and 50 tons (Hegge et al. 1990; Rustadbakken et al. 2010). During winter, November to February, the total catch was normally around 4 tons where most of the fish were caught in deeper waters (Rustadbakken et al. 2010). The total annual yield in Randsfjorden and Dokka-Etna could be more than 60 tons of whitefish in a good year (Rustadbakken et al. 2010). The fishery decreased rapidly between 1985 and 1995 and resulted in an overpopulated and stunted whitefish population of low value for human consumption (Lindås et al. 1996; Rustadbakken et al. 2010). A report of the annual catches from the fishery in Randsfjorden between 1978 and 1995, and Dokka-Etna from 1967 to 1995 is given by (Lindås et al. 1996). Reports of the culling conducted annually in the lake since 2007 are given by Høitomt (2013) and Randsfjorden Grunneierforening (2014) (Table 1).

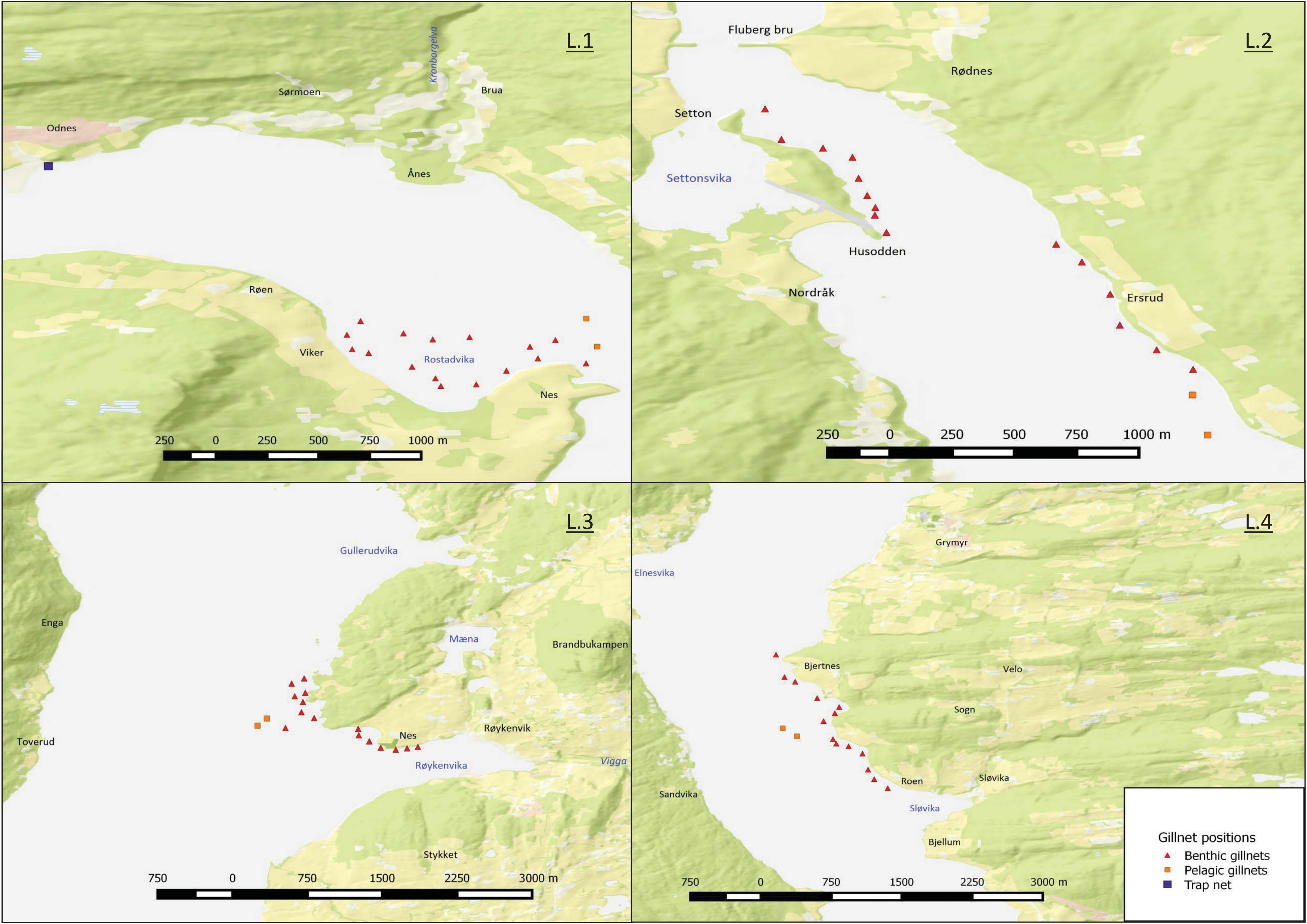
Table 1: Annual catches from the culling programme conducted in Randsfjorden between 2007 and 2014 (Høitomt 2013; Randsfjorden Grunneierforening 2014).

Year	Catches in kg
2007	700
2008	16 026
2009	23 585
2010	21 662
2011	29 830
2012	46 530
2013	35 023
2014	34 986

2.3. Sampling locations

Fish samplings were conducted at the 4 locations Fluberg (L.1 + L.2), Røykenvika (L.3) and Sløvika (L.4) (Figure 4). Because of low gillnet catches; additional whitefish was acquired from a large trap net close to L.1, which was used in the culling project. Zooplankton was sampled at Z between L.2 and Hov (Figure 4). The hydro acoustic survey was covering more or less the whole lake through taking a zig-zag transect pattern. The sampling locations were the same as used by Rustadbakken et al. (2010) in 2007. All surveys were conducted between September 15 and 30 (Appendix 2).

Figure 4: Sampling locations for fish survey (L.1-L.4), zooplankton sampling (Z.) and trap net position. See next page for the specific gillnet positions at each location.


L.1
Odnes
Sørmoen
Kronborgelva
Brua
Ånes
Røen
Viker
Rostadvika
Nes
250 0 250 500 750 1000 m
L.2
Fluberg bru
Rødnes
Setton
Settonsvika
Husodden
Nordråk
Ersrud
250 0 250 500 750 1000 m
L.3
Gullerudvika
Enga
Toverud
Mæna
Brandbukampen
Røykenvik
Nes
Røykenvika
Vigga
Stykket
750 0 750 1500 2250 3000 m
L.4
Grymyr
Elnesvika
Bjertnes
Velo
Sogn
Roen
Sløvika
Sløvika
Sandvika
Bjellum
750 0 750 1500 2250 3000 m
Gillnet positions
Benthic gillnets
Pelagic gillnets
Trap net

2.4. Fish survey

The fish survey was conducted by using Nordic multi-mesh benthic survey gillnets and Nordic multi-mesh pelagic survey gillnets (Appendix 3). The effort was 16 benthic gillnets and 4 pelagic gillnets during one night at each station. Unfortunately, two benthic gillnets got severe damaged during fishing, and these were removed from the survey with no replacements. The benthic gillnets were 1.5 m high, 30 m wide and had mesh sizes ranging from 5-55 mm (Appelberg et al. 1995). They were distributed and oriented randomly at each location, but equally assigned to strata -> 6 m and <-6 m depth within each location, and placed covering depths from 1.5 to 25 m. The pelagic gillnets were 6 m high, 30 m wide and had mesh sizes ranging from 5-55 mm (Appelberg et al. 1995). The pelagic gillnets were connected into two chains and placed at depths of 0-6 m and 10-16 m in mid parts of the lake. All gillnets were made from monofilament nylon.

2.5. Fish sampling

All fish caught in gillnets and acquired from the trap net were determined for species, weighed and length measured (from snout to mid part of tail, i.e., fork length). The fish were also determined by sex and reproductive stadium. Age- and growth patterns were assessed by readings of scales and otoliths in trout and whitefish, operculums from roach and pike, otoliths and operculums from perch, and otoliths from smelt and minnow. The otoliths were cut in half and heated over an open flame to accentuate the winter zones. The otoliths were then immersed in propane1.2-diol and read with a Leica MS 5 stereo microscope. The age readings from scales were performed by using a microfilm reader. The age was determined for all whitefish, roach, pike, trout and minnow, while 50 individuals of perch and smelt were selected from all length groups for age determination. Gender and reproductive stadium were determined by examining the size of the gonads. The reproductive stages were measured on a scale from I-VII, where stage I and II are fish that will not spawn during the upcoming spawning season. Fish at stage III to V are sexually maturing and will spawn during the upcoming spawning season. Fish at stage VI are ready to spawn, and fish at stage VII has already spawned (Jonsson & Matzow 1979).

Figure 5: Analysis of the parasitic content in a whitefish (Rustadbakken et al. 2010)

The parasite state of the whitefish was also examined. The examinations were performed by cutting 3 cross-sections at the back of the fish (Figure 5). The number of parasites in each section was counted and the degree of parasitism was calculated by dividing *no. of fish infected* by total *no. of fish*. By summing the total number of parasites visible in each cross-section, the intensity of parasitism was determined for each individual whitefish. The whitefish caught in this survey was not further determined to morph.

2.6. Zooplankton sampling

Zooplankton was sampled quantitatively by using a 15 L Schindler Trap with filter mesh size of 90 µm. Samples were collected at the depths: 1 m, 5 m, 10 m, 15 m and 20 m. All samples were conserved by using Lugol's solution and the organisms were later counted and species determined in the lab. A representative number of each species was measured by length, and specific dry weights were calculated from standard length/weight regressions. The biomass of the profile 0 to 20 m was calculated based on individual numbers and specific weights.

2.7. CTD-Ox-measurement

Oxygen- and temperature profiles were measured with an EXO2 Multiparameter Sonde at 4 deep areas in the lake (Appendix 4). The EXO2 was equipped with 6 sensors that measured temperature, pH, depth, turbidity, oxygen and conductivity (Figure 6) (YSI 2015). The Sonde was acclimated in surface waters for 5 minutes before profiling. Then the Sonde was lowered at a speed of 30 cm pr. second and two measurements were sampled every second. The measurements were later used when interpreting data collected in the hydroacoustic survey and fish survey.

Figure 6: The EXO2 Multiparameter Sonde used in the survey (YSI 2015).

2.8. Hydroacoustic survey

A hydroacoustic night survey was conducted between September 16 and 18. We used a 70 kHz SIMRAD EK60 scientific echo sounder with a transceiver, and a SIMRAD ES70-11 circular split beam transducer transmitting sound pulses vertically through the water in an $11^{o}{}_{-3dB}$ narrow beam. The transmission power was 240 W with a pulse width of 0.256 µs. The ping interval during survey was 1 ping s^{-1}. According to the European Hydroacoustic CEN standard, a "scientific" sounder is as a calibrated quantitative fisheries echo sounder operating at an appropriate frequency for the water body and target fish species, most likely between 38 kHz and 1.8 MHz (Urick 1996). Further it should enable calibrated data storage and processing in order to generate abundance and size distribution outputs (CEN 2014).

The equipment and 70 kHz frequency setup in this survey was chosen to optimize fish detection in Norwegian lakes and to do abundance/biomass estimations of fresh water fish. Prior to the survey, the echo sounder was calibrated through a standard target calibration procedure using a copper sphere with known acoustic scattering properties. The transducer was mounted on the bulwark of the survey boat and lowered 30 cm down into the water. Data was collected by doing zig-zag transects of the whole lake with a coverage of $\Lambda = L/\sqrt{A} = 8.7$, where L is the total transect length in km, and A is the total area of the lake in km^2. All collected raw data were stored on a computer by using the software SIMRAD ER60.

The hydroacoustic data was processed by using the post-processing software Sonar5-Pro (S5) from Lindem Data Acquisition A/S (Balk 2015) in accordance with the CEN standard (CEN 2014). Analysis of abundance and target strength (TS)-distributions were performed in S5, while further statistical analyses i.e. comparing results from 2007 to 2014, was done by using R (R Core Team 2014). Before analyzing the data, a bottom detection procedure was performed. A bottom margin of 0.3 m was set to avoid unreliable data collected from or near the bottom. A 3 m surface margin was set to avoid unreliable data collected in the upper part of the water, close to the transducer. Noise was removed from the echogram both by manually deletion and by using noise detection procedures in S5 (Figure 7). However, some low intensity noise remained as it was difficult to separate from fish. In some areas with much electric noise, removing the noise without removing fish was difficult. The SED-threshold in this survey was set to -62 dB in order to separate fish from noise. Single echo detections (SED), are believed to origin from single targets like fish. The amplitude echoes (AMP) includes also detections which have not been approved as single fish, such as dense schools, but also diffuse noise signals. The AMP- threshold was set to -68 dB according to the recommendations in the Great lakes SOP (Parker-Stetter et al. 2009). A split beam transducer receives the echoes with four channels making it possible to calculate the exact position of an object in the beam. The intensity of the received single echo is measured as target strength (TS) in dB re 1 m^2. By adding off-axis compensation to the TS, the true target strength of the fish is calculated. TS is in a logarithmic form a reference value which represents the size of the fish typically in the range from -60 (small) to -25 (large) dB. AMP-echoes are measured as Volume Backscattering Strength (S_v) in dB re 1 m^{-1} (Simmonds & MacLennan 2005).

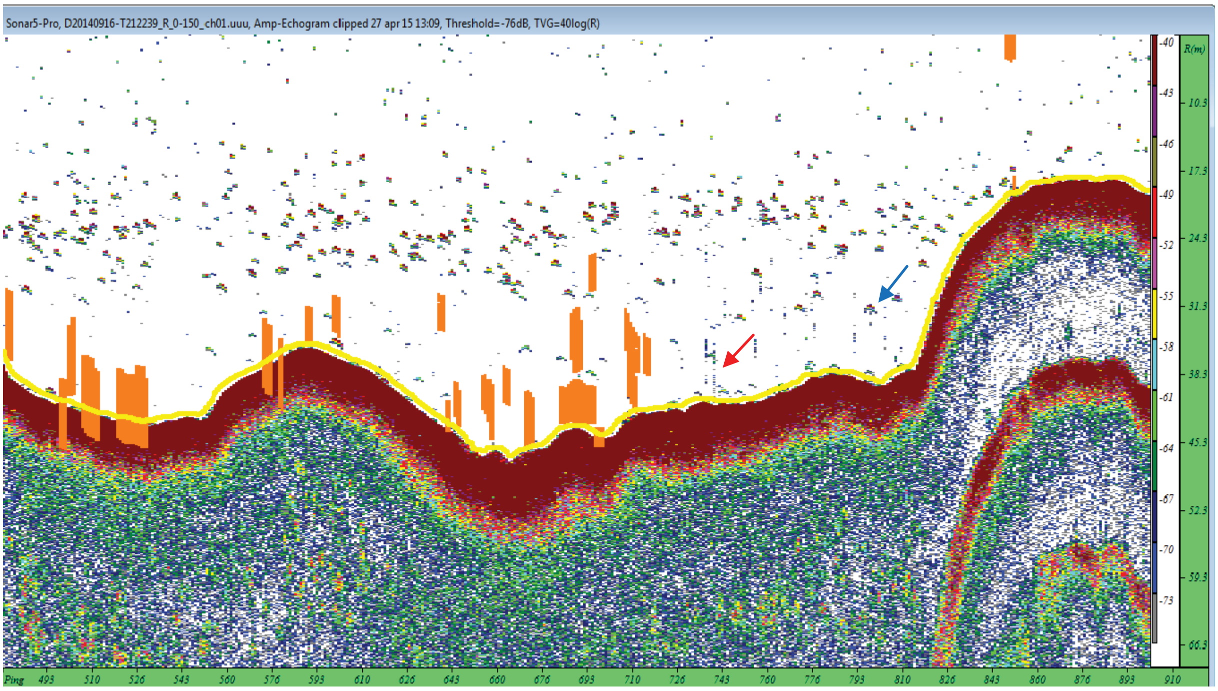


Figure 7: Echogram from the vertical transducer. The orange fields are electronic noise removed from the analysis. Fish appear as banana-shaped figures (blue arrow) in the echogram, while electronic noise often appears as long columns (red arrow). The yellow line represents the bottom with a margin of 0.3 m.

The relationship between TS in dB and fish length (L) in cm is species specific or at least species group specific. However, it may differ between different morphs or populations within a species (Simmonds & MacLennan 2005). The TS-L-equation follows the traditional linear regression formula TS=A*logL+B, where A and B are constants. For Randsfjorden A=25.67 and B=-97.2 has been found to give the best fit to the length distribution of a mixture of smelt and whitefish when length was measured in mm (Haugen & Rustadbakken, unpublished data of consecutive trawl catch and hydroacoustics in 2009). Biomass estimates were calculated from the abundance numbers and size distributions obtained from hydroacoustics and weight-length relationships of smelt and whitefish obtained from gillnet catches. Other TS-L-equations were found to be inaccurate by giving unlikely length distributions of smelt or whitefish and hence unreliable biomass estimates. The fish distribution could be separated into in three depth layers in the lake where fish in layer 1 (3-15 m) and layer 2 (15-50 m) had different target strength and apparently were different species (Figure 8). Biomass estimates were accordingly assessed for each separate layer, although layer 3 contained very little fish and was not further analyzed. The fish distribution was closely related to the temperature stratification of the lake, and most of the fish were detected around the metalimnion (Figure 9). The distribution of fish in relation to depth was more or less similar for 2007 and 2014.

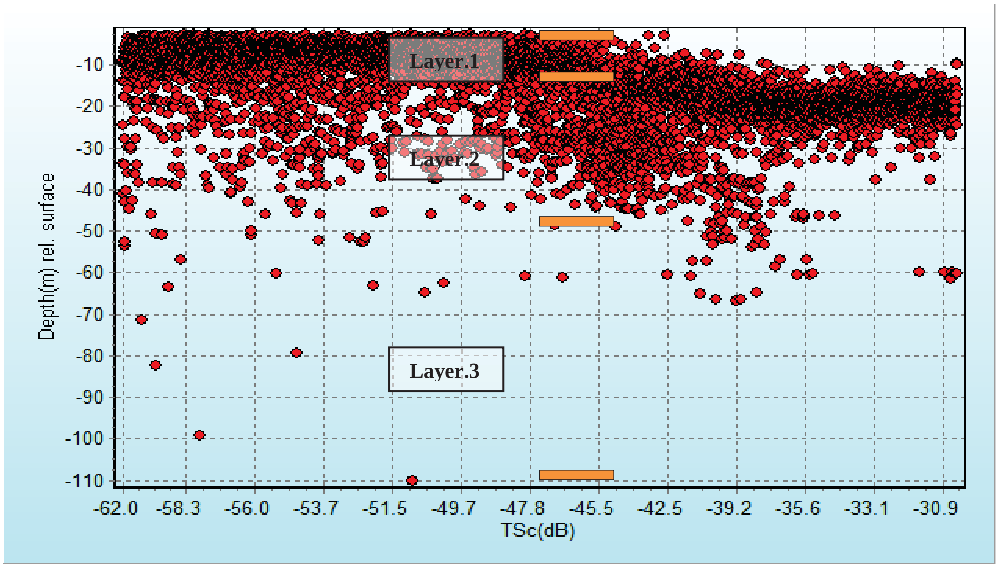


Figure 8: An overview of the fish detected in Randsfjorden during the 2014-survey where fish distributions are presented in three layers as a function of depth (m) and target strength (TS).

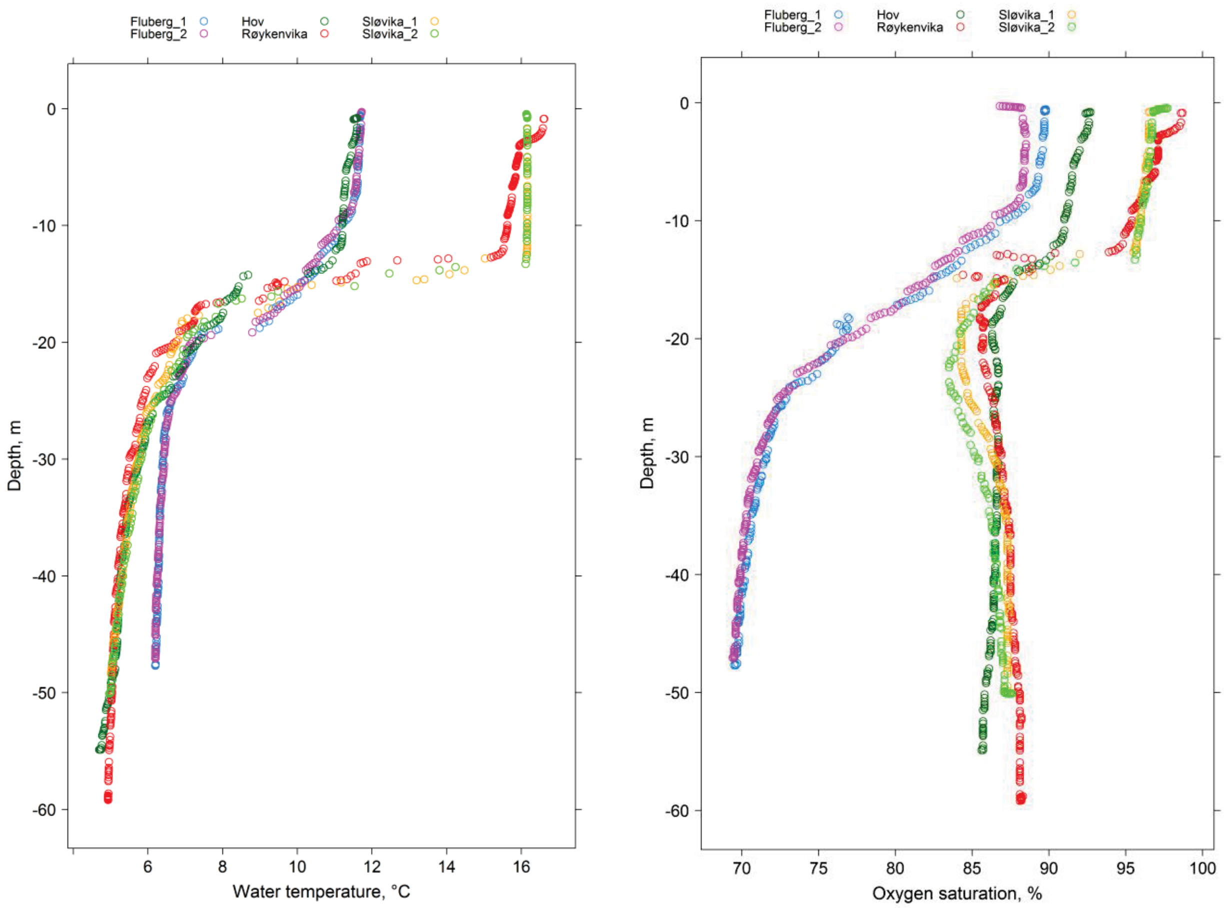


Figure 9: Samples of oxygen saturation and water temperature in relation to depth (m). The samples were collected with an EXO2-Sonde in Randsfjorden during the 2014-survey. Two samples were collected at Fluberg and Sløvika.

2.9. Data analysis

All statistical analyses were performed in R (R Core Team 2014). The raw data was compiled using Microsoft Excel 2007.

Lea (1910) found out that there was a proportional connection between the growth of the scale and the length of the fish. The annual growth of the fish was measured from center to each annuli of the scale by using the Dahl-Lea method:

$L_c = L_i \left(\frac{S_i}{S_c}\right)$, **Equation 1**

Where L_c is length when captured, L_i is back-calculated length at annulus i, S_i is scale radius to annuli i and S_c is the total scale radius (Dahl 1910; Lea 1910).

The growth pattern of whitefish was of great interest when analyzing the effects of the intensive culling. The growth pattern was found by fitting the von Bertalanffy model to the back-calculated length data:

$l_t = L_\infty \left[1 - e^{-k(t-t_0}\right]$, **Equation 2**

Where l_t is length of an individual at age t, L_∞ is the theoretical maximum length the fish will achieve, K is Brody's growth coefficient (yr^{-1}) and t_0 is hypothetical age at length 0 (Gulland 1977).

In order to explore and quantify effects from individual characteristics on parasite infection intensity (i.e., number of parasites per individual), generalized linear models (GLM) (MacCullagh & Nelder 1989) were fitted for the infection data under Poisson-distribution assumptions (log-link). A number of candidate models were fitted including combinations of length, weight, age, gender and condition factor, as predictors. I also included standardized age-specific length as a predictor to test and quantify if fast-growing individuals within an age class, had different infection intensities than slow-growing individuals. The standardization was performed at age level where:

$st.l_t = \frac{(l_t - \bar{l}_t)}{\sigma^2_{l_t}}$, **Equation 3**

Where l is length at age t, $\bar{l}_t$ is the mean over all lengths at age t and $\sigma^2_{l_t}$ is the standard deviation of lengths at age t. These standardized values are on standard deviation units, normally falling between -3 and 3. Model selection among candidate models was performed by using Akaike Information Criterion (AIC) (Akaike 1974) following routines described in (Burnham & Anderson 1998). A similar GLM-approach was followed when modeling individual character effects on parasite infection prevalence (i.e., probability of having one or more parasites). These analyses were performed using logit-link to the either-or responses (0=no parasites; 1=has parasite(s)). The GLM models were fitted using the GLM-procedure in R.

Differences in echo sounding-derived biomass densities between water layers in 2007 and 2014, were tested and quantified by fitting linear models (LM) and corresponding ANOVAs. These tests were performed using the lm-procedure in R.

Tests of year differences in TS-derived length distributions were undertaken by using an updated version of the Kolmogorov-Smirnov test (Sokdal & Rohlf 1995) by running a "bootstrapping" routine available in the ks.boot-procedure in R-package Matching. This bootstrapping routine reports p-values that allow for ties (i.e., cross-over of the cumulated distributions) (Abadie 2002).

The results from 2007 presented in this thesis are based on data published by Rustadbakken et al. (2010), in addition to some unpublished data from the same year. Large portions of the raw data from the fish- and hydroacoustic surveys conducted in 2007 were reanalyzed by same methods as used for the 2014-data. Additional scales collected from whitefish in 2007 were used for age determination in order to increase the data amount when back-calculating whitefish growth. Zooplankton data from 2012 are unpublished data collected by Atle Rustadbakken and was included in my thesis to get a better understanding of the developments in the zooplankton community.

3. Results

The total catch from the fish survey was 738 fish; 138 whitefish (share of 106 from trap net), 364 perch, 54 roach, 175 smelt, two trout, four pike and one minnow (Table 2). Compared to the 2007-catches, the number of perch, whitefish, pike and minnow was lower in 2014, while there was an increase in smelt and roach since 2007. For 2014-catches, the number of whitefish individuals caught per unit effort (NPUE) was highest at location 1 and lowest at location 3 (Table 3). In 2014, the total whitefish catch pr 100 m^2 gillnet (CPUE) was 0.5 fish for Nordic pelagic gillnets, and 2.5 fish for Nordic benthic gillnets. In 2007, the total whitefish catch pr 100 m^2 gillnet was 0.9 fish for Nordic pelagic gillnets and 0.37 fish for Nordic benthic gillnets. The catch of smelt pr 100 m^2 Nordic pelagic gillnet was 4.0 in 2007 and 6.1 in 2014.

Table 2: The total catch from the fishing survey in autumn 2014, showing distribution of the different species with max, min and mean weights/lengths and gillnet efforts.

Gillnets/weight / length	Number of gillnets	Number of net nights	Whitefish		Perch		Roach		Smelt		Trout		Pike		Minnow		Total	
			count	g/cm	count	g/cm	count	g/cm	count	g/cm	count	g/cm	count	g/cm	count	g/cm	count	g/cm
Nordic benthic	16	60	18	2804.4	362	33675.5	54	10969.5	26	237.77	2	954	4	3010	1	2.32	467	51653.54
Nordic pelagic	4	16	14	1631.3	2	5.78	0	0	149	588.25	0	0	0	0	0	0	165	2225.32
Large fish trap	*	*	106	22505.2	0	0	0	0	0	0	0	0	0	0	0	0	106	22505.17
Total number	20	76	138	26940.8	364	33681.3	54	10969.5	175	826.02	2	954	4	3010	1	2.32	738	76384.03
Mean weight (g)				195		92.53		203.1		6.029		477		752.5		2.32		109.21
Min weight (g)				5.7		0.58		1.03		1.89		97		25.0		2.32		0.58
Max weight (g)				914		637		450		16.26		857		2706		2.32		2706
Mean length (cm)				24.25		16.51		22.26		9.392		30.65		32.85		6.2		17.02
Min length (cm)				8.7		3.8		4.8		7.0		20.2		15.1		6.2		3.8
Max length (cm)				38.5		36.5		29.3		13.2		41.1		65.8		6.2		65.8

Table 3: Nordic benthic (NB) and Nordic pelagic (NP) gillnet efforts and number of individuals caught per net night (NPUE) for all species at all locations in 2014. Whitefish from the trap net are excluded.

				Number of individuals per net night (NPUE)						
Location	Gillnet	Effort	m^2	Perch	Pike	Roach	Smelt	Whitefish	Trout	Minnow
1	NB	16	720	4.19	0.19	0.31	0.06	0.44	0.06	0.00
1	NF	4	720	0.25	0.00	0.00	11.25	2.50	0.00	0.00
2	NB	15	675	5.93	0.07	0.47	0.20	0.27	0.00	0.07
2	NF	4	720	0.25	0.00	0.00	16.00	0.50	0.00	0.00
3	NB	15	675	13.07	0.00	2.80	0.87	0.40	0.00	0.00
3	NF	4	720	0.00	0.00	0.00	3.75	0.00	0.00	0.00
4	NB	14	630	0.71	0.00	0.00	0.64	0.07	0.07	0.00
4	NF	4	720	0.00	0.00	0.00	1.00	0.50	0.00	0.00

3.1 Whitefish age, size and growth

The length of whitefish caught in the 2014-survey varied from 8.7 to 38.5 cm with a mean length of 24.25 cm. Approximately 80 % of the whitefish had lengths between 26 and 30 cm (Figure 10). The length distributions for 2007 and 2014 are very similar for fish smaller than 30 cm, while there has been a significant decrease in larger fish between 2007 and 2014 (Figure 10).

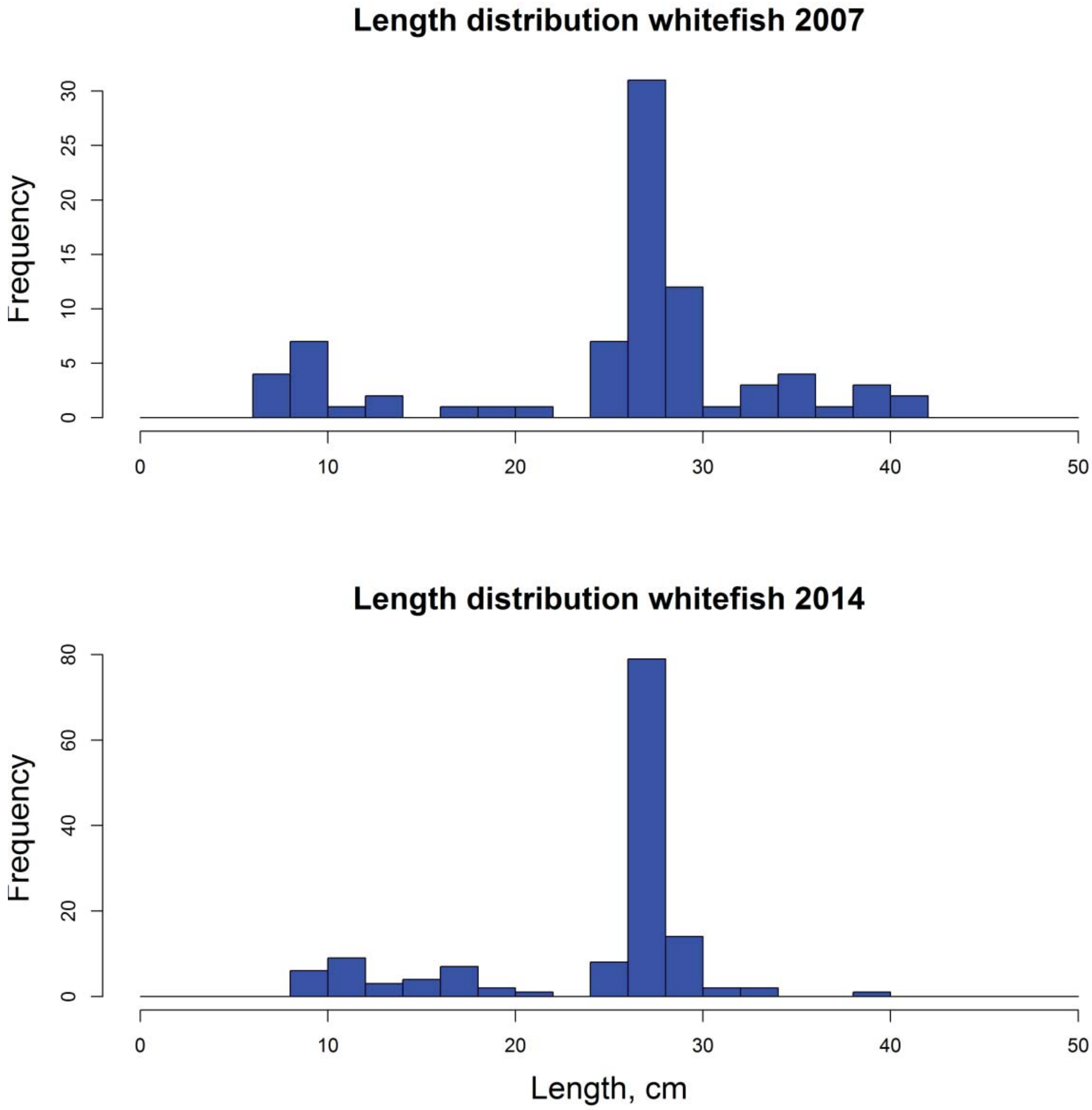


Figure 10: Length distribution of the whitefish caught in 2007 and 2014.

The age distribution seems to have changed between 2007 and 2014. The number of fish older than 8 years old had clearly declined between 2007 and 2014 (Figure 11). There were although some missing data as age was not determined for the smallest fish (8-10 cm) caught in 2007. These individuals were assigned age 1 (Figure 11).

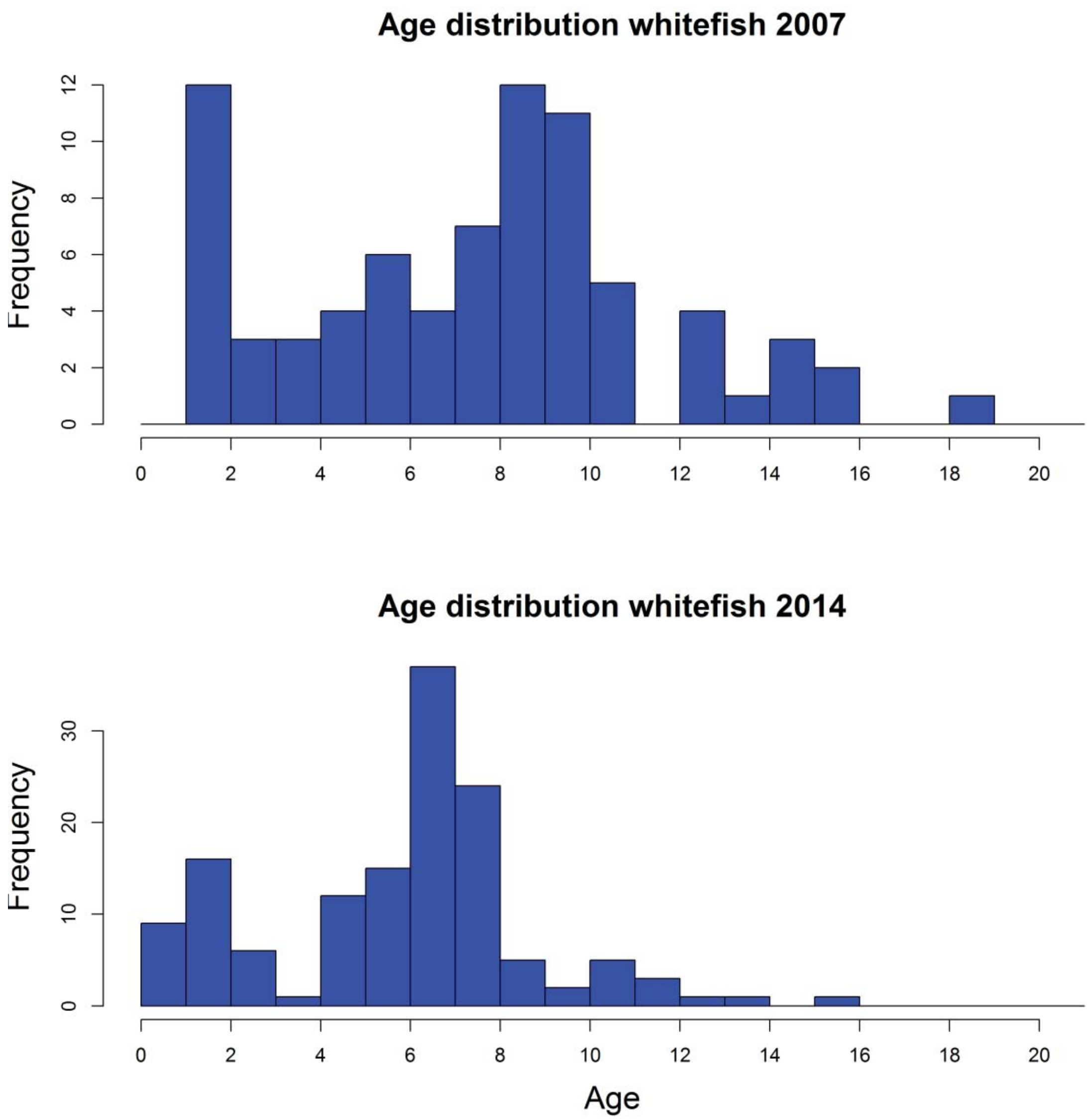


Figure 11: Age distribution of the whitefish caught in 2007 and 2014.

The whitefish seemed to have a rapid growth reaching more than 25 cm the first 3 years (Figure 12). When the whitefish reaches age 4-5 years, the growth is strongly reduced and almost ceases when the fish has reached 26-28 cm. This growth pattern had not changed between 2007 and 2014 (Figure 12 & Figure 14). The back-calculated lengths showed large differences in individual size within the same age classes (Table 4 & Figure 13). The lengths for 1+ whitefish varied from 4.5 to 11 cm, and such differences in size were common through all age classes for both years (Figure 13). The back-calculated growth showed that whitefish caught in 2007 and 2014 had very similar growth pattern through all years with only minor differences (Figure 14).

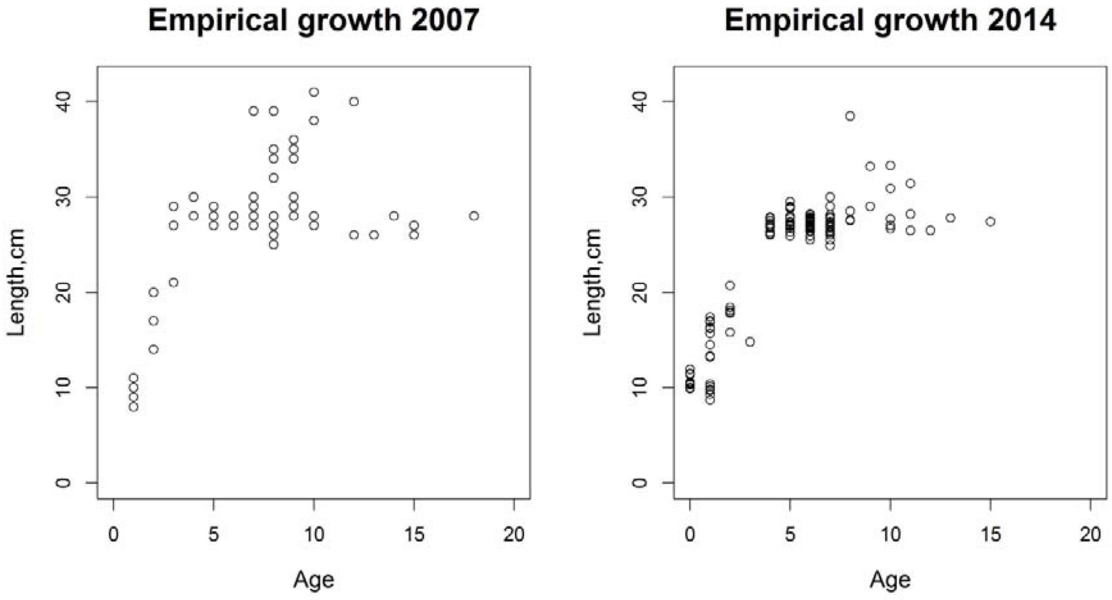


Figure 12: Empirical growth of the whitefish caught in 2007 and 2014.

Table 4: The von Bertalanffy estimates and 95 % confidence intervals for the back- calculated growth for whitefish caught in 2007 and 2014.

	2007			2014		
Parameter	Estimate	LCL	UCL	Estimate	LCL	UCL
L_∞	30.432	28.756	32.570	31.082	29.634	32.733
K	0.370	0.304	0.447	0.320	0.281	0.364
t_0	0.222	0.021	0.391	0.078	-0.028	0.180

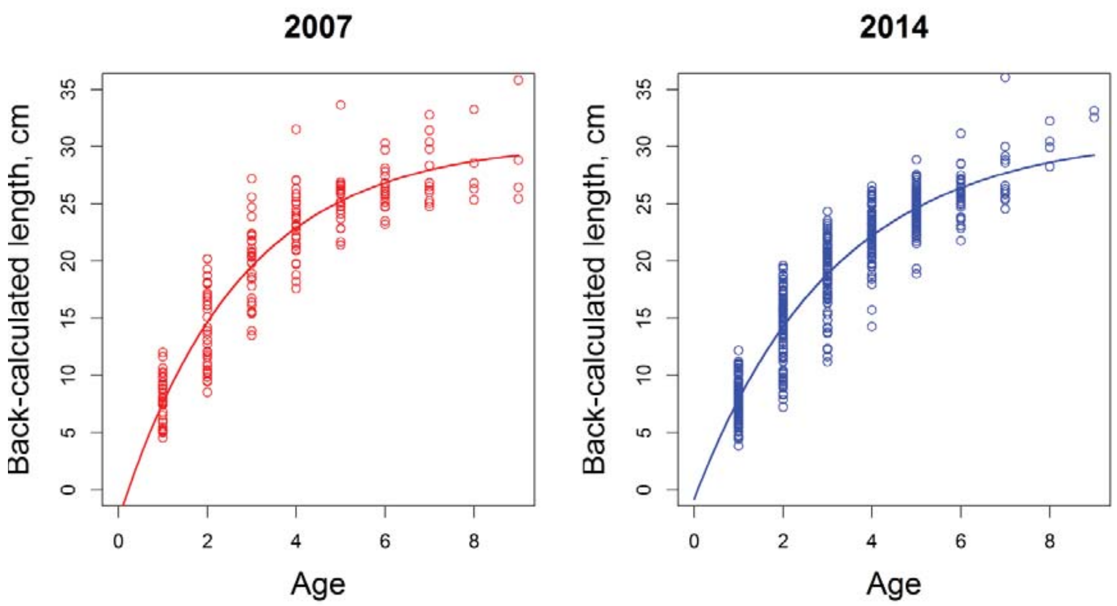


Figure 13: Back-calculated lengths in cm based on age determined from scales for whitefish caught in 2007 and 2014.

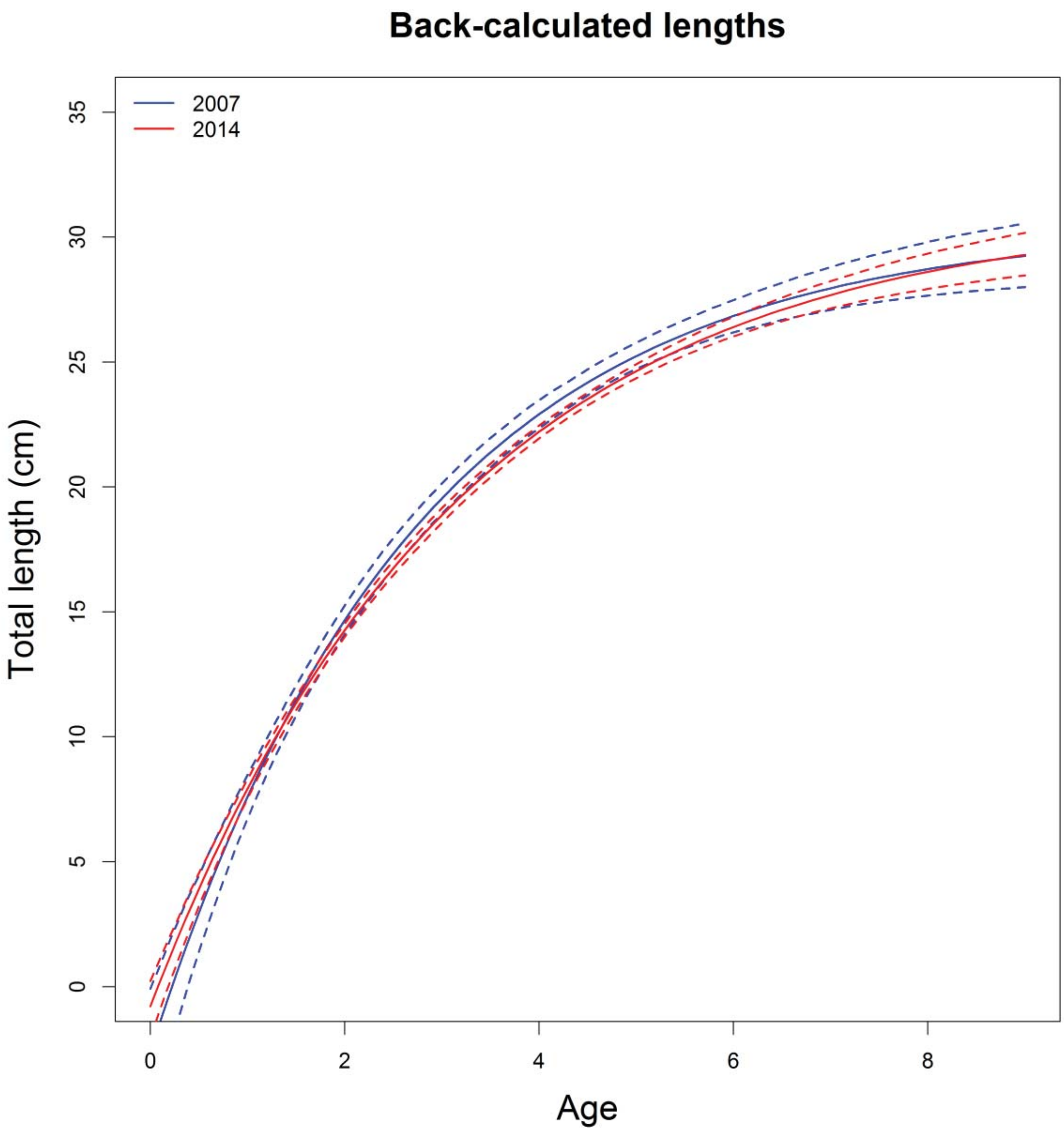


Figure 14: Predicted back-calculated growth of whitefish from 2007 (blue line) and 2014 (red line), based on age determined from scales. Dashed lines represent 95% confidence intervals.

3.2 Whitefish and parasites

Since 2007, the proportion of whitefish not infected by *T. crassus* had decreased from around 20 to 10 percent. However, there also seems to have been a slight shift from higher proportions of fish with high infection intensity to a higher proportion of fish with lower infection intensity (Figure 15). The maximum value of parasites was highest in 2014 with one whitefish containing 18 parasites (Figure 15).

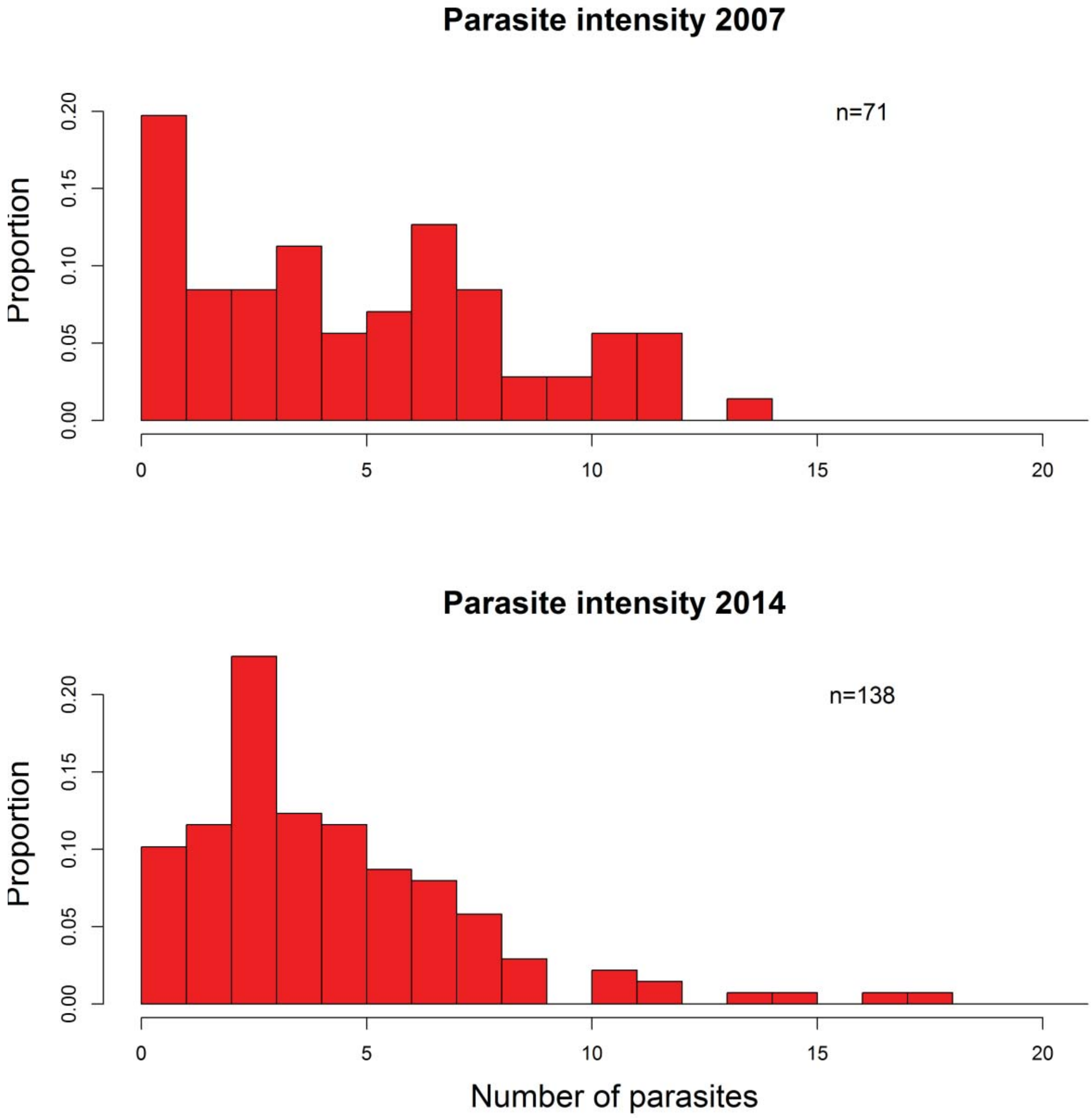


Figure 15: Parasitic intensity for all whitefish caught in 2007 and 2014.

The AIC model selection showed that a quadratic expression of age combined with an interaction term of standardized length (st.length) and year is the most supported model describing the variation in parasitic intensity amongst the whitefish (Table 5 & 6).

Table 5: Results from the AIC model selection for GLM-models were fitted to predict the parasite infection intensity in whitefish.

Model nr:	Model elements	df	AIC	Δ AIC
Model 7.1.1	Age^2*standardized length*Year[a]	10	972.30	0
Model 7.1	Age^2*standardized length*year	12	973.95	1.65
Model 11	Age^2*weight	6	1013.76	41.46
Model 7	Age^2*standardized length	6	1015.08	42.78
Model 7.2	Age^2*standardized length+year	7	1017.09	44.79
Model 12	Age^2+weight	4	1028.19	55.89
Model 8	Age^2*condition factor	6	1072.51	100.21
Model 4	Age^2*gender	6	1075.57	103.27
Model 2	Age^2	3	1080.77	108.47
Model 9	Age^2+condition factor	4	1082.50	110.20
Model 3	Age^2+gender	4	1082.70	110.40
Model 1	Age	2	1083.68	111.38
Model 10	Weight	2	1113.40	141.10
Model 5	Gender	2	1117.57	145.27
Model 6	Condition factor	2	1117.61	145.31

a = after removing the term Age^2:standardized length:year (backward selection).

Table 6: The parameter estimates **A** and anova table **B** of the most supported infection intensity model (Table 5). Parameter estimates are provided on log-scale due to the Poisson-distribution assumed for the infection intensity.

A	Estimate	Std. Error
Intercept	2.225610	0.261629
Age^2	-0.223094	0.060484
Age^2	0.012742	0.003131
St.length	0.236293	0.182085
Year [2014]	-2.132845	0.337634
Age^2*st.length	-0.212573	0.051024
Age^2*st.length	0.011333	0.003501
Age^2*year [2014]	0.561985	0.087464
Age^2*year [2014]	-0.031768	0.005585
St.length*year [2014]	0.437179	0.101344

B	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
Age^2	2	39.076	193	536.14	$3.271*10^{-9}$
St. length	1	47.209	192	488.93	$6.382*10^{-12}$
Year	1	0.092	191	488.84	0.7614
Age^2*st. length	2	24.388	189	464.45	$5.061*10^{-6}$
Age^2*year	2	31.498	187	432.95	$1.446*10^{-7}$
St. length*year	1	19.279	186	413.67	$1.130*10^{-5}$

A contour plot of the predicted values shows that the infection intensity in whitefish varies with the age, standardized length and the year of catch (Figure 16). For older fish there is a trend that fish with low standardized lengths hold more parasites than fish with high standardized lengths. The trend is reverse for younger whitefish where individuals with high standardized lengths seem to hold more parasites than young fish with low standardized lengths (Figure 16). It was also a tendency that the infection intensity had slightly decreased at least for older whitefish since 2007. However, lack of parasitic data from young whitefish in 2007 makes it difficult interpret the result for the youngest age groups (Figure 16).

Figure 16: Predicted infection intensity of whitefish in relation to st.length and age. Each blank symbol represents a whitefish of certain st.length and age. The lines represent predicted numbers of parasites isolines for the predicted infection intensity.

The AIC model selection showed that a quadratic expression of age combined with an interaction term of standardized length and year is the most supported model describing the parasitic prevalence amongst the whitefish (Table 7 & 8).

Table 7: Results from the AIC model selection for GLM-models were fitted to predict the parasite prevalence in whitefish.

Model nr:	Model elements	df	AIC	ΔAIC
Prevalens mod 7.1.1	Age^2*standardized length*year[a]	11	88.66	0
Prevalens.mod7.2	Age^2*standardized length+year	7	126.14	37.78
Prevalens.mod7	Age^2*standardized length	6	128.56	39.90
Prevalens.mod11	Age^2*weight	6	128.86	40.20
Prevalens.mod12	Age^2+weight	4	139.14	50.48
Prevalens.mod6	Condition factor	2	152.99	64.33
Prevalens.mod10	Weight	2	153.65	64.99
Prevalens.mod8	Age^2*condition factor	6	154.60	65.94
Prevalens.mod9	Age^2+condition factor	4	155.50	66.84
Prevalens.mod5	Gender	2	159.86	71.20
Prevalens.mod1	Age	2	159.89	71.23
Prevalens.mod2	Age^2	3	160.53	71.87
Prevalens.mod3	Age^2+gender	4	161.76	73.10
Prevalens.mod4	Age^2*gender	6	162.74	74.08

a = after removing the term standardized length:year (backward selection).

Table 8: The parameter estimates **A** and anova table **B** of the most supported parasite prevalence model (Table 7). Parameter estimates are provided on log-scale due to the Poisson-distribution assumed for the parasite prevalence.

A	Estimate	Std. Error
Intercept	$2.347*10^{3}$	$2.087*10^{5}$
Age^2	$-5.638*10^{2}$	$5.045*10^{4}$
Age^2	$3.319*10^{1}$	$3.023*10^{3}$
St.length	$5.866*10^{-1}$	$8.357*10^{-1}$
Year [2014]	$-2.346*10^{3}$	$2.087*10^{5}$
Age^2*st.length	$5.036*10^{1}$	$8.095*10^{3}$
Age^2*st.length	-7.399	$1.150*10^{3}$
Age^2*year [2014]	$5.639*10^{2}$	$5.045*10^{4}$
Age^2*year [2014]	$-3.312*10^{1}$	$3.023*10^{3}$
Age^2*st.length*year [2014]	$-5.051*10^{1}$	$8.095*10^{3}$
Age^2*st.length*year [2014]	7.421	$1.150*10^{3}$

B	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
Age^2	2	2.612	193	154.528	0.270892
St.length	1	10.135	192	144.393	0.001455
Year	1	4.397	191	139.996	0.036000
Age^2*st.length	2	27.852	189	112.144	$8.955*10^{-7}$
Age^2*year	2	37.730	187	74.414	$6.412*10^{-9}$
Age^2*st.length*year	2	7.756	185	66.659	0.020697

For whitefish caught in 2007, the predicted probability of having parasites was 90 % for a large proportion of the fish (Figure 17). All individuals without parasites are located as a concentrated group of older fish with high growth which explains the strange shape of the predicted contour isolines. For whitefish caught in 2014 it is a clear tendency that the probability of being infected with the parasite increases with increasing standardized lengths for whitefish with age between 0 and 6 years (Figure 17). The predicted probability of being infected by the parasite was more than 90 % for whitefish older than 7 years, while it was between 50 % and 90 % for younger whitefish, except those with higher growth rate. For whitefish between 0 and 3 years with low growth the predicted prevalence was less than 50 % (Figure 17).

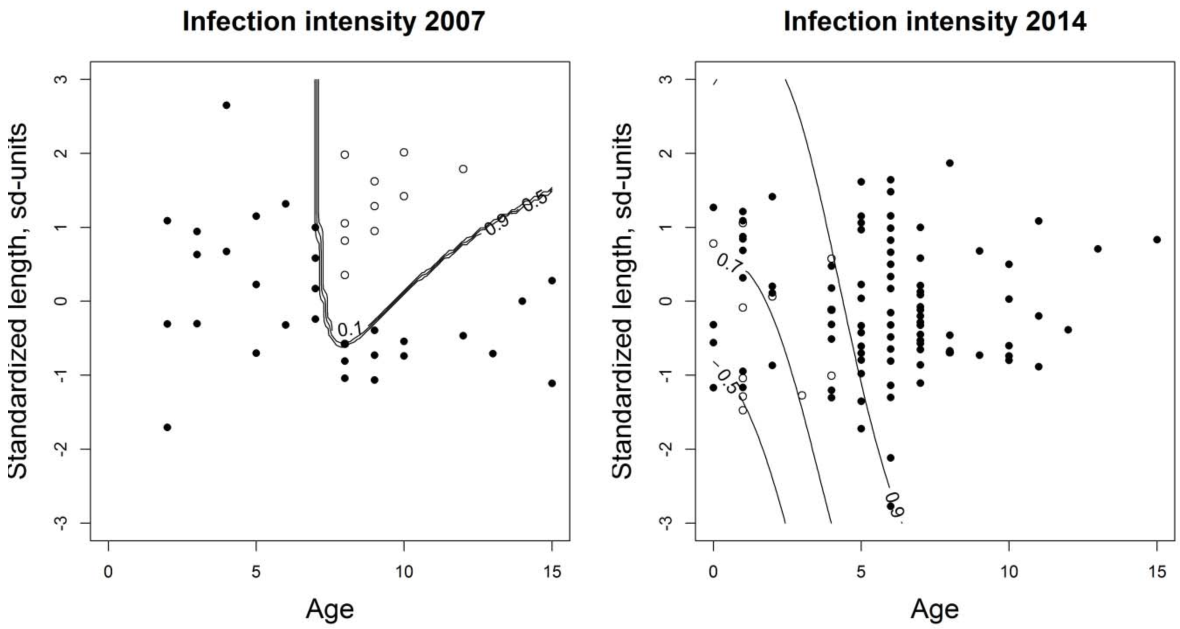


Figure 17: Predicted probabilities for a whitefish of certain age and st.length being infected with *T. crassus*. Black symbols represent the whitefish infected with the parasite, while open symbols represent whitefish without parasites. The lines represent predicted probability isolines for the predicted parasitic prevalence.

3.3 Zooplankton

The proportion of cladocerans in the samples was significantly higher in 2007 than for 2012 and 2014 (Table 9 & Figure 18). The proportion of copepods was almost the same for all three years with a slight increase in 2014 (Figure 18). The proportion of cyclopoid copepods was low in the samples from all three years (Table 9). In 2014-samples, 891 indetermined naupleus larva of Cyclopoida was found among the zooplankton.

Table 9: Density and biomass pr. m^3 of species registered in zooplankton samples collected at sampling location Z between Fluberg and Hov in 2007, 2012 and 2014.

Species	Density Number of individuals pr. m^3			Biomass mg dry weight pr. m^3		
	08.08.2007	24.09.2012	17.09.2014	08.08.2007	24.09.2012	25.09.2014
Copepoda						
Limnocalanus macrurus	8	8	0	0.34	0.34	0
Heterocope appendiculata	16	8	13	0.68	0.34	0.59
Eudiaptomus gracilis	1560	688	785	7.11	5.63	4.28
Cyclops scutifer	72	0	0	0.24	0	0
Mesocyclops leuckarti	136	240	825	0.26	0.14	0.76
Thermocyclops oithonoides	184	1360	545	0.2	0.64	0.89
Copepoda total:	**1968**	**2304**	**3032**	**8.83**	**7.09**	**6.52**
Cladocera						
Leptodora kindtii	24	0	0	0.18	0	0
Holopedium gibberum	48	32	40	0.37	0.12	0.16
Daphnia galeata	2328	48	0	13.87	0.79	0
Daphnia cristata	776	64	80	4.37	0.17	0.34
Bosmina longispina	352	432	1530	1.44	3.23	9.62
Polyphemus pediculus	16	0	0	0.04	0	0
Bosmina longirostris	0	0	13	**0**	**0**	0.02
Cladocera total:	**3544**	**576**	**1676**	**20.27**	**4.31**	**10.14**
Total:	**5520**	**2880**	**4708**	**29.1**	**11.4**	**16.66**

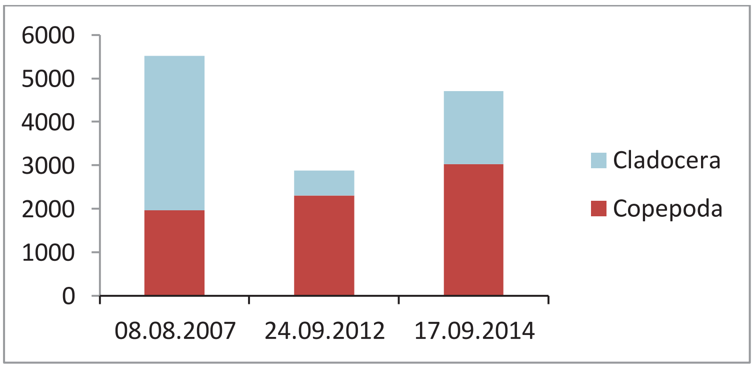


Figure 18: The distribution of Cladocera and Copepoda in samples collected from sampling location Z between Fluberg and Hov in 2007, 2012 and 2014.

3.4 Hydroacoustics

The total biomass in Randsfjorden had significantly increased between 2007 and 2014 (Figure 19 & Table 10). The mean (over 100 m segments) biomass in 2007 was found to be 4.6 kg/ha, while the biomass estimate for 2014 was found to be 13.3 kg/ha. Accordingly, the total biomass in the lake had almost tripled (2.89) between 2007 and 2014.

Table 10: Anova table showing of the test showing changes in biomass in Randsfjorden between 2007 and 2014.

	Df	Sum Sq	Mean Sq	F - value	P - value
year	1	31.40	31.3957	39.981	$5.194*10^{-10}$
Residuals	568	446.03	0.7853		

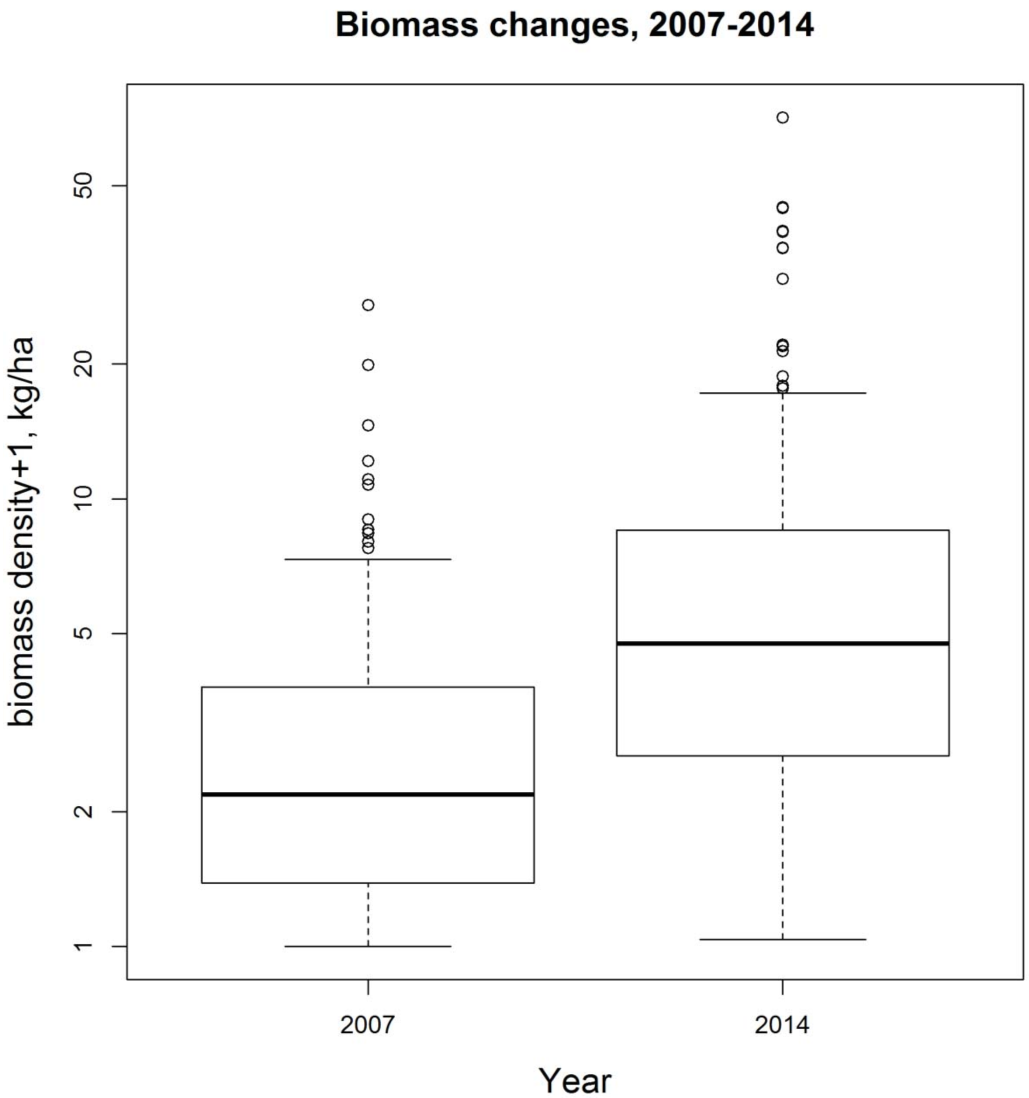


Figure 19: Box plot showing an increase of biomass in Randsfjorden between 2007 and 2014. The increase in total biomass (kg/ha) is given on log scale for the estimated value +1.

A test combining year and layer depth showed that there was a significant change in total biomass for both layer 1 and 2 in the lake between 2007 and 2014 (Table 11). The increase was most significant in layer 2 (Table 1). Layer 3 contained very little fish and was therefore excluded from the test.

Table 11: The parameter estimates **A** and anova table **B** for the model describing changes in biomass in layer 1 and layer 2 in Randsfjorden between 2007 and 2014.

A	Estimate	Std.error
Intercept	1.007	0.077
year	0.269	0.107
layer[2]	0.244	0.110
year2014*layer[2]	0.938	0.151

B	Df	Sum Sq	Mean Sq	F - value	P - value
year	1	51.621	51.621	95.438	$2.2*10^{-16}$
layer	1	5.90	5.90	10.908	0.001
Year *layer	1	20.849	20.849	38.546	$1.416*10^{-9}$
Residuals	376	203.372	0.541		

The TS-derived length distribution differs significantly between the two years (Kolmogorov-Smirnov test: D=0.32, p<0.0001). From the cumulative length-distribution one can see that the proportion of fish smaller than 10 cm was significantly higher in 2007 than 2014, and especially the proportion of fish approximately 3-4 cm was higher in 2007 (Figure 20 & 21). The proportion of fish between 13 and 28 cm was higher in 2014 compared with 2007 and the proportion of fish larger than 30 cm was higher in 2007 compared with 2014 (Figure 21).

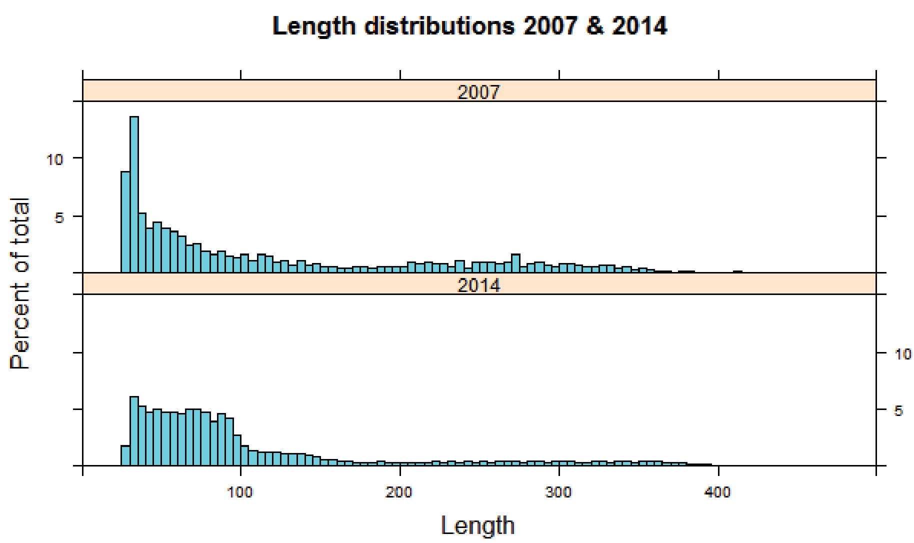


Figure 20: The length distribution (mm) of all fish registered in the hydroacoustic surveys in 2007 and 2014.

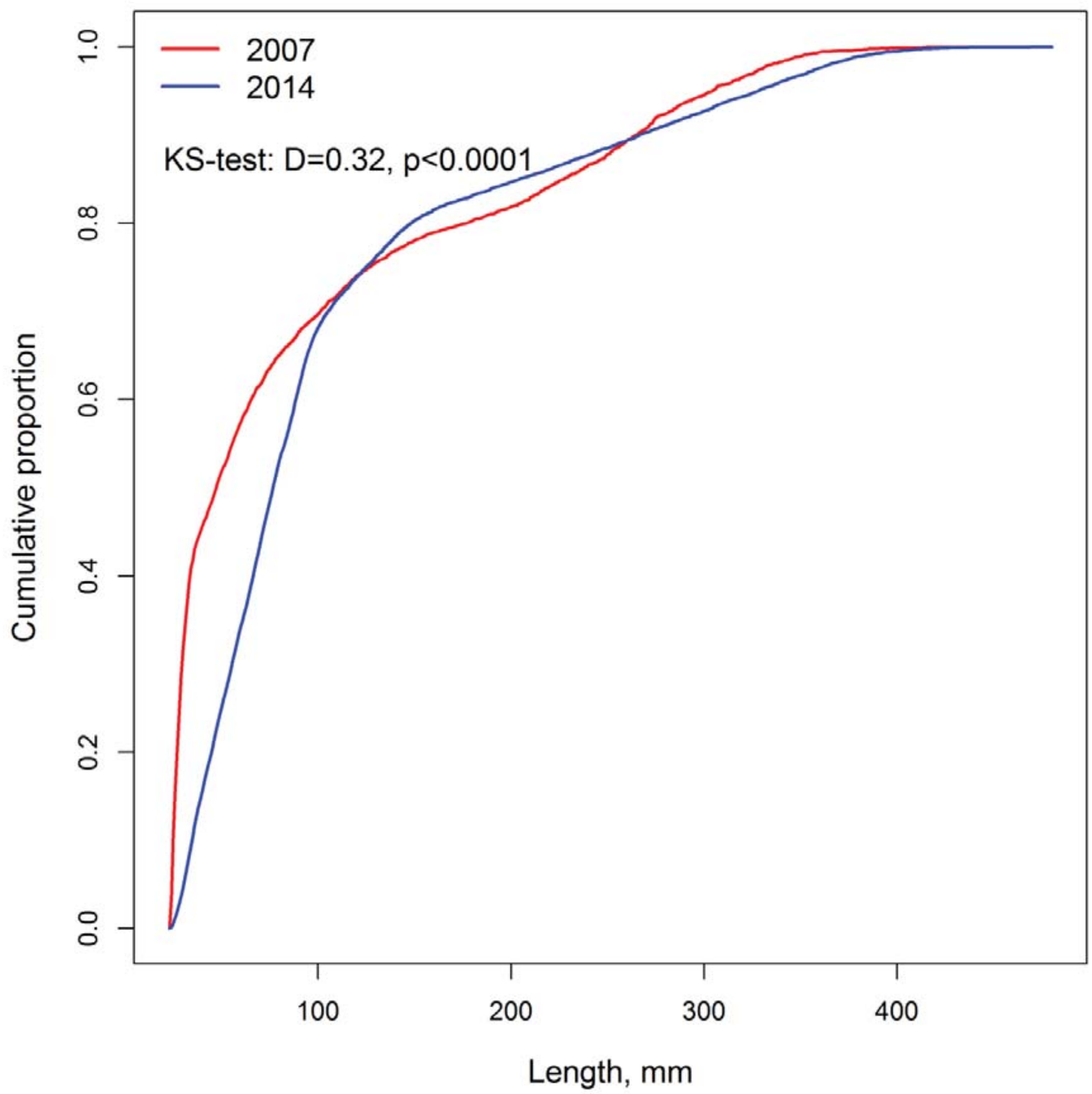


Figure 21: The cumulative length distribution (mm) of fish detected in the 2007-survey (red) and 2014-survey (blue). Kolomogorov-Schmirnoff-test statistics (KS-test) is provided.

4. Discussion

4.1. Fish density

It was expected that a comprehensive culling of whitefish in Randsfjorden would reduce the fish density as earlier shown in Sølensjøen (Museth et al. 2007) and Stuorajavri (Amundsen 1988). In Randsfjorden, the whitefish CPUE for Nordic benthic gillnets was higher in 2014 than 2007 and indicates an increase in the fish density. However, this result may be inaccurate as the effort in 2007 was much lower than the effort in 2014. The Nordic benthic gillnets do also largely catch the benthic morph of the whitefish (Lindås et al. 1996), which is of lower interest in a commercial fishery compared to the pelagic morph. A comparison in whitefish CPUE for the Nordic benthic gillnets is therefore not further assessed. For Nordic pelagic gillnets, the whitefish CPUE had decreased by almost 50 % between 2007 and 2014. This decline may indicate that the culling programme had managed to reduce whitefish density since 2007. However, whitefish catches in Nordic pelagic gillnets were low in 2007 and particularly low in 2014. Therefore, reliable conclusions concerning changes in whitefish density cannot be based on the gillnet catches alone.

The low whitefish catches in 2014 may be explained by a possible aggregation of whitefish in limited areas of the lake. During spawning season, normally starting in Randsfjorden from mid September, the pelagic whitefish aggregates in limited areas around the river estuaries before migrating up river (Enge 1956). Accordingly, the fish density might have been underestimated since the fish survey was conducted in beginning of the spawning period with relatively low effort and randomized locations and stratifications of gillnets. There were also some problems with gillnet failures at sampling location 4 which may explain the very low catches at this location. A strong current in the area is thought to be the main factor affecting the gillnet catches. Several Nordic benthic gillnets had apparently changed direction during the night by drifting along the bottom and attached to rocks and logs. Some gillnets were stuck at the bottom and got severe damage when collected. One of the Nordic pelagic gillnets was also observed standing more or less horizontally in the water and had accordingly very low catches. Therefore, current is a problem that might affect gillnet catches and areas with strong currents should be avoided when conducting a fish survey.

According to the results from the hydroacoustic surveys, the total biomass density in Randsfjorden had almost tripled between 2007 and 2014. This result was not expected as the intensive culling programme was believed to have reduced the density of whitefish and hence the total biomass density in the lake. The cumulative proportion of fish between 13 and 28 cm were higher in 2014 compared to 2007. It is likely that whitefish constitutes the majority of the fish in this length group as the maximum length of smelt caught in gillnets was found to be 13.2 cm. The increase in smaller whitefish might be explained as an effect of reduced competition from larger individuals. Larger individuals more than 28 cm had significantly decreased in the lake since 2007, and as documented by Jensen (1981), reduced competition from larger individuals may be an important factor increasing recruit survival. Thus, the increase in biomass density in Randsfjorden between 2007 and 2014 might be explained by an increase in whitefish recruits.

In 2007, the lake was surveyed with coverage of 7.9 while the coverage was 8.7 in 2014. As coverage affects the precision of the results, a survey design with coverage of more than 2-4 is recommended (Guillard & Vergès 2007; Godlewska et al. 2009). Both the 2007- and 2014 survey met this recommendation so I may assume that the coefficient of variation (CV = standard deviation of the abundance estimate divided by the mean) is well below 0.5. However, there are some major issues that must be taken into account when comparing the hydroacoustic surveys from 2007 and 2014. The 2007-survey was conducted in daylight during early afternoon between 6 and 9 August, while the 2014-survey was conducted during night between 16 and 18 September. According to Sandlund and Lindem (1984) and Sandlund et al. (1992), daytime surveys do often give lower estimates of biomass density than night surveys as pelagic planktivorous fish often form dense schools during daytime and make single fish detection harder. Schooling fish close to the surface may also more frequently try to avoid the boat than single fish (Sandlund & Lindem 1984). During night, the schools dissolve and single fish are more easily detected (Sandlund & Lindem 1984; Sandlund et al. 1992). In Lake Mjøsa, population estimates from night surveys has been documented to be more than twice as high compared with day surveys (Sandlund et al. 1992). Also CEN (2014) recommends the hydroacoustic surveys to be conducted during night avoiding dusk and dawn. Accordingly, the day survey conducted in 2007 might have underestimated the fish density and is therefore less suitable for comparison with the night survey conducted in 2014. Hence, reliable conclusions concerning changes in biomass and length distribution of fish in Randsfjorden cannot be based on a comparison of these two surveys alone.

A partial time series of hydroacoustic surveys conducted in Randsfjorden show tendencies of a decline in biomass density since 1990 (Figure 22). An examination of this time series also shows that the decline had occurred before the initiation of the culling programme.

Torgersen and Gregersen (2009) claimed that the whitefish in Randsfjorden gradually showed some recovery from mid of the 1990s after suffering from recruitment failure in the early 1990s.

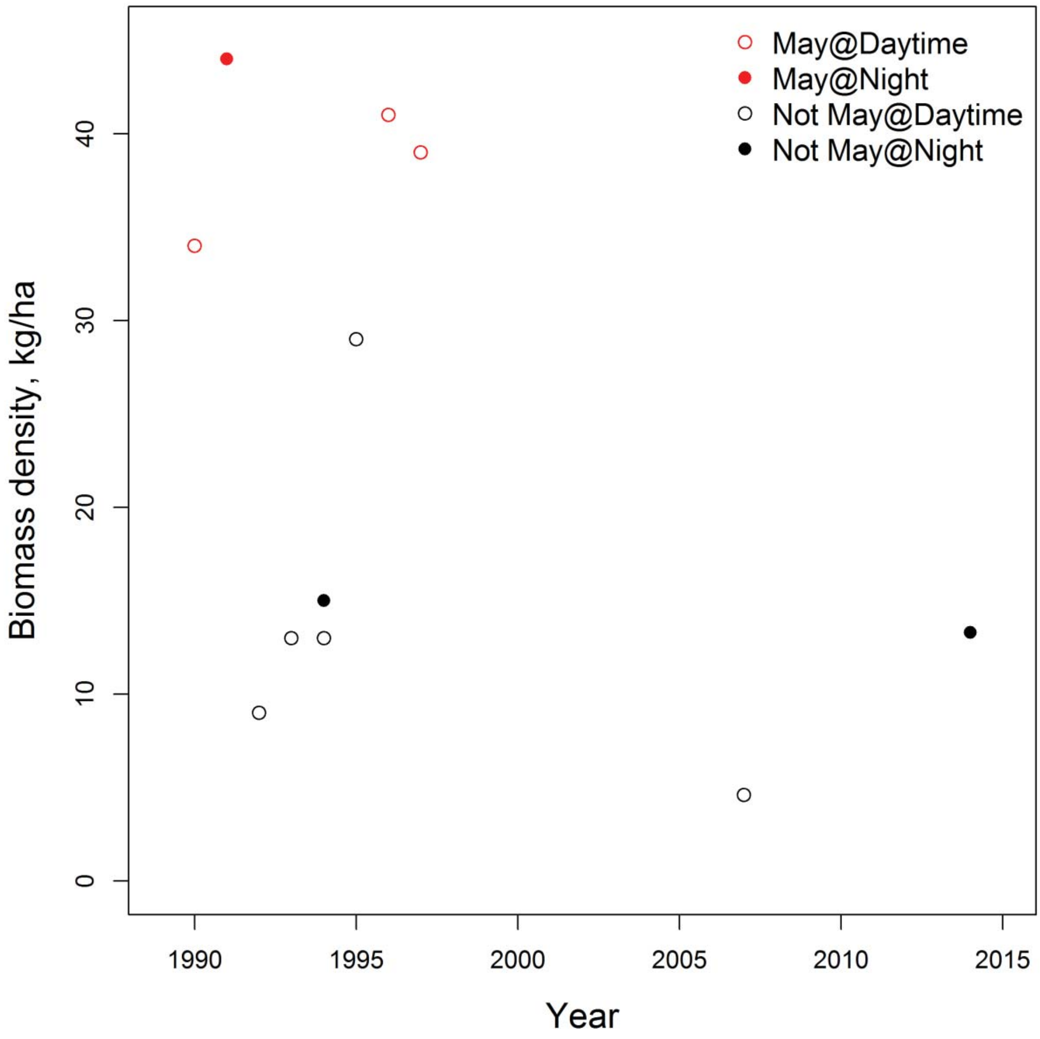


Figure 22: Time series of hydroacoustic surveys conducted in Randsfjorden since 1990 showing changes in biomass density (kg/ha). Filled symbols represent night surveys while blank symbols represent day surveys. Red symbols represent surveys conducted during May. Data from 1990 to 1997 is acquired from (Eriksen et al. 1998).

Between 1990 and 1994, the whitefish were in particularly bad condition due to high population densities and had problems of developing gonads and even reaching the spawning locations upriver (Torgersen & Gregersen 2009). The decline in whitefish density between 1997 and 2007 has no clear explanation, but might be due to by enhanced conditions in the lake as the whitefish condition slightly increased during the end this period (Torgersen & Gregersen 2009) (Figure 23).

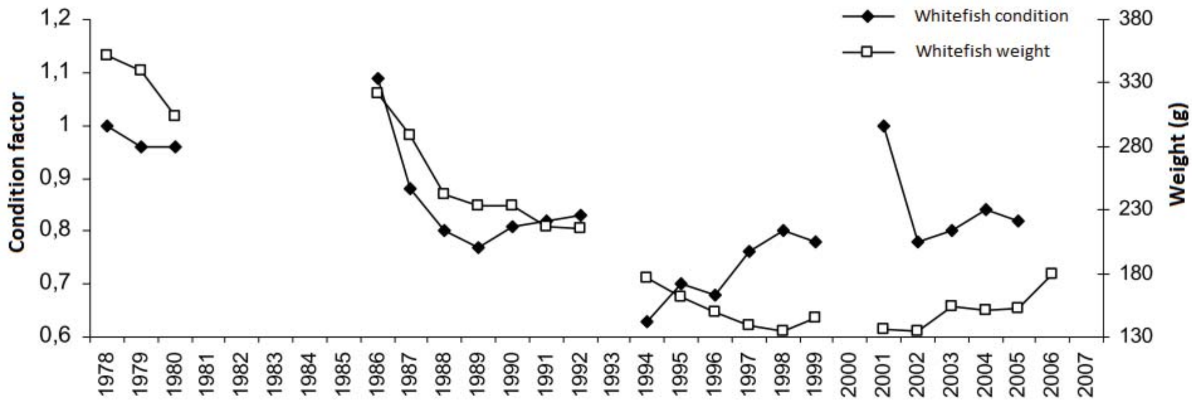


Figure 23: Development in whitefish weight and conditions between 1978 and 2007 based on whitefish caught in pelagic gillnets with mesh sizes 26 and 39 mm. After (Torgersen & Gregersen 2009).

The high degree of annual fluctuations in the estimated biomass densities can be explained by large differences in annual recruitment. However, differences in biomass density may also be a result of seasonal variations as the hydroacoustic surveys have been conducted in different seasons, from mid of May to mid of September (Eriksen et al. 1998; Rustadbakken et al. 2010). According to Sandlund and Lindem (1984) and (Sandlund et al. 1992), the distributions of fish in pelagic areas differ throughout the year and often peak during late summer and autumn when populations of preferred zooplankton species is highest. However, the highest biomass densities recorded in Randsfjorden have been documented from hydroacoustic surveys conducted during spring (Lindås et al. 1997) (Figure 22).

Eriksen et al. (1998) announced that the estimates of annual changes in biomass density do not reflects real changes in fish density, but rather errors in the methods used when conducting the hydroacoustic surveys. This situation reflects the importance of standardizing the sampling methods when doing population monitoring. Accordingly, new standardized methods for hydroacoustic survey performance in Randsfjorden are crucial in order to collect more comparable data.

4.2. Whitefish age, size and growth

The whitefish population in Randsfjorden showed some improvements in age structure between 2007 and 2014. Prior to the initiation of the culling programme, Rustadbakken et al. (2010) found that the whitefish population was generally old where 60 % of the fish was eight years or older in 2007. A similar situation were reported by Styrvold et al. (1981) and Lindås et al. (1996). However in 2014, more than 70 % of the fish was younger than 8 years which supports the predicted juvenilisation outcome of the intensive culling programme. The same juvenilisation effect from whitefish culling has also been documented by Amundsen (1988) in

Stuorajavri and Museth et al. (2007) in Sølensjøen. The back-calculated growth for whitefish showed however no significant changes in annual average growth for any age groups between from 2007 and 2014 and the stagnation length of 28 cm was also the same as documented by (Rustadbakken et al. 2010). In 1978-1979, Styrvold et al. (1981) found that the whitefish stagnated at lengths between 32-34 cm. There was although found a slight increase in average whitefish weight between 2007 and 2014 as the average length of 195 g in 2014 was higher than the average length of 180 g reported in 2007 by Torgersen and Gregersen (2009). The average weight of 235 g reported by Rustadbakken et al. (2010) the same year is less relevant as these catches are believed to contain a significant number of large benthic whitefish. The intensive culling programme in Randsfjorden had apparently not managed to attain any major recovery of whitefish growth between 2007 and 2014, and further actions are necessary for achieving sufficient growth improvements.

In contrast, Museth et al. (2007) documented rapid improvements in whitefish growth in Sølensjøen after removing more than 50 tons of fish during a three years period. In Randsfjorden, the fishing programme had removed 208 tons of whitefish between 2007 and 2014 without attaining any significant growth improvements. The culling must therefore be considered unsuccessful in mitigating density dependent factors that inhibit whitefish growth. In fact, successful culling and recovery of whitefish populations has largely been documented from much smaller lakes such as Stuorajavri (Amundsen 1988; Amundsen & Kristoffersen 1990) and Sølensjøen (Museth et al. 2007) with total areas of 25 and 21 km^2. Hence, an underestimation of the effort needed for reducing the population density might be an explanation of why the whitefish growth has failed to improve in such a large lake as Randsfjorden. Prior to the initiation of the culling programme, Rustadbakken et al. (2010) announced that the whitefish population needed to be culled at least 50 tons annually in order to restore the quality and size of the fish. This recommendation has not been met any of the years since the culling programme was initiated. Reaching or even surpassing this limit may therefore be crucial for a sufficient recovery of growth in the whitefish population.

4.3. Smelt and roach

According to Taugbøl et al. (2004), it may be a great challenge to estimate the effort needed in order to successfully cull a fish population. The area and depth of the lake as well as competition and predation from other individuals or species, are some of the factors that must be taken into account when assessing the effort (Taugbøl et al. 2004). Especially, it may be hard to predict how unintentional interference from other species may become a problem when working with a species-rich system such as Randsfjorden. According to the gillnet catches, the populations of roach and smelt had significantly increased in Randsfjorden between 2007 and 2014. A comprehensive study from Finnish lakes has shown that roach often has a negative impact on whitefish growth (Raitaniemi et al. 1999). Young individuals are especially vulnerable as they compete with roach over the same food resources (Raitaniemi et al. 1999). Although Randsfjorden is deep compared to many Finnish lakes, and the competition relationship may differ from Finnish lakes, further increases in the roach population may affect the whitefish population and require more attention. The population of smelt had also increased in Randsfjorden between 2007 and 2014. This species may have a large impact on the fish community as it consumes both phytoplankton, zooplankton and other individuals (Sandlund et al. 2005). Smelt is documented to influence the food resources of other species such as whitefish and vendace *C. albula* (Sandlund et al. 2005). More research is therefore required to understand how the smelt is interacting with whitefish in Randsfjorden as they use the same habitat and also may compete over the same food resources.

4.4. *T. crassus* and zooplankton community

The infection of *T. crassus* had shown some improvements since 2007 with a slightly higher proportion of young whitefish without parasites and an overall decreased infection intensity in the population. However, the infection of *T. crassus* was still a problem in Randsfjorden as 90 % of the whitefish was found to be infected by the parasite. In contrast, Styrvold et al. (1981) found that only 1 % of the whitefish in Randsfjorden were infected with the parasite in early 1980s. The parasite infection was highest in old, slow-growing individuals, but also fast-growing young individuals were heavily infected. This situation was also observed in Canadian lakes by Miller (1952) and later described from a Finnish lake by Pulkkinen and Valtonen (1999) in a more extensive study. Pulkkinen and Valtonen (1999) found that the accumulation of parasites was closely related to age and growth. In Randsfjorden, the infection intensity or accumulation of parasites in whitefish increased with increased growth for younger fish while the opposite was the case for older fish. The high infection intensity in young and fast growing fish might be explained by a higher intake of food, potentially including infected copepods, which again increases the accumulation of parasites. Slow-growing fish may consume fewer copepods and is therefore less exposed to parasite infection. As the fish accumulate more and more parasites the damage caused by the parasite will eventually inhibit the growth. This hypothesis is supported by Pulkkinen and Valtonen (1999) who also claim that whitefish seems to reach a certain threshold level of parasitic intensity were the accumulation of parasites is rapidly increased and further growth is inhibited. In

Randsfjorden, the parasitic threshold level seems to be reached when the fish is around five years old as the parasite accumulation seems to increase from this age. Pulkkinen and Valtonen (1999) found no connection between infection intensity and increased whitefish mortality, but laboratory experiments has shown that infection of *T. crassus* may cause severe damage and increased mortality to whitefish, especially young individuals (Dick & Rosen 1982).

An intensive exploitation of whitefish has earlier been described as a possible strategy in mitigating the infection intensity of *T. crassus* (Amundsen & Kristoffersen 1990). Brooks and Dodson (1965) documented that a comprehensive reduction in fish density may change the composition of the zooplankton fauna from smaller copepods to larger cladocerans due to reduced selective predation on larger cladocerans. An increase in large cladocerans may therefore result in a whitefish dietary shift from infected copepods to larger and more preferred cladocerans and accordingly reduced infection intensity of *T. crassus* in the fish (Amundsen & Kristoffersen 1990). However, the high infection intensity in whitefish in Randsfjorden indicates that infected copepods still constitute a significant part of the whitefish diet.

According to Miller (1952), Pulkkinen and Valtonen (1999) and Sichrowsky et al. (2013), copepods of the genus *Cyclops* are the most suitable intermediate hosts for *T. crassus. Cyclops*-species such as *C. streenus* and *C. scutifer* are widely known as suitable host for *T. crassus* (Miller 1952; Lawler 1955; Pulkkinen & Valtonen 1999; Pulkkinen et al. 2000). There are also a few records showing that *Eudiaptomus gracilis* might be infected by the parasite (Pulkkinen et al. 1999). However, this species is not documented to be an important host for *T. crassus* (Sichrowsky et al. 2013).

In 2007, Rustadbakken et al. (2010) documented a large proportion of large cladocerans such as *Daphnia galeata* in the zooplankton samples, and found only a small number of *Cyclops*. In comparison, the samples collected in 2014 and especially 2012 had a considerably lower proportion of cladocerans, although the fraction of *Cyclops* and other copepods were almost similar as found by (Rustadbakken et al. 2010). However, the zooplankton samples from 2012 and 2014 were collected in late autumn, and a lower proportion of cladocerans is most likely a result of seasonal fluctuations rather than increased feeding pressure (Faafeng et al. 1979). According to Løvik et al. (2005) and Løvstad (2014), there has been a relatively high proportion of large cladocerans in samples collected annually since 2001 and there are also indications of an improvement in the zooplankton fauna in the lake since the end of the 1980s

(Løvik et al. 2005; Løvstad 2014). The proportion of cyclopoid copepods has accounted for only 10% or less of the total biomass in zooplankton samples since 2001(Løvik et al. 2005; Rustadbakken et al. 2010; Løvstad 2014). Such a low fraction of *Cyclops* do not correspond with the high infection intensity of *T. crassus* found in the whitefish in Randsfjorden. According to Miller (1952), *T. crassus* is transmitted from pike to cyclopoid copepods during a short period during spring and early summer when pikes are spawning. As the zooplankton samplings in Randsfjorden are conducted during autumn, there are no records of the abundance of cyclopoid copepods in the lake during springtime. Therefore, zooplankton samplings should also be conducted during springtime in order to find that a larger population of cyclopoid copepods during this transmission period might explain the high infection intensity of *T. crassus* in the whitefish.

Cyclops scutifer is the only cyclopoid copepod found in the zooplankton samples between 2001 and 2014 in Randsfjorden (Løvik et al. 2005; Løvstad 2008; Løvstad 2011; Løvstad 2014). Nielsen et al. (1985) and Rognerud et al. (1989) had earlier documented scattered individuals of *C. abyssorum* in pelagic areas of the lake. However, this species has not been documented in zooplankton samples collected the last twenty years and cannot be a major host for *T. crassus* in Randsfjorden. The most effective host for *T. crassus* in many European lakes is considered to be *C. streenus* (Miller 1952), and was earlier found to be one of several hosts for *T. nodulosus* in Bogstad Lake near Oslo, southern Norway (Halvorsen 1967). This species is also reported from Lake Jarenvatnet (Norwegian Biodiversity Information Centre 2015) which distributes into Randsfjorden. However, *C. streenus* is not yet documented from Randsfjorden and *C. scutifer* must therefore be considered as the first intermediate host for *T. crassus* in the lake. Additional examination of this species and its seasonal abundance in Randsfjorden may provide valuable information when developing new strategies aiming at reducing the infection intensity of *T. crassus* in the whitefish.

4.5. Management implications

The intensive culling programme has managed to attain some positive results on whitefish age and infection intensity since it was initiated in 2007. However, further actions are necessary for a sufficient recovery of the whitefish stock. Increasing the fishing effort is required in order to meet the recommendations of an annual removal of 50 tons whitefish from the lake. The effort may be increased by installing additional trap nets, although introduction of new gears should also be evaluated. The pelagic whitefish tend to migrate in large schools during summer in search for food and may therefore be easily caught during this season. By using large purse seines or Danish seines, the fish can effectively be removed in large quantities at low costs. Economy is always a limiting factor in such projects and new strategies should always be developed without unnecessary use of expensive manpower.

The hydroacoustic surveys conducted in Randsfjorden have shown to be less valuable for comparisons as they were performed in different seasons during the year and by using different methods, often with significant errors. New standardized methods of conducting the hydroacoustic surveys are required in order to collect more comparable data of the biomass density. Future surveys should always be based on the new CEN-standard for hydroacoustic surveys (CEN 2014). The hydroacoustic surveys should therefore be conducted at night and during August in order obtain more precise estimations of biomass densities in the lake. Additional surveys may also be conducted during May as biomass estimations also seem to be high during this month. Conducting hydroacoustic surveys during late autumn should be avoided as aggregation of spawn fish in the river estuaries may give lower estimates of biomass density.

The increase of roach and smelt in the lake must be taken into account because competition from these species may inhibit whitefish growth. The population development of these species should therefore be monitored and their position as competitors to whitefish should be evaluated.

An extended zooplankton sampling during springtime is required to understand if the composition of cladocerans and cyclopoid copepods in the zooplankton community differ from the samples conducted in autumn. Zooplankton sampling in shallow waters during spring time may be valuable to achieve better knowledge about the transmission of *T. crassus* between pike, *C. scutifer* and whitefish. The zooplankton sampling should also be combined with stomach samplings of whitefish in order to understand how *C. scutifer* may act as an important food resource for whitefish during this period. *C. streenus* infected by *T. crassus* has been found to change its behavior by swimming closer to the surface and becoming more vulnerable to predation (Pulkkinen et al. 2000). If *T. crassus* has the same manipulating effect on *C. scutifer*, this *Cyclops*-species may become a more preferred prey for as it is easy to catch. Stomach sampling of whitefish in Randsfjorden is therefore crucial in order to find if infected *C. scutifer* is a more preferred prey during spring in comparison with other copepods or cladocerans. To more effectively handle the parasite, removal of pike must be evaluated for Randsfjorden. An extensive reduction in the pike population might reduce the parasitic reservoir and the transmission rate of parasites to whitefish. The removal of pike was the key factor of reducing the infection intensity of *T. crassus* in Stuorajavri (Amundsen & Kristoffersen 1990). As mentioned, the transmission of *T. crassus* to cyclopoid copepods is limited to a only short period of time during spring and early summer as the parasite release its eggs when pike enters shallow waters to spawn (Miller 1952). The pike can effectively be removed during this period by using benthic gillnets. The removal should be focused on large pike more than three years old since younger pikes seem to be little infected by the parasite (Miller 1952; Lawler 1955).

4.6 Conclusions

Low gillnet catches and hydroacoustic surveys less suitable for comparison made it difficult to state a reliable conclusion concerning changes in whitefish density between 2007 and 2014. A time series of hydroacoustic surveys conducted in Randsfjorden since early the 1990s show indications of a long term reduction in biomass density between 1990 and 2015. However, new standardized methods of conducting the hydroacoustic surveys are required in order to collect more comparable data of the biomass density. The intensive culling programme has only managed to attain minor growth improvements in the whitefish population since 2007. Thus, the intensive culling programme needs extensive improvement and new strategies in order to achieve sufficient growth recovery in the whitefish population. The parasite *T. crassus* is still a major problem in the in the lake as 90 % of the pelagic whitefish population is found to be infected. Extensive sampling of the zooplankton community during springtime combined with stomach sampling of whitefish is recommended for obtaining more knowledge concerning the high infection intensity of *T. crassus* in whitefish in Randsfjorden. Extensive removal of pike should be evaluated as a new strategy for reducing the infection intensity of the parasite in whitefish. Summarized, the whitefish stock in Randsfjorden needs further improvements before a commercial fishery can be established.

5. References

Abadie, A. (2002). "Bootstrap Tests for Distributional Treatment Effects in Intrumental Variable Models.". *Journal of the American Statistical Association*, 97: 284-292.
Akaike. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716-723.
Amundsen, P. A. (1988). Effects of an intensive fishing programme on age structure, growth and parasite infection of stunted whitefish (Coregonus lavaretus L. s.l.) in Stuorajavri, northern Norway. *Finnish Fish*, 9: 425-434.
Amundsen, P. A. & Kristoffersen, R. (1990). Infection of whitefish (Coregonus lavaretus L. s.l.) by Triaenophorus crassus Forel (Cestoda: Pseudophyllidea): a case study in parasite control. *Can. J. Zool.*, 68: 1187-1192.
Appelberg, M., Berger, H. M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J. & Rask, M. (1995). Development and intercalibration of methods in Nordic freshwater fish monitoring. *Water, Air and Soil Poll.*, 85: 401-406.
Balk, H. (2015). *Sonar 4 and Sonar 5-pro post processing systems*: Lindem Data Acquisation A/S.
Borgstrøm, R. & Hansen, L. P. (2000). Fiskeforsterkningstiltak og beskatning. In Borgstrøm, R. & Hansen, L. P. (eds) *Fisk i ferskvann - Et samspill mellom bestander, miljø og forvaltning*, pp. 277-290. Oslo: Landbruksforlaget.
Brooks, J. L. & Dodson, S. I. (1965). Predation, Body Size, and Composition of Plankton. *Science*, 150: 28-35.
Burnham, K. P. & Anderson, D. R. (1998). *Model Selection and Inferences*. New York: Springer Verlag.
CEN. (2014). Water quality - Guidance on the estimation of fish abundance with mobile hydroacoustic methods. *Report European Committee for Standardization* 2014:15910. 43 pp.
Dahl, K. (1910). *Alder og vekst hos laks og ørret belyst ved studier av deres skjæl.* Kristiania: Centraltrykkeriet. 115 pp.
Dick, T. A. & Rosen, R. (1982). Experimental infections of whitefish, Coregonus clupeaformis (Mitchill), with Triaenophorus crassus Forel. *Journal of Fish Diseases*, 5: 83-86.
Dick, T. A. & Watson, R. (1977). *The whitefish-pike parasite.* Wringley, R. E. (ed.). Manitoba Nature Winter 1077. Winnipeg: Manitoba Nature pp. 26-31.
Eknæs, Å. (1979). *Innlandsfiske.* Oslo: Det Norske Samlaget.
Enge, K. (1956). *Undersøkelse av de systematiske forhold hos Sik i Randsfjorden.* Master degree. Oslo: University of Oslo. 56 pp.
Eriksen, H., Lindås, O. R. & Hegge, O. (1998). Bedre bruk av fiskeressursene i regulerte vassdrag i Oppland. *Fagrapport 1997. Fylkesmannen i Oppland, miljøvernavdelingen*, 1998:4. Lillehammer. 69 pp.
Faafeng, B., Alsaker-Nøstdahl, B., Gøsta, K., Løvik, J. E., Sahlqvist, E.-Ø. & Tjomsland, T. (1979). Randsfjorden 1978 *Årsrapport Norsk institutt for vannforskning-NIVA*, 0-78014. Oslo. 164 pp.
Godlewska, M., Dlugoszewski, B., Doroszczyk, L. & Jozwik, A. (2009). The relationship between sampling intensity and sampling error-empirical results from acoustic surveys in Polish vendace lakes. *Fisheries Research*, 96: 17-22.
Guillard, J. & Vergès, C. (2007). The repeatability of fish biomass and size distribution estimates obtained by hydroacoustic surveys using various sampling strategies and statistical analyses. *Hydrobiologia*, 92: 605-617.
Gulland, J. A. (1977). *Fish Population Dynamics.* 2nd ed. London: John Wiley & Sons Ltd.
Halvorsen, O. (1967). Studies of the helminth fauna of Norway. X. Triaenophorus Nodulosus (Pallas, 1760) (cestoda) in Bogstad Lake. I. Copepods as first intermediate hosts *Nytt Magasin for Zoologi*, 15: 124-129.
Hegge, O., Qvenild, T. & Skurdal, J. (1990). Sikfisket i Randsfjorden 1978-1988. *Rapport Fylkesmannen i Oppland Miljøvernavdelingen*, 1990:10. Lillehammer. 20 pp.
Huitfeldt-Kaas, H. (1918). *Ferskvandsfiskenes utbredelse og indvandring i Norge: med et tillæg om krebsen.* Kristiania: Centraltrykkeriet.

Høitomt, G. (2013). Innlandsfiske i Randsfjorden - Oppsummering av tynningsfiskeprosjekt gjennomført i 2013. *Rapport. Kistefos Skogtjenester AS*, 2013:14. 16 pp.

Jensen, A. L. (1981). Population regulation in lake whitefish, Coregonus-clupeaformis (Mitchill). *Journal of Fish Biology*, 19: 557-573.

Jonsson, B. & Matzow, D. (1979). *Fisk i vann og vassdrag.* Oslo: Aschehoug

Klemetsen, A. & Amundsen, P. A. (2000). Fiskesamfunn i nord-norske innsjøer. In Borgstrom, R. & Hansen, L. P. (eds) *Fisk i ferskvann - Et samspill mellom bestander, miljø og forvaltning*, pp. 89-101. Oslo: Landbruksforlaget.

Kottelat, M. & Freyhof, J. (2007). *Handbook of European freshwater fishes.* Berlin: Kottelat, Carnol, Switzerland and Freyhof, Berlin, Germany.

Lawler, G. H. (1955). Life history studies of Triaenophorus at Heming Lake, Manitoba. Part I. The life of *T. crassus* and *T.nodulosus* in the final host, *Esox lucius* with special reference to changes in infection rate from year to year. *Manuscript reports of the biological stations*, 1955:604. 17 pp.

Lea, E. (1910). On the methods used in herring investigations. *Publs. Circonst. Cons. perm. int. Explor. Mer 1910*, 53: 7-174.

Lekang, O.-I. (1988). *Innlandsfiske.* Oslo: Landbruksforlaget.

Lindås, O. R., Eriksen, H. & Hegge, O. (1996). Fiskeribiologiske undersøkelser i Randsfjorden og Dokka-Etna etter regulering av Dokka. *Rapport Fylkesmannen i Oppland Miljøvernavdelingen*, 1996:8. Lillehammer. 40 pp.

Lindås, O. R., Eriksen, H. & Hegge, O. (1997). Bedre bruk av fiskeressursene i regulerte vassdrag i Oppland. *Fagrapport 1996. Fylkesmannen i Oppland, miljøvernavdelingen*, 1997:2. Lillehammer. 68 pp.

Løvik, J. E., Kjelberg, G. & Brettum, P. (2005). Overvåkning av vannkvalitet og biologiske forhold i Randsfjorden med tilløpselver - Samlerapport for 2001-2004. *Rapport. Norsk institutt for vannforskning-NIVA*, 2005:4957. Oslo. 54 pp.

Løvstad, Ø. (2008). Vassdragsovervåkning i Randsfjorden og sidevassdrag 2007. *Rapport. Limno-Consult - Norwegian Institute of Applied Limnology*. Oslo. 22 pp.

Løvstad, Ø. (2011). Vassdragsovervåkning i Randsfjorden 2011. *Rapport Limo-Consult, Norwegian Institute of Applied Limnology*. Oslo. 18 pp.

Løvstad, Ø. (2014). Vassdragsovervåkning i Randsfjorden og sidevassdrag - Randsfjorden 2013. *Rapport. Limno-Consult, Norwegian Institute of Applied Limnology*. Oslo. 21 pp.

MacCullagh, P. & Nelder, J. A. (1989). *Generalized Linear Models* 2ed. London: Chapman & Hall.

Miller, R. B. (1952). *A review of the Triaenophorus problem in Canadian lakes.*, vol. 95. Ottawa: Bull. Fish Res. Boars Can. 42 pp.

Museth, J., Sandlund, O. T. & Borgstrom, R. (2007). Coexistence between introduced whitefish (Coregonus lavaretus) and native Arctic charr (Salvelinus alpinus) depends on heavy whitefish exploitation. In Jankun, M., Brzuzan, P., Hliwa, P. & Luczynski, M. (eds) Advances in Limnology, vol. 60 *Biology and Management of Coregonid Fishes - 2005*, pp. 343-350. Stuttgart: E Schweizerbart'sche Verlagsbuchhandlung.

Nielsen, P. S., Saltveit, S. J., Brittain, J. E. & Brabrand, Å. (1985). Randsfjorden: undersøkelse og vurdering av fiskeribiologiske forhold. *Rapport Laboratorium for ferskvannsøkologi og innlandsfiske*, 1985:79. Oslo. 70 pp.

Norwegian Biodiversity Information Centre. (2015). *Species Map service 1.6.* Available at: http://artskart.artsdatabanken.no/FaneArtSok.aspx (accessed: 27.04.2015).

Parker-Stetter, S. L., Rudstam, L. G., Sullivan, P. J. & Warner, D. M. (2009). *Standard operating procedures for fisheries acoustic surveys in the Great Lakes*: Great Lakes Fishery Commission Special Publication.

Pulkkinen, K., Pasternak, A. F., Hasu, T. & Valtonen, E. T. (2000). Effect of Triaenophorus crassus (Cestoda) infection on behavior and susceptibility to predation of the first intermediate host Cyclops strenuus (Copepoda). *Journal of Parasitology*, 86: 664-670.

Pulkkinen, K. & Valtonen, E. T. (1999). Accumulation of plerocercoids of Triaenophorus crassus in the second intermediate host Coregonus lavaretus and their effect on growth of the host. *Journal of Fish Biology*, 55: 115-126.

Pulkkinen, K., Valtonen, E. T., Niemi, A. & Poikola, K. (1999). The influence of food competition and host specificity on the transmission of Triaenophorus crassus (Cestoda) and Cystidicola farionis (Nematoda) to Coregonus lavaretus and Coregonus albula (Pisces:Coregonidae) in Finland. *International Journal for Parasitology*, 29: 1753-1763.

R Core Team. (2014). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raitaniemi, J., Malinen, T., Nyberg, K. & Rask, M. (1999). The growth of whitefish in relation to water quality and fish species composition. *Journal of Fish Biology*, 54: 741-756.

Randsfjorden Grunneierforening. (2014). *Tynningsfiske 2014*: Randsfjorden Grunneierforening. Available at: http://randsfjord.org/text1_41.html (accessed: 01.05.2015).

Rognerud, S., Brettum, P. & Romstad, R. (1989). Undersøkelser av Randsfjorden og Dokka 1988-92: årsrapport for undersøkelsen i 1988. *Overvåkningsrapport Norsk institutt for vannforskning-NIVA*, 1989:360. Oslo. 40 pp.

Rustadbakken, A., Haugen, T. O. & Løvik, J. E. (2010). Høstfisk-utvkling av innlandsfiske 2007-2010, Delrapport 1, Fiskebiologiske undersøkelser i Engeren og Randsfjorden : bestandsstatus for siken før iverksetting av tiltak. *Rapport. Norsk institutt for vannforskning-NIVA*, 2010:5962. Hamar. 32 pp.

Sandlund, O. T., Hesthagen, T. & Brabrand , Å. (2011). Coregonid introductions in Norway: well-intended andsuccessful, but destructive. *Advances in Limnology*, 64: 341-358.

Sandlund, O. T. & Lindem, T. (1984). Ekkoloddregistrering av pelagiske fiskebestander i innsjøer. *Fauna*, 37: 105-111.

Sandlund, O. T. & Næsje, T. F. (2000). Komplekse, laksefiskdominerte fiskesamfunn på Østlandet. In Borgstrom, R. & Hansen, L. P. (eds) *Fisk i ferskvann Et samspill mellom bestander, miljø og forvaltning.*, pp. 109-129. Oslo: Landbruksforlaget.

Sandlund, O. T., Næsje, T. F. & Lindem, T. (1992). Ekkoloddregistrering av pelagisk fiskebestand i Mjøsa 1990-91. *Oppdragsmelding Norsk institutt for naturforskning-NINA*, 1992:138. Trondheim. 15 pp.

Sandlund, O. T., Stang, Y. G., Kjellberg, G., Naesje, T. F. & Hambo, M. U. (2005). European smelt (Osmerus eperlanus) eats all; eaten by all: Is it a key species in lakes? In Jones, J. (ed.) vol. 29 *International Association of Theoretical and Applied Limnology, Vol 29, Pt 1, Proceedings.*, pp. 432-436. Stuttgart: E Schweizerbart'sche Verlagsbuchhandlung.

Sichrowsky, U., Schabetsberger, R., Gassner, H., Kaiser, R., Boufana, B. & Psenner, R. (2013). Cradle or plague pit? Illuminated cages increase the transmission risk of parasites from copepods to coregonids. *Aquaculture*, 392-395: 8-15.

Simmonds, E. J. & MacLennan, D. N. (2005). *Fisheries Acoustics. Theory and Practice.* Oxford: Blackwell.

Sokdal, R. R. & Rohlf, F. J. (1995). *Biometry.* 3 ed. New York: W. H. Freeman and Company.

Styrvold, J.-O., Brabrand, Å. & Saltveit, S. J. (1981). Fiskeribiologiske undersøkelser i forbindelse med reguleringsplanene for vassdragene Etna og Dokka, Oppland. III, Studier av ørret og sik i Randsfjorden og elvene Etna og Dokka / Jan-Olav Styrvold, Åge Brabrand og Svein Jakob Saltveit. *Rapport Laboratorium for ferskvannsøkologi og innlandsfiske*, 1981:46. Oslo. 103 pp.

Sumich, J. L. & Morrissey, J. F. (2004). *Introduction to the Biology of Marine life.* 8 ed. London: Jones and Bartlet Publishers International.

Svärdson, G. (1976). Interspesific population dominance in fish communities of Scandinavian Lakes. *Rep. Inst. Freshw. Drottningholm* 55: 144-171.

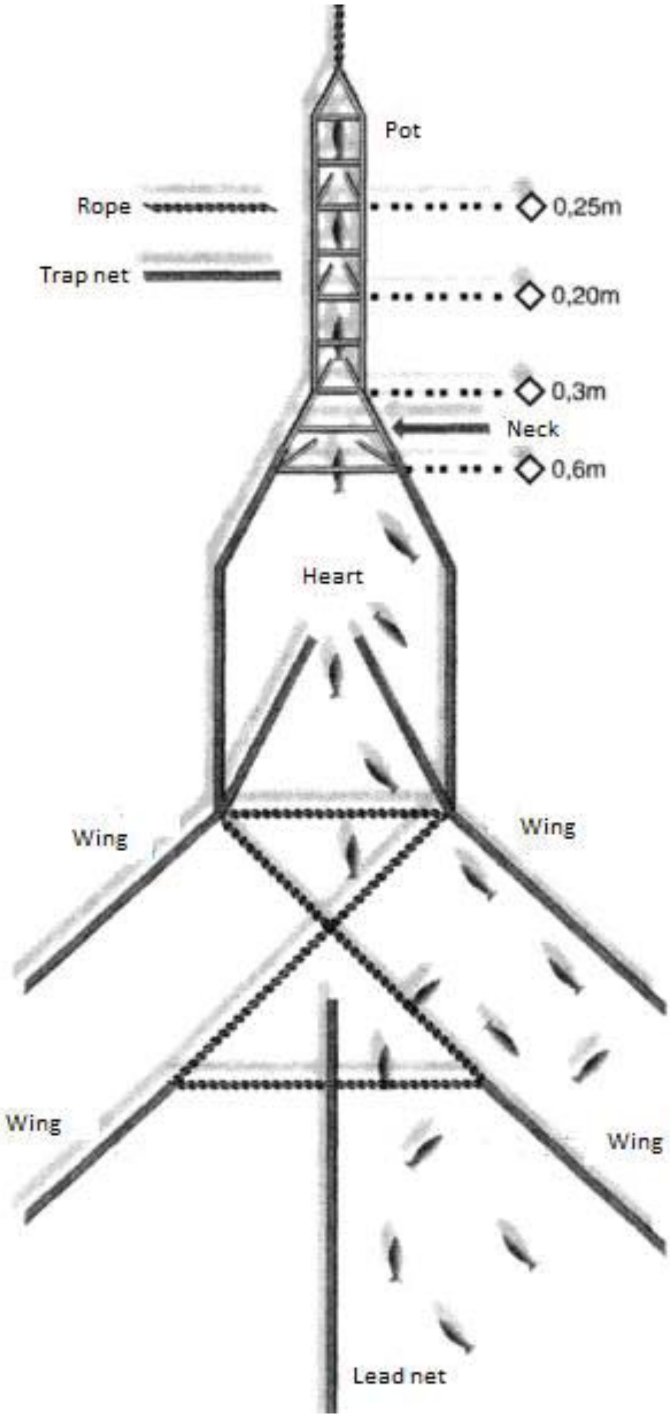
Taugbøl, T., Andersen, O. & Grøndahl, F. A. (2004). Erfaringer med storruse til nærings- og kultiveringsfiske. *Rapport. Norsk institutt for naturforskning-NINA*, 2004:827. Trondheim. 60 pp.

Torgersen, P. & Gregersen, F. (2009). Fangstregistreringer i regulerte vassdrag i Oppland. *Rapport. Fylkesmannen i Oppland, miljøvernavdelingen*, 2009:5. Lillehammer. 76 pp.

Urick, R. J. (1996). *Principles of underwater sound*. 3 ed. Los Altos. California: Peninsula Publ.
YSI. (2015). *EXO2 Water Quality Sonde*: Xylem Inc. Available at: http://www.ysi.com/productsdetail.php?EXO2-Water-Quality-Sonde-90 (accessed: 01.05.2015).

Appendix 1

Sketch of a trap net similar to those used in the intensive culling programme in Randsfjorden.



Appendix 2

Overview of gillnet position, depth and date of fishing at each sampling location.

Gillnet locations					
Gillnet nr:	Mesh size (NB or NP)	Location	Depth (m)	Coordinates (x,y)	Date of fishing
1	NB	1	5.6	60°77.981 , 10°23.258	15.09.2014
1	NB	2	15.4	60°74.784 , 10°24.364	16.09.2014
1	NB	3	3.0	60°43.489 , 10°43.942	17.09.2014
1	NB	4	6.0	60°18.833 , 10°22.472	29.09.2014
2	NB	1	2.0	60°78.030 , 10°22.827	15.09.2014
3	NB	1	2.3	60°77.909 , 10°22.545	15.09.2014
3	NB	2	4.2	60°74.883 , 10°24.304	16.09.2014
3	NB	3	2.5	60°43.791 , 10°43.739	17.09.2014
3	NB	4	12.0	60°17.602 , 10°23.470	29.09.2014
4	NB	1	5.0	60°77.773 , 10°22.275	15.09.2014
4	NB	2	6.8	60°75.026 , 10°24.241	16.09.2014
4	NB	3	13.0	60°43.599 , 10°43.712	17.09.2014
4	NB	4	20.0	60°17.170 , 10°23.761	29.09.2014
5	NB	1	3.8	60°77.757 , 10°21.959	15.09.2014
5	NB	2	10.5	60°73.444 , 10°26.704	16.09.2014
5	NB	3	2.5	60°43.791 , 10°43.739	17.09.2014
5	NB	4	6.0	60°18.005 , 10°23.021	29.09.2014
6	NB	1	9.1	60°77.833 , 10°21.910	15.09.2014
6	NB	2	10.5	60°75.199 , 10°24.196	16.09.2014
6	NB	3	18.0	60°43.898 , 10°43.589	17.09.2014
6	NB	4	7.0	60°17.693 , 10°23.309	29.09.2014
7	NB	1	2.8	60°77.947 , 10°21.701	15.09.2014
7	NB	2	4.5	60°75.348 , 10°23.673	16.09.2014
7	NB	3	21.0	60°44.135 , 10°43.533	17.09.2014
8	NB	1	2.6	60°78.083 , 10°21.313	15.09.2014
8	NB	2	1.6	60°75.275 , 10°23.979	16.09.2014
8	NB	4	18.5	60°17.725 , 10°23.167	29.09.2014
8	NB	3	3.0	60°43.962 , 10°43.781	17.09.2014
9	NB	1	1.8	60°78.120 , 10°21.166	15.09.2014
9	NB	2	24.4	60°75.601 , 10°23.552	16.09.2014
9	NB	3	5.7	60°43.231 , 10°43.761	17.09.2014
9	NB	4	15.0	60°17.781 , 10°23.129	29.09.2014
10	NB	1	3.6	60°78.263 , 10°21.118	15.09.2014
10	NB	2	4.7	60°73.605 , 10°26.436	16.09.2014
10	NB	3	4.0	60°42.921 , 10°45.632	17.09.2014
10	NB	4	10.0	60°18.104 , 10°23.151	29.09.2014

11	NB	1	6.4	60^o78.400 , 10^o21.240	15.09.2014
11	NB	2	20.0	60^o73.810 , 10^o26.165	16.09.2014
11	NB	3	6.0	60^o42.895 , 10^o45.426	17.09.2014
11	NB	4	2.1	60^o18.181 , 10^o23.201	29.09.2014
12	NB	1	10.8	60^o78.278 , 10^o21.624	15.09.2014
12	NB	2	3.5	60^o74.066 , 10^o26.094	16.09.2014
12	NB	3	2.2	60^o42.932 , 10^o45.152	17.09.2014
12	NB	4	20.0	60^o18.292 , 10^o22.947	29.09.2014
13	NB	1	11.0	60^o78.218 , 10^o21.886	15.09.2014
13	NB	2	5.5	60^o74.332 , 10^o25.885	16.09.2014
13	NB	3	10.0	60^o43.050 , 10^o44.943	17.09.2014
13	NB	4	5.0	60^o18.496 , 10^o22.693	29.09.2014
14	NB	1	11.4	60^o78.146 , 10^o22.756	15.09.2014
14	NB	2	5.0	60^o74.577 , 10^o24.446	16.09.2014
14	NB	3	3.0	60^o43.287 , 10^o44.743	17.09.2014
14	NB	4	8	60^o18.554 , 10^o22.570	29.09.2014
15	NB	1	24.0	60^o78.240 , 10^o22.215	15.09.2014
15	NB	2	14.2	60^o74.479 , 10^o25.696	16.09.2014
15	NB	3	13.0	60^o43.166 , 10^o44.753	17.09.2014
15	NB	4	12	60^o17.283 , 10^o23.605	29.09.2014
16	NB	1	16.0	60^o78.211 , 10^o22.983	15.09.2014
16	NB	2	2.9	60^o74.721 , 10^o24.361	16.09.2014
16	NB	3	16.0	60^o43.303 , 10^o43.421	17.09.2014
16	NB	4	10.2	60^o17.402 , 10^o23.534	29.09.2014
17	NP	1	10-16	60^o78.423 , 10^o23.260	15.09.2014
17	NP	2	10-16	60^o72.899 , 10^o26.811	16.09.2014
17	NP	3	10-16	60^o43.345 , 10^o42.912	17.09.2014
17	NP	4	10-16	60^o17.818 , 10^o22.717	29.09.2014
18	NP	1	0-6	60^o78.146 , 10^o23.357	15.09.2014
18	NP	2	0-6	60^o73.231 , 10^o26.701	16.09.2014
18	NP	3	0-6	60^o43.479 , 10^o43.081	17.09.2014
18	NP	4	0-6	60^o17.916 , 10^o22.550	29.09.2014

Appendix 3

Panel distribution in Nordic pelagic and Nordic benthic survey gillnets.

Nordic benthic and pelagic survey gillnet												
Panel nr:	1	2	3	4	5	6	7	8	9	10	11	12
Mesh size (mm):	43.0	19.5	6.25	10.0	55.0	8.0	12.5	24.0	15.5	5.0	35.0	29.0

Appendix 4

The locations for temperature- and oxygen profiling.