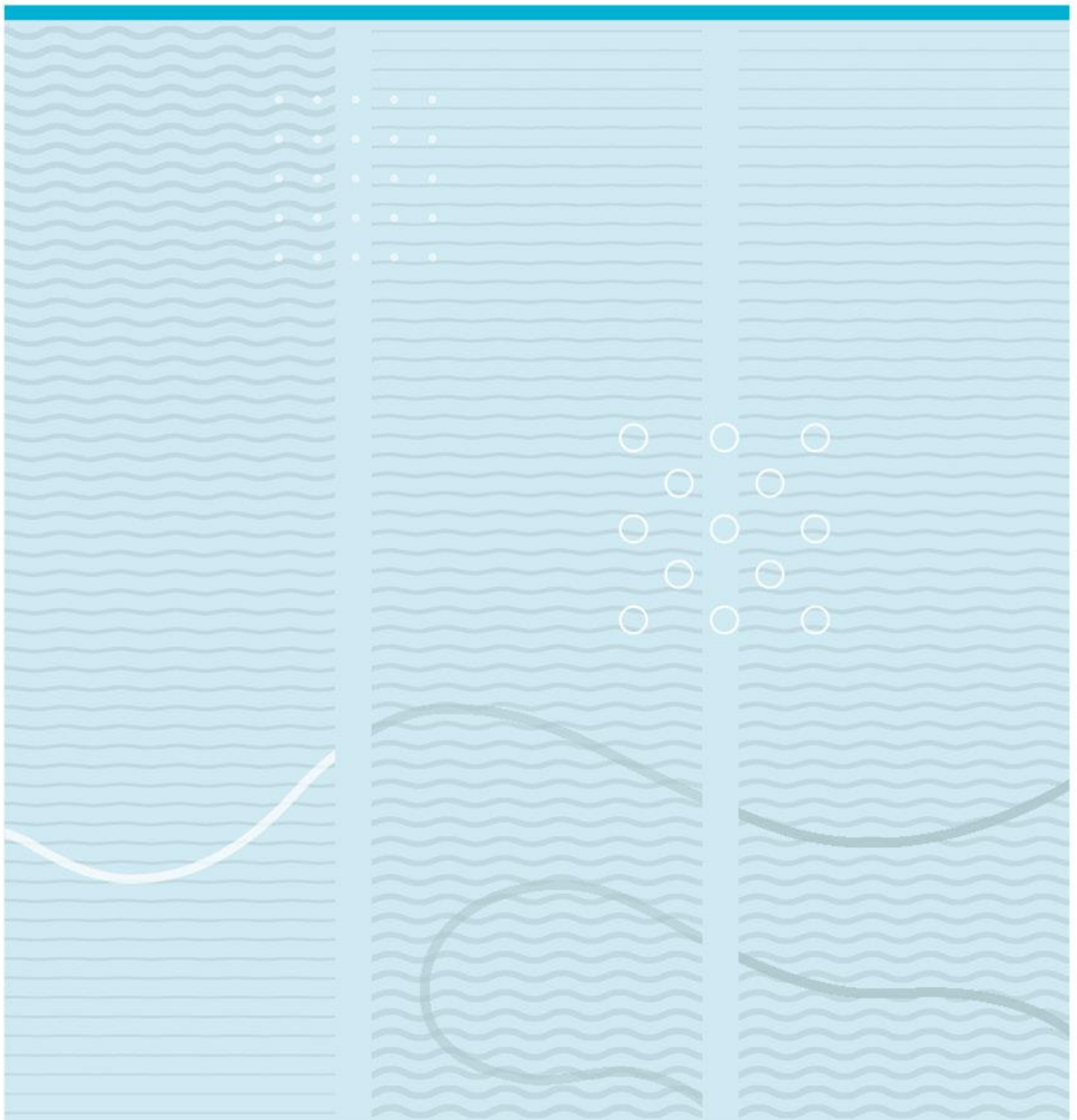


Solveig Irene Dolven

Macroparasite investigations of European perch (*Perca fluviatilis*) and European whitefish (*Coregonus lavaretus*) in Lake Norsjø, South-Eastern Norway



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This thesis is worth 60 study points

Abstract

In 2018, the abundance of macroscopic ectoparasites and intestinal endoparasites was investigated in European perch (*Perca fluviatilis*) and European whitefish (*Coregonus lavaretus*) collected in three seasons and three sites from Lake Norsjø, South-Eastern Norway. The main objectives were to reveal factors known to affect freshwater parasite abundance in fish, like host specificity, season, water temperature, habitat, diet, fish length and age. Totally 2113 parasite individuals were found in the 258 perch and 101 whitefish investigated. The most abundant parasites found in both species were acanthocephalans and *Proteocephalus* spp., constituting 95 % of the total parasite load. The remaining 5 % were individuals of *Triaenophorus crassus*, *Dibothriocephalus* spp., nematodes, trematodes, *Salmincola* sp. and *Argulus coregoni* in European whitefish, and *Triaenophorus crassus*, *Triaenophorus nodulosus*, *Dibothriocephalus* spp., *Eubothrium* sp., nematodes and *Argulus coregoni* in European perch.

Significantly higher abundance of *Proteocephalus* spp. was found in whitefish than in perch, while significantly higher abundance of acanthocephalans was found in perch. This indicates differences in fish diet, as acanthocephalans are transmitted by benthic macroinvertebrates, while *Proteocephalus* spp. are transmitted by pelagic copepods. Furthermore, the cestode fauna was more diverse in perch than in whitefish. The most important parasite predictors were fish length and season. The abundance of acanthocephalans in both fish species, *Proteocephalus* sp.1 in whitefish, and cestodes in perch, all increased significantly by increasing fish length. This is likely a consequence of longer time feeding histories and need of more food and more diverse food, in increasingly larger and older fish. Acanthocephalans were significantly less abundant in autumn than spring in both fish species, while in perch these parasites were significantly more abundant in summer than in spring. *Proteocephalus* sp.1 was significantly more abundant in summer and autumn than in spring in whitefish, while *Proteocephalus* sp.2 of perch was found only in spring. The different seasonalities are likely effects of various life cycles among the parasite species in the lake.

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Preface

This thesis was conducted at the University of South-Eastern Norway, Campus Bø, under the supervision of Professor Espen Lydersen (USN) and Senior Research Scientist Tor Atle Mo (Norwegian Institute for Nature Research). I would like to thank my supervisors for the help and guidance in the very interesting fields of freshwater ecology and parasitology. Conducting this study was as inspiring as it was challenging, having limited parasitological knowledge prior to the field work and with an extremely steep learning curve. This was only possible with your excellent guidance.

All field work, lab work and species identification were done in collaboration with Ann-Cecilie Henriksen. I am grateful for the productive and rewarding collaboration. The many long days in the lab were both educational and enjoyable in your company. I also want to thank Tone Jøran Oredalen for the good company during both the laboratory and field work. Thank you to Karin Brekke Li for the valuable help and instructions in the water chemistry laboratory. Moreover, I am thankful to Christian Robstad, Frode Bergan, Martin Ring and Jonas Berg for participation in the field work.

I would like to thank my current workplace, Larvik og Omegns Turistforening, for the encouragement and for the flexibility making it possible to conduct field work, lab work and to attend mandatory lectures and thus combining my studies with a job.

Finally, I want to thank my husband, Joachim Dolven, both for supporting me in frustrating times and for listening to my overwhelming enthusiasm when I had read just another interesting article. Thank you also to my adoring six months old daughter, Agnete, for boosting my motivation to get this thesis finished with your joyful smiles.

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1 Introduction

Parasitism is a form of symbiosis found in all ecosystems. All species are probable hosts to parasites, and free-living species are likely outnumbered by parasites (Windsor, 1998). Parasitism is present when different species, often far from each other phylogenetically, live in close association with each other for some time, where one of the species benefits and one is harmed (Dimijian, 2000). A parasite has one or several hosts throughout its life cycle and is usually dependent on the host to complete its life cycle (Bykhovskaya-Pavlovskaya et al., 1964). Thus, parasites do not belong to a particular taxonomic group, but represents a common way of life.

Although the exact prevalence, intensity and abundance of different parasite species varies considerably between different lakes, the biology of the parasite species is the main cause for the variation of infections (Poulin, 2006). Different parasite species are adapted to different hosts causing the host specificity found in some species (Karvonen & Valtonen, 2004; Sobecka & Słomińska, 2007). However, similar feeding habitats can cause parasites to be found in paratenic or accidental hosts (Scholz, 1999; Taraschewski, 2000). Other factors determining the parasite abundances are seasonality (Chubb 1980, 1982), diet (Valtonen et al., 2010), fish size (Poulin, 2000; Zelmer & Arai, 1998) and age (Zelmer & Arai, 1998). Intestinal parasites will almost always cause some disturbances in the host, ranging from minor to lethal (Marcogliese, 2004). The pathological processes can be similar across a wide range of hosts and parasites, with examples of consequences being reduced food consumption, changes in metabolism, disturbances in digestive functions and local tissue damage (Hoste, 2001). In general, the host can seem unharmed at low intensities, while increased damage occurs with increasing parasite intensity.

Despite many previous studies, still limited knowledge about freshwater parasites exists, primarily due to sparse expertise in species identification and little promoting of why fish parasitism is important, including the ecological roles of parasites in aquatic systems. Due to their transmission patterns in hosts and their sensitivity for changes in the ecosystem, they can be used to study other effects than the parasitic fauna itself. For example, knowledge about intestinal parasites will give information about the fish's diet over a longer time than just stomach analyses, only being a snap-shot of fish diets. Parasites can

thus complement studies of foodweb structures, climatic conditions, environmental contaminants and other ecological stresses (Marcogliese, 2004, 2005).

This study focuses on macroscopic ectoparasites and endoparasites of the intestine (intestinal helminths) of European perch (*Perca fluviatilis*, hereafter perch) and European whitefish (*Coregonus lavaretus*, hereafter whitefish) in Lake Norsjø, South-Eastern Norway. Macroparasites, in this context, are defined as fish parasites that can be observed with the naked eye, including both mature and immature stages. While the ectoparasites are present on external surfaces of fish, the endoparasites are present internally in most organs and structures. The aim of the study was to describe the ecto- and endo-macroparasite abundances, to reveal potential differences in the parasite fauna between the two fish species, seasonal and spatial variations, parasite abundance in relation to water chemical parameters like lake trophic status and water temperature, and correlations between intensity of infection and fish size. No previous studies have focused on the parasite fauna of whitefish and perch in Lake Norsjø.

2 Material and method

2.1 Sampling site

This study was conducted in the oligotrophic, dimictic Lake Norsjø, located in Vestfold and Telemark county, Norway (Figure 1). It is situated at about 59°17' N, 9°18' E and located at 15 m a.s.l. It is a large lake with a surface area of 55.2 km², stretching about 29.6 km from the northernmost point at Gvarv, to the southernmost point at Åfoss. Maximum depth is 171 m, mean depth 87 m. Lake Norsjø is regulated at Skotfoss, but the regulation height is small, i.e. 15 cm (The Norwegian Water Resources and Energy Directorate, 2019). Three major rivers drain into Lake Norsjø, River Bøelva at Gvarv, River Sauarelva at Akkerhaugen and River Eidselva at Ulefoss. These three rivers drain large areas, including considerable parts of the Hardangervidda mountain plateau. Lake Norsjø drains to River Skienselva at Skotfoss, and enters into sea, Frierfjorden, at Porsgrunn.

The fish community in Lake Norsjø have been reported to consist of perch, whitefish, Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), northern pike (*Esox lucius*), European smelt (*Osmerus eperlanus*), crucian carp (*Carassius carassius*), three-spined stickleback (*Gasterosteus aculeatus*), European eel (*Anguilla Anguilla*), European river lamprey (*Lampetra fluviatilis*) and tench (*Tinca tinca*) (Borgstrøm, 1974; Jensen, 1954; Lydersen & Moreno, 2016).

Fish and water samples from Lake Norsjø were collected in 2018, during spring, summer and autumn, at three different sites, referred to as North, Middle and South (Figure 1). The site North was in the Årnes bay (59°22'14"N, 9°11'30"E), the site Middle was located outside Ulefoss (59°17'10" N, 9°17'00" E), while the site South was in Fjærekilen (59°11'50" N, 9°29'00" E). In summer, site South included deployment of gillnets near Skotfoss (59°12'32" N, 9°30'00" E) in addition to Fjærekilen.

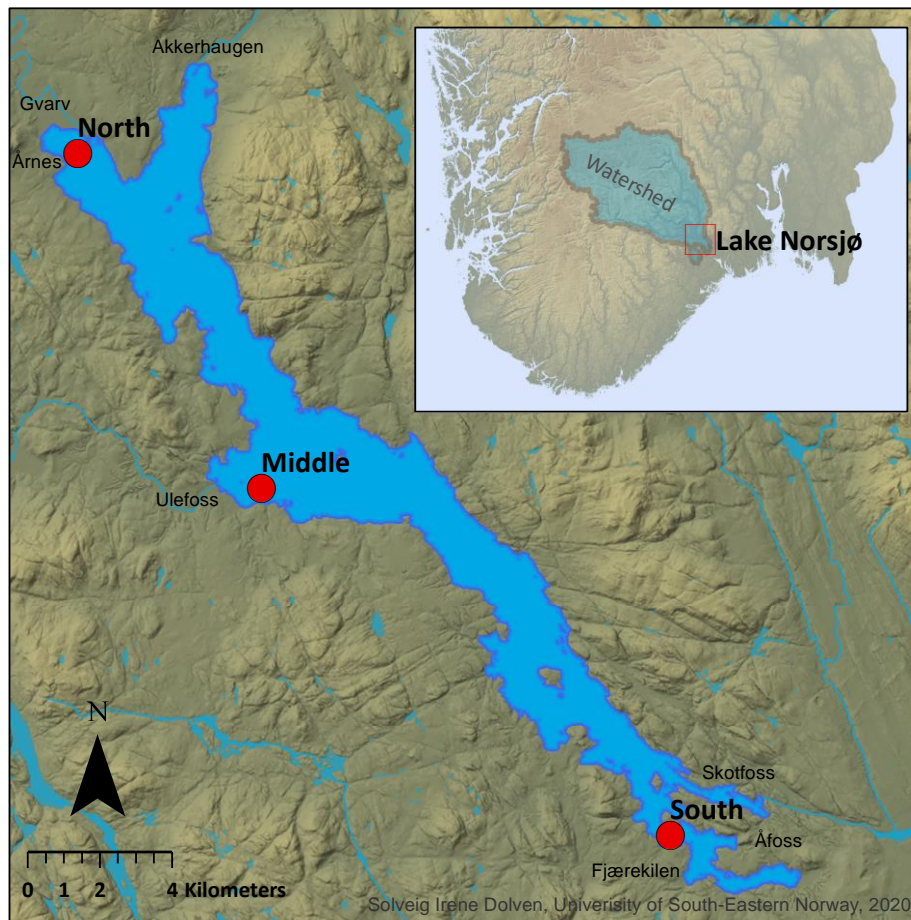


Figure 1. Map of Lake Norsjø with the three sampling sites North, Middle and South marked with red circles. In the upper right corner is the lake watershed, and marked with a red rectangle is the location of the lake in South-Eastern Norway. Map generated with ArcMap version 10.6.1 (Esri, 2018), using the datasets Terrain model WMS (Norwegian Mapping Authority, 2020), Nevina Watershed (The Norwegian Water Resources and Energy Directorate, 2020b) and Lake and Main River (The Norwegian Water Resources and Energy Directorate, 2020a).

2.2 Fish sampling

At all three sampling sites of the lake (North, Middle and South), fishing was implemented three times in 2018: 28.–30.05., 30.07.–01.08. and 10.–12.09., i.e. during spring, summer and autumn. Two bottom gillnet chains, each consisting of eight gillnets (length: 25 m; height: 1,5 m) with mesh sizes ranging from 13.5 to 45.0 mm were used at all sites and seasons. All gillnet chains were set from the shore at shallow water and out into deeper water of the lake. The gillnets fished overnight for approximately 24 hours, and the fish

was taken out of the gillnets at Årnes as soon as they were retrieved (about 1-2 hours). Weight was measured on a digital weight (nearest gram), while premade measuring boards were used for total length measurements (nearest mm). Total length was measured from the tip of the snout to the tip of the longest lobe of the tail/caudal fin. After measuring length and weight and registration and sampling of ectoparasites (see chapter 2.3), each fish was marked with a unique number and individually stored in plastic zipper bags, before transported in cooling boxes from Årnes to Campus Bø (University of South-Eastern Norway) and stored in a freezer (-18°C) until further analyses.

Fulton's condition factor K (K_f) was calculated for whitefish, i.e. $K_f = 100 * W / L^3$ (W = weight (g), L = length (cm)).

One main objective was to catch minimum 30 fish of each species at each sampling site and seasons, i.e. a total catch of 270 individuals of each species. If less, another 24 hours gillnet fishing were implemented. This was needed at site South during spring and summer, at site Middle during summer and autumn, and at site North during autumn. At site South, both gillnet chains were sabotaged during the summer fishing at Skotfoss, which caused reduced catch and subsequent reduced data quality from this site.

If more than 30 fish of one species were caught, only 30 fish were included in the investigated material. This selection was done partially in the field to reduce the duration of the field work, and partially after storage. In field, more than 30 fish were selected before registration in a semirandom selection, by including fish of various size based on visual judgement. Before the laboratory work, this material was further reduced to 30 fish by random selection using the web service random.org (Haahr, 2018).

2.3 Subsampling of parasites

In field, subsampling of ectoparasites was done by external inspection of gills, fins and skin on fresh fish material. All ectoparasites were registered and stored in number marked vials containing technical ethanol (96 %). The numbering of vials corresponded

to the unique fish numbers. Scalpels, scissors and tweezers were used to remove skin or fins surrounding the attachment organ of ectoparasites where applicable.

Subsampling of endoparasites was done in the laboratory in the period 20.09.–10.12.2018. The fish was taken out of the freezer the day before and kept in a cooling room overnight to thaw before the dissection. The fish abdomen was cut open with scissors with rounded tip. This was done by a small cut transversely below the gills, followed by a long incision longitudinal from this point and to the anus. The sex of the fish was registered. The organs were gently removed, and the intestinal tract was taken out by cutting over close to the oesophagus. The intestinal tract was put in a petri dish with 9 % saline water to avoid dissolving of the parasites. The coelom-side of the intestinal tract and organs, and the coelom itself, were inspected for encysted nematodes and plerocercoids (larval stage of cestodes), as well as parasites lying free in the coelom. The cysts were opened and the parasites collected.

The intestinal tract was cut open from the oesophagus to the anus with scissors, while consecutively collecting the parasites that was found not encysted. The parasites were temporarily stored in saline water in petri dishes while they were collected and examined. Tweezers were used to handle the fish organs and the parasites. A selection of the parasites was thereafter preserved in technical ethanol (96 %) for later examination.

Parasitological examination was conducted under a stereo microscope or light microscope to identify species. Equipment used was Swift SM80 stereo microscope with magnification power of 10–40x and Olympus CX21FS1 compound light microscope with magnification of 40–1000x. A Micro Capture camera was used to take pictures of the parasites through the magnifying lenses for documentation or for later examination of the morphology characteristics before alcohol preservation. In a few occasions, the digital motorized stereo microscope Zeiss Stereo Discovery V20 was used to get improved pictures. The number of each parasite species was counted. To avoid counting the same individual twice, for example if a cestode had been cut over, the counting of cestodes was based on scolices. The total length of a selection of parasites were measured to the nearest mm. Some of the acanthocephalans with retracted proboscises were delicately

squeezed with tweezers at the anterior part of the body to expose the proboscis and count the hooks.

To get a general overview of registered parasites in the Norwegian fauna and their fish hosts, the book *Limnofauna Norvegica* (Aagaard & Dolmen, 1996) and the report *Parasitter hos norske ferskvannfisk* (Sterud, 1999) was used. The book *Key to parasites of freshwater fish of the USSR* (Bykhovskaya-Pavlovskaya et al., 1964), covering a broad area of freshwater parasitology, was used to narrow down on the species. *Proteocephalus* spp. was identified according to Scholz et al. (1998), *Dibothriocephalus* spp. (formerly *Diphyllobothrium* spp., revised according to Waeschenbach et al., 2017) was identified according to Andersen & Gibson (1989), *Eubothrium* sp. according to Andersen & Kennedy (1983), *Salmincola* sp. according to Kabata (1969) and *Argulus* sp. according to Bykhovskaya-Pavlovskaya et al. (1964) and Økland (1985). The remaining taxa, including Acanthocephala and *Triaenophorus* spp. were identified according to Bykhovskaya-Pavlovskaya et al. (1964). In the case of different unspecified parasite species of the same genus found in both fish species, a numbering of sp.1 and sp.2 was used for whitefish and perch, respectively, to separate them in the following text. The mentioned resources were studied in combination with other relevant articles for specific fish host species and parasite species. Literature searches to find relevant scientific articles were conducted in PubMed (<https://www.ncbi.nlm.nih.gov/pubmed>), Google Scholar (<https://scholar.google.no>) and Oria (<https://www.oria.no>).

2.4 Water analyses

At all sites and seasons, water samples were taken at 1 m and 20 m, by use of a Limnos water sampler. Simultaneously water temperatures were measured. 500 mL of water was transferred from the Limnos sampler into prewashed polyethylene bottles, and immediately stored dark and cold, until back from field, where the bottles were stored in a dark cooling room (4°C) until analysed. Water chemical analyses were conducted at the Institute of Nature, Health and the Environment, Campus Bø, at the University of South-Eastern Norway. The equipment and standard methods used are listed in Table 1. Furthermore, the analytical results were interpreted according to the Norwegian quality

guidance document for fresh waters characterization (Direktoratsgruppen vanndirektivet, 2018).

Table 1. Overview of water chemical parameters analysed, analytical equipment and standard methods used.

Parameter	Equipment/Machine	Standard
pH	Mettler Toledo SevenCompact S210	NS 4720
Conductivity	WTW Cond 3110 TetraCon 325	NS-ISO 7888
Alkalinity	Mettler Toledo G20 Compact Titrator and Mettler Toledo DG 115-SC electrode	NS 4754
Turbidity	Turbiquant 1100 IR	NS-EN ISO 7027-1
Ca ²⁺ , Mg ²⁺ , Na ⁺ , K ⁺ , NH ₄ ⁺	Dionex ICS-1100 Ion Chromatography System	NS-EN ISO 14911
SO ₄ ²⁻ , Cl ⁻ , NO ₃ ⁻	Dionex ICS-1100 Ion Chromatography System	NS-EN ISO 10304-1
Tot-N	Certoclav-Tisch-Autoclav, FIAlyzer 1000 and AIM3200 Autosampler	NS 4743
Tot-P	Certoclav-Tisch-Autoclav and Perkin Elmer Lambda 25 UV/VIS Spectrofotometer	NS 1189
True colour	Perkin Elmer Lambda 25 UV/VIS Spectrofotometer	NS-EN ISO 7887:2011C

2.5 Statistical analyses

Calculations of parasite prevalence, mean intensity and mean abundance were conducted in Excel 2019, Version 1902. The definitions of these parasitological terms follow Bush et al. (1997). Mean intensity and abundance are given as mean per fish individual. Other statistical calculations and modelling were conducted using R, version 3.6.1 (R Core Team, 2019) and RStudio, version 1.2.1335 (RStudio Team, 2018). Packages installed to R and used for data visualization and modelling were: pacman for package managing (Rinker & Kurkiewicz, 2017), rio for importing data (Chan et al., 2018), tidyr and dplyr for reformatting data (Wickham & Henry, 2019a; Wickham et al., 2019b), AER for dispersion tests (Kleiber & Zeileis, 2008), car for VIF testing for collinearity (Fox & Weisberg, 2019), MASS for negative binomial GLM and confidence intervals (Venables & Ripley, 2002), glmmTMB for zero inflation modelling (Brooks et al., 2017) and DHARMA for Residual plotting, Kolmogorov-Smirnov test, outlier test and zero inflation test (Hartig, 2019).

Estimates are given with measures of spread and uncertainty. Fish length and weight are given with standard deviation (SD), parasite prevalence and estimates of statistical

models are given with 95% confidence intervals (CI) according to the Agresti-Coull method, and mean parasite intensity and abundance are given with standard errors of the mean (SE). Difference in fish length between sampling sites was tested with one-way ANOVA and Tukey test.

Generalized linear models (GLMs) were used to describe the variations in parasite abundance. The number of infected fish decided which parasite species to model. Cestodes (all copepod-transmitted, both adult and plerocercoids in the class Cestoda) were modelled as one group when too few parasite individuals were present of the respective cestode species to model separately. The statistical models of interest are shown in Table 2, and further model selection was done on these. Overdispersion tests were run on the fitted Poisson-models to choose the distribution type for the response variable. Negative binomial distributed models were used for all models.

Correlation tests between fish length and weight was done with Kendall's Tau Coefficient, and collinearity was tested by generalized variance-inflation factors (VIF). To avoid collinearity in the models, limit was set at a correlation of 0.7 and a VIF of 5 to be included. The variable fish weight was omitted from the statistical models due to collinearity.

Table 2. Statistical models (fish and parasite species) and the predictors included in the model selection process (+). Predictors are site, season, length, sex, Fulton's K (K_f), *Proteocephalus*, fish species and interactions between predictors.

Fish species	Models	Predictors											
		Site	Season	Length	Sex	Fulton's K	<i>Proteocephalus</i>	Fish species	Site, Length ^a	Season, Length ^a	Species, Season ^a	Species, Site ^a	Species, Length ^a
W	<i>Acanthocephala</i>	+	+	+	+	+	+		+	+			
W	<i>Proteocephalus</i>	+	+	+	+	+			+	+			
P	<i>Acanthocephala</i>	+	+	+	+		+		+	+			
P	Cestoda	+	+	+	+				+	+			
B	<i>Acanthocephala</i>	+	+	+				+			+	+	+
B	<i>Proteocephalus</i>	+	+	+				+			+	+	+
B	Cestoda	+	+	+				+			+	+	+

Note. W = Whitefish, P = Perch, B = Both fish species.

+ Predictors included in the model selection process.

^a Interactions

Model selection was done with backwards stepwise regression using the drop1(..., test = "Chi") command. The least significant predictors were removed, and the model was refitted until it resulted in a model that was not significantly more informative at the 5 % significance level by removing more predictors. After model selection, model validation was done by plotting the scaled residuals to detect lack of fit. The deviance residuals were plotted against the fitted values, each explanatory variable in the model and each explanatory variable not used in the model. Zero-inflation tests, Kolmogorov-Smirnov tests for uniformity and outlier tests were run on all models. Zero-inflation (mixture) models and zero-altered (two-part/hurdle) models were fitted regardless of those results, to see if they had a better fit than the GLMs.

For all models the reference levels were site Middle, spring season, female, perch. Variables with complete separation were included in the models to get the best fit, but the results are not reported. For each predictor, the estimate, standard error (SE), 95% confidence interval (CI), z-value and p-value are reported. The significance of predictors in the final models for explaining the variation in parasite abundance was judged by a p-value below 0.05 and a confidence interval not spanning zero.

2.6 Delimitations of the study

Several boundaries were set for this study. Firstly, the focus of the thesis was macroscopic parasites, since a study including parasites undetectable by the naked eye would have demanded much more time in the laboratory. Parasites were identified to the lowest taxonomic rank possible with the equipment and investigation time available. Only the intestinal tract, the coelom-side of organs and external surfaces of the fish were studied, while no other organs or musculature were dissected. Other analyses like genetics to determine parasite species, age determination of fish and stable isotope analyses were not performed, as the very time-consuming parasite determination was preferred. However, age determination and stable isotope analyses have later been performed, but was not incorporated in this thesis. Also, a distinguishing between the three morphs of whitefish was not implemented.

3 Results

3.1 Water quality of Lake Norsjø

According to the quality guidance document for characterization of Norwegian freshwaters (Direktoratsgruppen vanndirektivet, 2018), Lake Norsjø is characterized as a very big, deep, (very) calcium poor and clear lake. Based on the total phosphorous (Tot-P) and total nitrogen (Tot-N) analyses, Lake Norsjø is an oligotrophic lake in good ecologic state (Table 3). All water chemical data are present in Annex 6 and 7.

Surface temperatures (1 m depth) in Lake Norsjø were recorded slightly higher at site North compared with site South in all three seasons. Surface water temperature varied 13.0–15.4°C in spring, 21.5–23.1°C in summer, and 16.6–16.9°C in fall. At 20 m depth, all three stations had low spring temperatures (4.8–6.8°C), slightly higher temperatures during summer (7.4–11.5°C), and highest temperatures during fall (12.5–15.7°C), due to a particularly warm and long-lasting summer. The small temperature differences between 1 and 20 m during fall indicate the onset of autumn water turnover.

Table 3. Essential physical data and water chemistry (mean values) of Lake Norsjø in accordance with the criteria set by the guidance document 02:2018.

Parameter	Norsjø (mean value)	Water type
Depth	87 m	Deep, > 15 m
Size	55,48 km ²	Very big, > 50 km ²
Climate region	15 m a.s.l	Lowland, <200 m a.s.l
Eco region	Telemark	Eastern Norway
Alkalinity	0,012 mekv/L	Very calcium poor, < 0,05 mekv/L
Calcium	2,24 mg/L	Calcium poor, 1–4 mg/L
Turbidity	0,3 FNU	Clear, < 1,5 FNU
Colour	13,5 mg Pt/L	Clear, 10–30 mg Pt/L
Total phosphorus	4 µg/L	Very good ecologic state, 1–4 µg/L
Total nitrogen	206 µg/L	Good ecologic state, 200–400 µg/L

3.2 Fish sampling

A total of 1358 fish of six species were caught, whereas 857 were stored. Three species were caught in sufficient numbers for further analysis, i.e. perch, whitefish and Arctic charr. Only the parasites of perch and whitefish were studied in this thesis, while Arctic charr was studied in a separate master's thesis (Henriksen, 2019). The material consisted

of 334 perch and 116 whitefish. Compared to the intention of catching 30 fish of both species at all three sites and all three seasons, this was not obtained in two out of nine samples for perch, and in eight out of nine samples for whitefish. Random selection resulted in a total of 258 perch and 101 whitefish being examined for the presence of parasites (Table 4). The whitefish consisted of 47 males and 54 females, while 103 perch were males and 154 females (Table 5).

Table 4. Number of whitefish and perch investigated from the three seasons and sampling sites North (N), Middle (M) and South (S) in Lake Norsjø.

Species	Spring			Summer			Autumn			Total
	N	M	S	N	M	S	N	M	S	
Perch	21	27	30	30	30	30	30	30	30	258
Whitefish	30	7	2	23	11	5	14	6	3	101

Table 5. Sex distribution of sampled whitefish and perch at the different sites and seasons in Lake Norsjø.

Species	Field season	Female	Male	Sampling site	Female	Male
Whitefish	Spring	19	20	North	34	33
	Summer	22	17	Middle	15	9
	Autumn	13	10	South	5	5
	Total	54	47	Total	54	47
Perch	Spring	34	44	North	55	25
	Summer	63	26	Middle	47	40
	Autumn	57	33	South	52	38
	Total	154	103	Total	154	103

Note. One summer perch was not sex determined by mistake and therefore not reported in the table.

The length of whitefish ranged 148–440 mm, with a mean of 279 ± 47 mm, while the weight ranged 22–757 g with a mean of 195 ± 109 g. It was no significant difference in whitefish length at the three sampling sites ($F(2, 98) = 0.643$, $p = 0.528$). The length of perch ranged 106–365 mm with a mean of 210 ± 53 mm, while the weight ranged 10–711 g with a mean of 131 ± 127 g (Table 6). It was a significant difference in perch length at the three sampling sites ($F(2, 255) = 53.46$, $p < 0.001$). The perch at site North was significantly larger than perch at site Middle ($p < 0.001$) and site South ($p < 0.001$), while site Middle did not significantly differ from site South ($p = 0.702$). Length and weight were significantly and strongly positively correlated for both fish species (whitefish $r_1(94) = 0.90$, $p < 0.001$; perch $r_1(253) = 0.91$, $p < 0.001$). VIF-testing indicated high collinearity (perch = 10–12, whitefish = 10–12). Three perch and five whitefish lack weight data and

subsequent K_f calculations, as weight was not measured before the gut was removed. As length was measured, their lengths were included in the data set.

Table 6. Range, mean and median values of length (mm) and weight (g) of the sampled whitefish and perch at the various sites and seasons in Lake Norsjø.

	Season/ Site	Length (mm)			Weight (g)		
		Range, min-max	Mean \pm SD	Median	Range min-max	Mean \pm SD	Median
Whitefish	Total	148–440	279 \pm 47	282	22–757	195 \pm 109	179
	Spring	148–331	253 \pm 37	244	22–334	136 \pm 71	117
	Summer	190–440	304 \pm 43	304	51–757	255 \pm 120	237
	Autumn	193–347	280 \pm 46	287	57–331	195 \pm 90	194
	North	186–440	284 \pm 48	284	47–757	208 \pm 120	187
	Middle	190–320	262 \pm 37	266	51–309	156 \pm 73	146
	South	148–345	285 \pm 54	296	22–333	207 \pm 86	206
Perch	Total	106–365	210 \pm 53	193	10–711	131 \pm 127	78
	Spring	106–338	200 \pm 55	180	10–560	110 \pm 114	63
	Summer	147–341	211 \pm 44	210	28–499	124 \pm 93	107
	Autumn	134–365	218 \pm 58	205	22–711	156 \pm 159	96
	North	130–365	253 \pm 59	258	22–711	236 \pm 166	214
	Middle	134–356	193 \pm 37	183	22–633	90 \pm 79	67
	South	106–285	188 \pm 33	184	10–221	80 \pm 45	69

3.3 Model selection

The dispersion tests on the fitted Poisson GLMs showed overdispersion ($p \leq 0.05$) in all seven response variables (Annex 1). A negative binomial dispersion was thus used. The model selection process resulted in seven fitted models (Table 7). These were two models of whitefish parasites (*Acanthocephala* and *Proteocephalus* sp.1), two models of perch parasites (*Acanthocephala* and *Cestoda*), and three parasite models for both fish species combined (*Acanthocephala*, *Proteocephalus* spp. and *Cestoda*). The predictors site, season, length, Fulton's K and fish species, including several of their interactions, were included in the statistical models, while fish sex did not significantly explain the variations in parasite abundance. Zero inflation tests, Kolmogorov-Smirnov tests and outlier tests were run on the seven selected models (Annex 1). The results showed only insignificant p-values for the two first mentioned tests. Thus, there were no more zeros than what could be expected to find in a fitted model, and a zero inflated model was not required. Zero-inflated models were nonetheless tested, but found to be less fitted than the generalized linear models. The Kolmogorov-Smirnov tests showed that the observed

residuals did not differ significantly from the expected residuals. The outlier test showed that for all but one model, there was not a larger than expected number of observations that were outside the range of simulated values.

Table 7. Predictors included (+) in the seven final statistical models.

Fish species	Models	Predictors												
		Site	Season	Length	Sex	Fulton's K	<i>Proteocephalus</i>	Fish species	Site, Length ^a	Season, Length ^a	Species, Season ^a	Species, Site ^a	Species, Length ^a	
W	Acanthocephala	-	+	+	-	-	-		-	-				
W	<i>Proteocephalus</i>	+	+	+	-	+			-	+				
P	Acanthocephala	+	+	+	-		-		-	-				
P	Cestoda	+	+	+	-				+	-				
B	Acanthocephala	-	+	+				+			+	-	+	
B	<i>Proteocephalus</i>	-	+	-				+			+	-	-	
B	Cestoda	-	+	-				+			+	-	-	

Note. Green cells (+): predictors included in the final model. Red cells (-): predictors excluded through model selection. W = Whitefish, P = Perch, B = Both fish species.

^a Interactions

3.4 Parasites

Complete parasite data broken down by season and sampling site are presented in Annex 2 and 3 for whitefish and in Annex 4 and 5 for perch. Here, all data for prevalence, mean intensity and mean abundance referred to in the text are reported. Together, 2113 parasites of at least 11 different species were found in the investigated fish. The only ectoparasite found in both fish species was *Argulus coregoni*, while the endoparasite taxa found in both fish species were *Proteocephalus* spp., *Acanthocephala*, *Dibothriocephalus* spp., *Triaenophorus crassus* and Nematoda. As the parasite intensity was very high in a few fish individuals of both fish species, these individuals affected the mean abundance greatly. The predominant parasites were *Acanthocephala* and *Proteocephalus* spp. They were the only parasites found in a higher number than 10 in one fish individual.

Totally 769 parasites of 8 species were found in the investigated whitefish (Figure 2), whereas 710 individuals were endoparasites (6 species), 59 ectoparasites (2 species). Of the 101 whitefish inspected, 69 fish were infected with one or more parasites. In addition

to the above mentioned endoparasites, also Trematoda was found in whitefish. The ectoparasite taxa were *Argulus coregoni* and *Salmincola* sp. The Acanthocephala and *Proteocephalus* sp.1 were most abundant endoparasites found in whitefish. The total prevalence of parasites was 68.3 % (CI 58.7–76.6), mean intensity 11.1 ± 2.4 and mean abundance 7.6 ± 1.7 . The summer season stands out with high parasite counts, while the distribution by sampling site was more even (Figure 3), but note the uneven sample sizes.

Totally 1344 parasite individuals of 8 species were found in the 258 investigated perch (Figure 4), whereas only one individual was an ectoparasite. Together, 200 perch were infected with one or more parasites, and Acanthocephala was most abundant. In addition to the endoparasites found in both fish species, *Triaenophorus nodulosus* and *Eubothrium* sp. was only found in perch. The total prevalence of parasites was 77.5 % (CI 72.0–82.2), mean intensity 6.7 ± 0.7 and mean abundance 5.2 ± 0.6 . Similar to whitefish, most parasites were found in the summer season, while the parasite load between sites was more even (Figure 5).

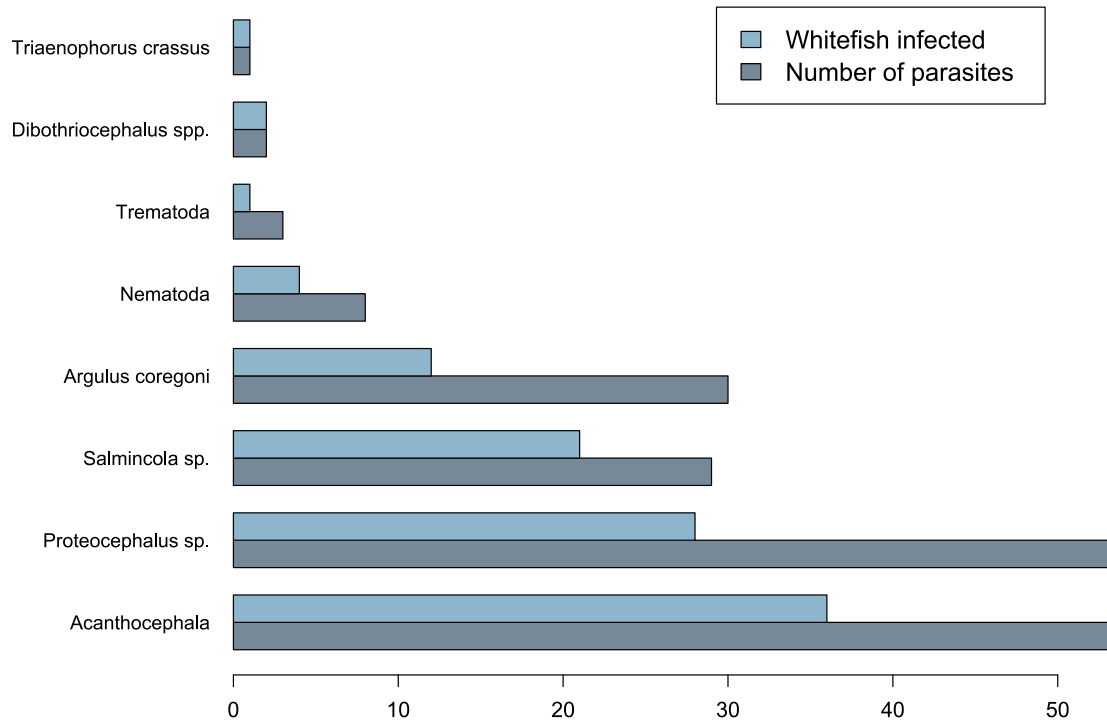


Figure 2. Parasite species found in whitefish in Lake Norsjø, with the number of whitefish infected and the total number of parasites shown. Note that the limit of the x axis is set at 50. The number of *Proteocephalus* sp.1 and *Acanthocephala* was 367 and 329, respectively.

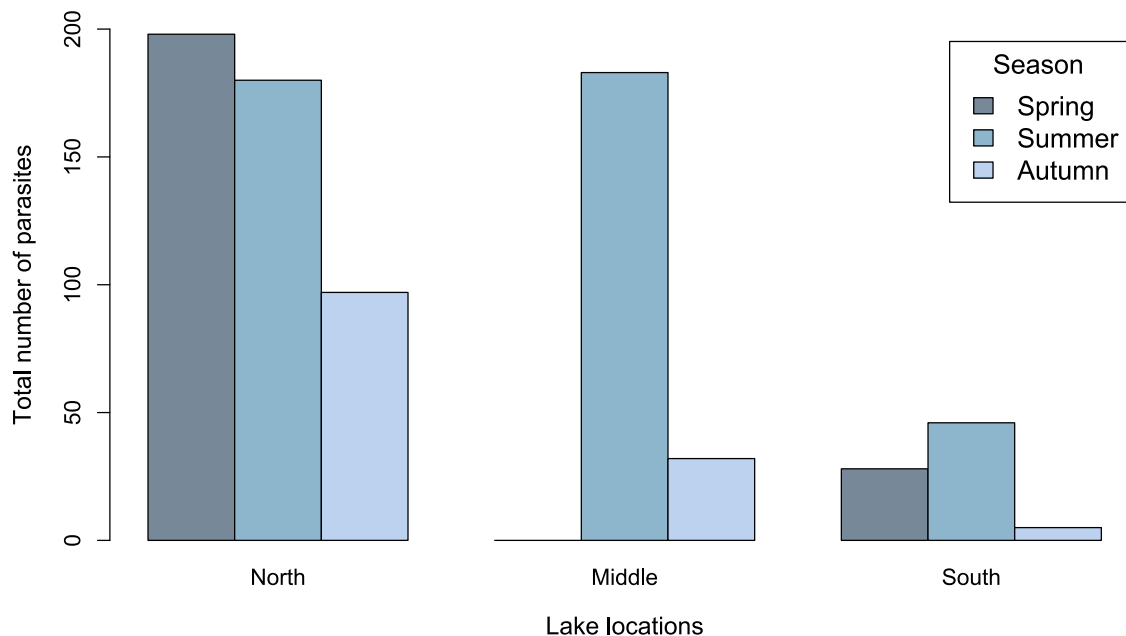


Figure 3. Whitefish parasite infection by seasons and sampling sites in Lake Norsjø. Season: spring n=39, summer n=39, autumn n=23. Site: North n=67, Middle n=24, South n=10.

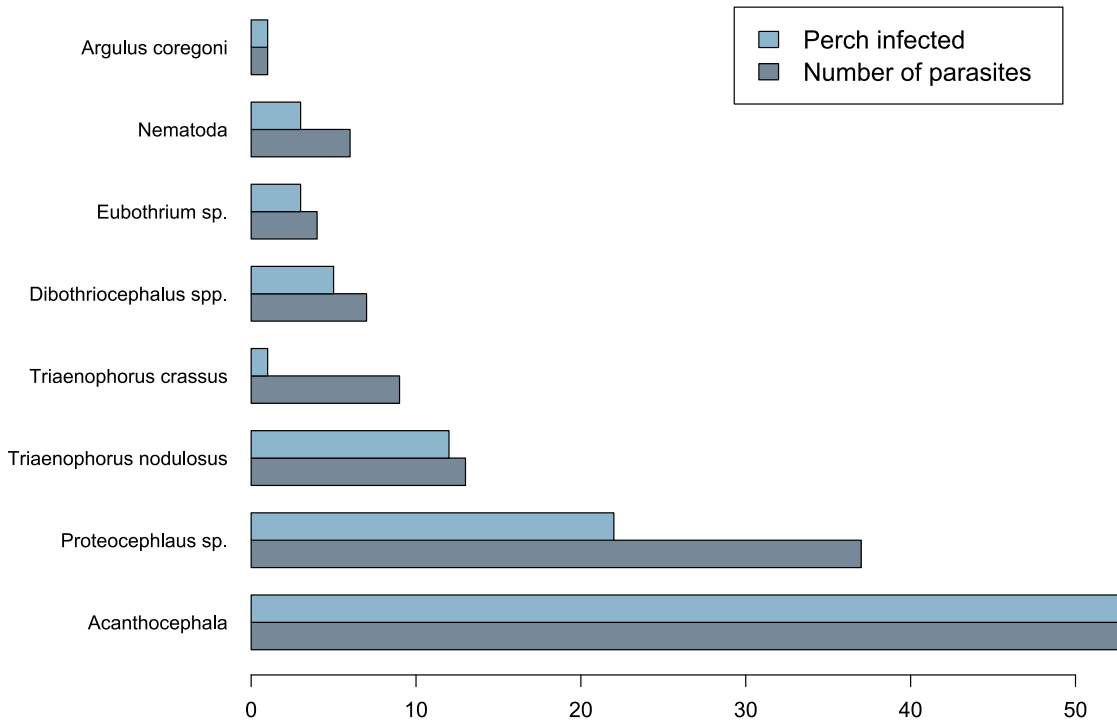


Figure 4. Parasite species found in perch from Lake Norsjø, with the number of perch infected and the total number of parasites shown. Note that the limit of the x axis is set at 50. The number of perch infected and number of Acanthocephala found were 189 and 1270, respectively.

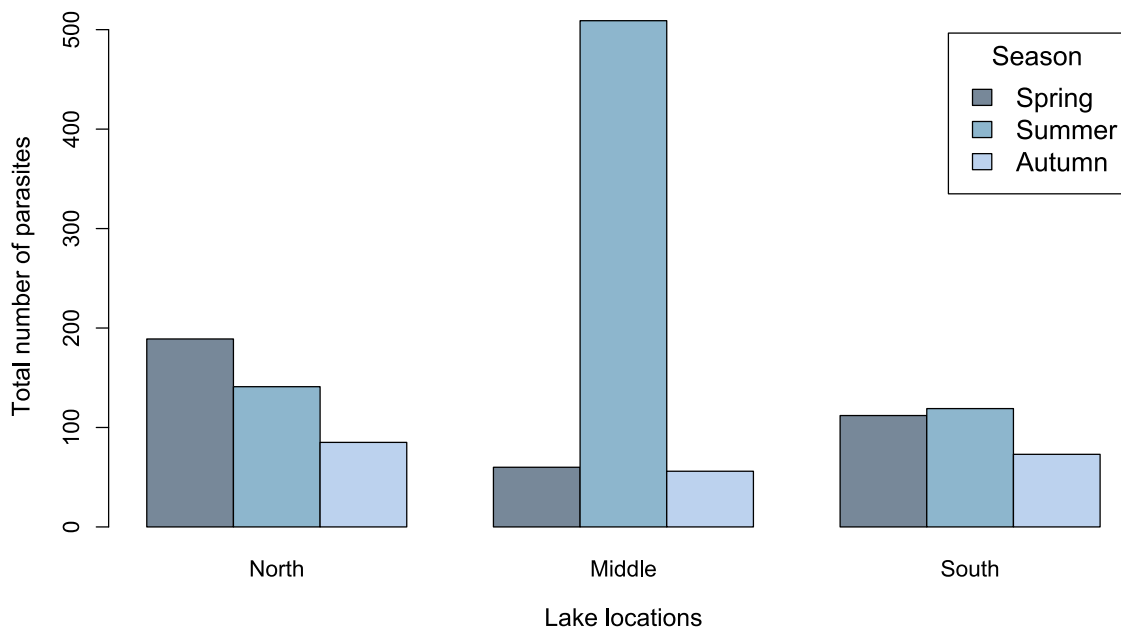


Figure 5. Perch parasite infection by seasons and sampling sites in Lake Norsjø. Season: spring n=78, summer n=90, autumn n=90. Site: North n=81, Middle n=87, South n=90.

Acanthocephala

Totally 329 acanthocephalans were found in 28 whitefish, while 1270 acanthocephalans were found in 189 perch. In whitefish, the prevalence was 27.7 % (CI 19.9–37.2), with a mean intensity of 11.8 ± 3.1 and mean abundance of 3.3 ± 1.0 . This mean intensity in whitefish was the highest found in this study, with 63 acanthocephalan individuals as the highest count in one whitefish.

In perch, the prevalence was 73.3 % (CI 67.5–78.3), with a mean intensity of 6.7 ± 0.8 and mean abundance of 4.9 ± 0.6 . This prevalence and mean abundance were the highest found in this study. The highest acanthocephalan count in one perch was 62.

In both fish species, the acanthocephalans were found in stomach and all parts of the intestine, and some of them came out of the anus while handling the fish in the field. In both perch and whitefish, some parasites were attached to the intestine, while many had unexposed proboscises and were unattached. In whitefish, some of the parasites were attached to the outside of the intestine, rather than the inside.

The parasites size ranged 3–14 mm in whitefish and <1–21 mm in perch. The acanthocephalans in perch had a robust body that was slightly wider close to the proboscis (Figure 6A). The proboscis was long with about 7–8 hooks in each row (Figure 6B). In contrast, the acanthocephalans in whitefish had a very soft body and some were wrinkled, others smooth (Figure 6C). Most acanthocephalans in whitefish normally had 6–7 hooks in each row (Figure 6D), while some appeared to have only 3–4 hooks, although this low count was uncertain, likely due to insufficiently exposed proboscis. Since the proboscises of the unattached individuals often were hidden, they were difficult to expose entirely, and accordingly the hooks difficult to observe/count. For some of the attached parasites, the hook count was also uncertain when the proboscises were covered in host tissue that was difficult to remove to make the hooks visible.

Season and length were the predictors that best explained the variations in parasite abundance in whitefish (Table 8). Significantly fewer parasites were found in autumn than in spring. Furthermore, fewer parasites were found in summer than in spring, but this

difference was not significant. Both prevalence and abundance were highest in summer, while the intensity was highest in spring, with more fish with high parasite loads. The parasite abundance exhibited a significant positive correlation with the length of whitefish.

Table 8. Output data from statistical modelling of Acanthocephala in whitefish from Lake Norsjø, showing the effect of season and fish length on parasite abundance.

Predictor	Estimate	SE	CI		z-value	p-value
			2.5%	97.5%		
Intercept	-11.1	2.28	-17.0	-5.67	-4.86	< 0.001
Summer (Season)	-1.29	0.766	-3.01	0.236	-1.69	0.093
Autumn (Season)	-3.51	0.984	-5.72	-1.48	-3.56	< 0.001
Length	0.045	0.009	0.025	0.068	5.19	< 0.001

Sampling site, season and length were the predictors best explaining the variation in parasite abundance in perch (Table 9). There was fewer parasites at site North and site South than at site Middle, but the differences were not significant. Compared with spring, there were significantly more parasites in summer and significantly fewer parasites in autumn. The parasite abundance exhibited a weak but significant positive correlation with the length of perch.

Table 9. Output data from statistical modelling of Acanthocephala in perch from Lake Norsjø, showing the effect of sampling site, season and fish length on parasite abundance.

Predictor	Estimate	SE	CI		z-value	p-value
			2.5%	97.5%		
Intercept	-0.493	0.417	-0.388	1.38	1.18	0.237
North (Site)	-0.310	0.242	-0.782	0.165	-1.28	0.200
South (Site)	-0.392	0.208	-0.823	0.040	-1.88	0.060
Summer (Season)	0.632	0.210	0.192	1.07	3.02	0.003
Autumn (Season)	-0.618	0.220	-1.05	-0.188	-2.81	0.005
Length	0.005	0.002	0.001	0.009	2.71	0.007

Evaluating the acanthocephalans in both fish species together, totally 1599 acanthocephalans were found in the 217 infected fish. Total prevalence was 60.4 % (CI 55.3–65.4), with mean intensity of 7.4 ± 0.8 and mean abundance of 4.5 ± 0.5 . Season, length and fish species were the predictors best explaining the variations in the parasite data (Table 10). Compared with spring, significantly more parasites were found in

summer and significantly fewer in autumn. Parasite abundance exhibited a weak but significant positive correlation with fish length. Also, significantly fewer acanthocephalans were found in whitefish than in perch. The effect of season on abundance was significantly smaller in whitefish than in perch, while the positive correlation between parasite abundance and fish length was significantly larger in whitefish than in perch.

Table 10. Output data from statistical modelling of Acanthocephala in both fish species combined, showing the effect of fish species, season, fish length, and their interactions on parasite abundance in Lake Norsjø.

Predictor	Estimate	SE	CI		z-value	p-value
			2.5%	97.5%		
Intercept	0.280	0.419	-0.643	1.22	0.668	0.504
Whitefish (Species)	-10.9	1.53	-14.9	-7.18	-7.14	< 0.001
Summer (Season)	0.780	0.242	0.305	1.25	3.23	0.001
Autumn (Season)	-0.590	0.251	-1.08	-0.103	-2.35	0.019
Length	0.005	0.002	0.001	0.009	2.67	0.007
Whitefish (Species) Summer (Season) ^a	-1.94	0.531	-3.02	-0.913	-3.65	< 0.001
Whitefish (Species) Autumn (Season) ^a	-2.82	0.716	-4.36	-1.39	-3.94	< 0.001
Whitefish (Species) Length ^a	0.038	0.006	0.024	0.053	6.57	< 0.001

^a Interactions

***Proteocephalus* sp.1 and sp.2**

All together 367 individuals of *Proteocephalus* sp.1 were found in the 34 infected whitefish. This was the parasite with the highest prevalence (33.7 %, CI 25.2–43.4) and mean abundance (3.6 ± 1.3) in whitefish. The mean intensity was 10.8 ± 3.5 , with 108 individuals of *Proteocephalus* sp.1 as the highest count in the pyloric caeca of one whitefish (counted scolices). In perch, totally 37 *Proteocephalus* sp.2 individuals were found in the 22 infected fish. The prevalence was 8.5 % (CI 5.7–12.7), with mean abundance of $0.1 \pm <0.1$ and mean intensity of 1.7 ± 0.3 . The highest parasite count in one perch was 7.

The *Proteocephalus* spp. in both fish species were most often found in the pyloric caeca, but also in the upper part of the small intestine. In perch, some parasites came out of the anus when handling the fish in the field. All were adult individuals.

In whitefish, some morphologic variability was observed among the *Proteocephalus* sp.1 individuals investigated, but only the most frequently found morphology is described. The scolex was most often rounded and large, visibly wider than the strobila (Figure 6E). Suckers seemed large as they were easily visible. The strobilae were segmented in both fish species (Figure 6F). The *Proteocephalus* sp.2 in perch seemed to have a different morphology than those found in whitefish. The *Proteocephalus* sp.2 individuals had a small scolex with decreasing width anteriorly, small suckers and a wide, almost non-visible neck (Figure 6G). Three parasite individuals in two perch had a very thin and long neck, with deviant characteristics from what described above. Despite this fact, they were included in the *Proteocephalus* sp.2 data.

In perch, both prevalence, intensity and abundance were highest at site North and lowest at site South. There was complete separation/perfect prediction in the season data of *Proteocephalus* sp.2, as all 37 *Proteocephalus* sp.2 individuals found in perch were present in spring, with a prevalence of 28 % (CI 19–39).

In whitefish, sampling site, season, length and K_f were the predictors that best explained the variation in the parasite data (Table 11). Significantly fewer parasites were found at site South compared with site Middle. Furthermore, more parasites were found at site North than at site Middle, but the difference was not significant, as the prevalence was highest at site Middle, while the intensity and abundance were highest at site North. Significantly more parasites were found in summer and autumn than in spring. Parasite abundance exhibited a significant negative correlation with the K_f value, while it exhibited a significant positive correlation with the length of the fish. The positive correlation between parasite abundance and fish length was significantly smaller in summer and autumn than in spring.

Table 11. Output data from statistical modelling of *Proteocephalus* sp.1 in whitefish from Lake Norsjø, showing the effect of sampling site, season, fish length, K_f (Fulton's K) and the interaction between season and fish length on parasite abundance.

Predictor	Estimate	SE	CI		z-value	p-value
			2.5%	97.5%		
Intercept	-30.0	9.92	-54.5	-14.4	-3.03	0.003
North (Site)	0.677	0.694	-0.875	2.10	0.976	0.329
South (Site)	-2.58	1.16	-5.03	-0.186	2.23	0.026
Summer (Season)	45.4	11.4	26.4	72.8	3.98	< 0.001
Autumn (Season)	34.8	11.3	15.8	62.0	3.06	0.002
Length	0.133	0.038	0.070	0.230	3.50	< 0.001
K_f	-11.4	4.52	-22.1	-1.18	-2.53	0.011
Summer (Season) Length ^a	-0.150	0.385	-0.244	-0.085	-3.89	< 0.001
Autumn (Season) Length ^a	-0.114	0.039	-0.208	-0.049	-2.95	0.003

^a Interactions

In both fish species combined, totally 404 *Proteocephalus* spp. individuals were found in the 56 infected fish. Total prevalence was 15.6 % (CI 12.2–19.7), with mean intensity of 7.2 ± 2.2 and mean abundance of 1.1 ± 0.4 . Fish species and season were the predictors best explaining the variation in the *Proteocephalus* spp. data (Table 12). Significantly more *Proteocephalus* individuals were found in whitefish than in perch.

Table 12. Output data from statistical modelling of *Proteocephalus* spp. in both fish species combined, showing the effect of fish species on parasite abundance in Lake Norsjø.

Predictor	Estimate	SE	CI		z-value	p-value
			2.5%	97.5%		
Intercept	-0.746	0.333	-1.37	-0.049	-2.24	0.025
Whitefish (Species)	1.45	0.540	0.425	2.58	2.69	0.007

Trienophorus nodulosus and *Trienophorus crassus*

Together 13 *Trienophorus nodulosus* individuals were found in 12 infected perch, none in whitefish. The prevalence was 4.7 % (CI 2.6–8.1). The species was found in the intestine, and in some cases, they came out of the anus while handling the fish in the field. The *T. nodulosus* were plerocercoids and thus immature and unsegmented. The hooks were thin and small (Figure 6H). The parasite was found in all seasons and at all

sites, but highest numbers were found in autumn at site North, with a prevalence of 10 % (CI 5.2–18) in autumn and a prevalence of 9.9 % (CI 4.9–19) at site North.

While only one *Triaenophorus crassus* individual was found in whitefish, nine individuals were found in one single perch. In whitefish, the parasite was found unencysted in the visceral cavity, while in perch all nine came out of the anus in the field. The hooks were large and broad in both fish species (Figure 6I), substantially larger than in the *T. nodulosus*. All individuals were plerocercoids. In perch, all individuals were found in spring at site South. In whitefish, the parasite was found in summer at site North.

***Dibothriocephalus* spp.**

Totally two *Dibothriocephalus* spp. individuals were found in two whitefish, while seven individuals were found in totally five infected perch. In whitefish the parasites were about 30–40 mm long and very wrinkled, while in perch, they were less wrinkled and all seven were short, well below 20 mm. The individuals in whitefish were found in summer and autumn at site Middle and South, while in perch, they were found in the spring and autumn, at site North and Middle.

***Eubothrium* sp.**

Totally four *Eubothrium* sp. individuals were found in three infected perch, none in whitefish. The four parasites were found in one perch from each of the three sampling sites, with three parasites in spring and one in autumn. The individuals were small, with a length of 4–8 mm.

Cestoda

The grouped response variable, within the class Cestoda, includes adults of *Proteocephalus* spp. and plerocercoid stages of *Triaenophorus nodulosus*, *Triaenophorus crassus*, *Eubothrium* sp., and *Dibothriocephalus* spp.

All the five cestodes listed above were found in perch. All together 70 individuals were present in the 38 infected perch. The prevalence was 14.7 % (CI 10.9–19.6), with mean intensity of 1.8 ± 0.3 and mean abundance of 0.3 ± 0.1 . Three cestode species were found

in whitefish, i.e. *T. crassus*, *Dibothriocephalus* spp. and *Proteocephalus* sp.1 All except three of the total 370 cestodes found in the 36 infected whitefish were *Proteocephalus* sp.1 individuals. Total prevalence was 35.6 % (CI 27.0–45.4), with a mean intensity of 10.3 \pm 3.4 and a mean abundance of 3.7 \pm 1.3.

In perch, the sampling site, season and length were the predictors best explaining the variations in cestode abundance (Table 13). Significantly more cestodes were found at site North than at site Middle judged by p-value, but the confidence interval includes zero, while fewer cestodes were found at site South than at site Middle, but this difference was not significant. The prevalence was highest at site North, i.e. 32 % (CI 17–35), while the intensity was highest at site South (3.2 \pm 1.8). Significantly less cestodes were found in summer and autumn compared with spring. The prevalence in spring was 32.1 % (CI 23–43), in summer 2.2 % (CI 0.2–8.3), and in autumn 12.2 % (CI 6.9–21). The cestode abundance exhibited a significant positive correlation with the length of the perch. This effect was significantly smaller at site North than at site Middle judged by p-value, but the confidence interval includes zero, and the length effect was even larger at site South than at site Middle, but not significant.

Table 13. Output data from statistical modelling of Cestoda in perch from Lake Norsjø, showing the effect of sampling site, season, fish length and the interaction between site and length on parasite abundance.

Predictor	Estimate	SE	CI		z-value	p-value
			2.5%	97.5%		
Intercept	-4.34	1.46	-8.48	-0.530	-2.97	0.003
North (Site)	4.01	2.00	-0.913	9.24	2.01	0.045
South (Site)	-3.01	2.48	-9.33	2.85	-1.21	0.225
Summer (Season)	-3.86	0.802	-5.82	-2.48	-4.81	< 0.001
Autumn (Season)	-1.71	0.404	-2.54	-0.938	-4.24	< 0.001
Length	0.020	0.007	<0.001	0.042	2.74	0.006
North (Site) Length ^a	-0.018	0.009	-0.042	0.005	-2.01	0.045
South (Site) Length ^a	0.013	0.012	-0.016	0.044	1.08	0.281

^a Interactions

Together 440 cestode individuals were found in 74 infected fish, i.e. 38 perch and 36 whitefish. The total prevalence was 20.6 % (CI 16.8–25.1), with a mean intensity of 5.9 \pm 1.7 and mean abundance of 1.2 \pm 0.4. Season and fish species were the predictors best

explaining the variation in total number of cestodes (Table 14). Significantly less individuals were found in summer and autumn compared with spring, and significantly more cestodes were found in whitefish than in perch. The effect of season on cestode abundance was significantly larger in whitefish than in perch.

Table 14. Output data from statistical modelling of Cestoda parasites in both fish species combined, showing the effect of fish species, season and their interaction on parasite abundance in Lake Norsjø.

Predictor	Estimate	SE	CI		z-value	p-value
			2.5%	97.5%		
Intercept	-0.386	0.309	-0.959	0.261	-1.25	0.211
Whitefish (Species)	1.09	0.511	0.121	2.15	2.14	0.032
Summer (Season)	-3.42	0.813	-5.35	-2.01	-4.21	< 0.001
Autumn (Season)	-1.41	0.478	-2.36	-0.479	-2.94	0.003
Whitefish (Species) Summer (Season) ^a	4.30	0.993	2.47	6.48	4.33	< 0.001
Whitefish (Species) Autumn (Season) ^a	2.18	0.814	0.610	3.85	2.69	0.007

^a Interactions

Salmincola sp.

Together 29 *Salmincola* sp. individuals were found on the 21 infected whitefish, with a prevalence of 20.8 % (CI 14.0–29.8), mean intensity of 1.4 ± 0.2 and mean abundance of 0.3 ± 0.1 . The individuals were found on pectoral fins, pelvic fins and dorsal fins, both on the fins and on the skin at the basis of the fins. The parasites had a long and anteriorly slender cephalothorax. The trunk was long, slender and smooth, with a length of 3–4 mm. The total length of the parasites was 4–6 mm (cephalothorax + trunk). Egg sacs were long and straight (Figure 6J). On the second antenna, both the exopod and the endopod were spinulated/denticulated. The claw of the maxilliped was greatly reduced with a small denticle visible near its base. The second maxilla had inflated tips. The bulla was spherical (Figure 6K). The parasite was found in all three seasons and at all three sampling sites.

Argulus coregoni

Together 30 *Argulus coregoni* individuals were found on the 12 infected whitefish, while only one individual was found on perch. In whitefish, the prevalence was 11.9 % (CI 6.8–19.8), with mean intensity of 2.5 ± 0.7 and mean abundance of 0.3 ± 0.1 . The species was found on the back, abdomen and fins (pectoral fins, pelvic fins and anal fin), and varied

both in size and colour (red to white). The individual found on perch was about 4 mm, while the individuals found on whitefish were larger. Their lobes were pointed and acuminate (Figure 6L). While the only individual on perch was found in summer at site North, 29 of the 30 individuals found on whitefish occurred in summer and at all three sampling sites, with a prevalence of 28 % (CI 16–44).

Nematoda

Together eight nematodes were found in the four infected whitefish, while totally six individuals were found in the three infected perch. Five of the individuals in whitefish were found encysted on the outside of either the swim bladder, stomach or oesophagus, while three were found unencysted. In perch, two were found encysted in two fish, while the remaining four were found in the intestine of one fish. The whitefish nematodes varied 12–23 mm in length, while the perch nematodes ranged 9–27 mm. The nematode morphology appeared to be different from each other, both between and within the two fish species. The nematodes were found in spring and autumn, at site North and Middle.

Trematoda

Three trematodes were found in one whitefish in autumn at site South. The individuals were not further described as they were too disintegrated.

Unidentified

Three cysts in three whitefish were not included in the parasite data. One was within the class Cestoda but not possible to identify in more detail, while the two remaining cysts were mistakenly not opened. In four perch, six unidentified unsegmented parasites were found, most likely immature cestode individuals, without any visible scolex or strobila, essential morphology for identification. There was also found another unidentified, segmented parasite in perch.

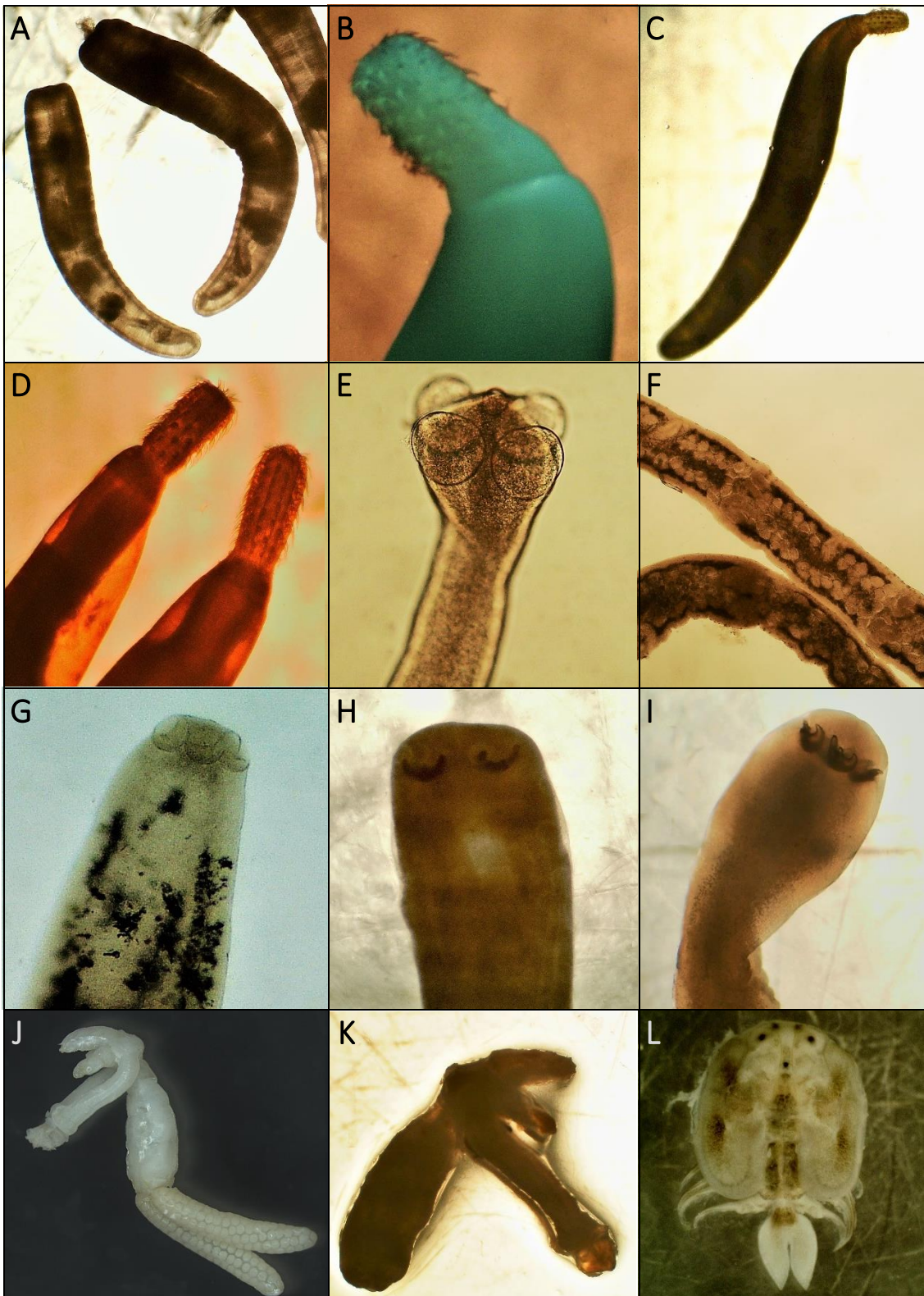


Figure 6. Photographs of parasites from whitefish and perch caught in Lake Norsjø in 2018. **A,B** – *Acanthocephala* from perch. **C,D** – *Acanthocephala* from whitefish. **E,F** – *Proteocephalus* sp.1 from whitefish. **G** – *Proteocephalus* sp.2 from perch. **H** – *Triaenophorus nodulosus* from perch. **I** – *Triaenophorus crassus* from whitefish. **J,K** – *Salmincola* sp. from whitefish (J, damaged bulla). **L** – *Argulus coregoni* from whitefish.

4 Discussion

4.1 Fish diet and habitat use

The diet and habitat use of the fish can affect what parasites the fish hosts acquire, since fish feeding on pelagic zooplankton typically will acquire more copepod-transmitted parasites, while fish feeding on benthic organisms will acquire more benthic macroinvertebrates transmitted parasites (Knudsen et al., 2004; Stutz et al., 2014). Thus, knowledge about fish diet and habitat is necessary for explaining the variation in parasite fauna.

The diet and habitat choice of perch varies between lakes (lake morphology and fish diversity), age/ontogeny, but also with season and availability. In general, perch are found in deeper profundal areas of deep lakes as Lake Norsjø during winter, and in shallower littoral areas during the remaining year. Perch are omnivorous, eating whatever easily available. Thus, their diet in general consists of both benthic organisms and zooplankton, and fish when they reach a certain size (Thorpe, 1977; Wang & Eckmann, 1994). Littoral perch of Lake Norsjø however, have been found to feed mainly on littoral, benthic organisms from spring to autumn (Lydersen & Moreno, 2016), while no diet data was reported from the winter period.

Whitefish differs from perch in that they often are found in segregated sympatric forms/morphs in many lakes (Enge, 1959; Siwertsson et al., 2013). Jensen (1954) described three potential morphs in Lake Norsjø, which he called “stream whitefish” (strømsik), “littoral whitefish” (grunnsik) and “winter whitefish” (vintersik). These whitefish morphs were reported to differ in size, somewhat different morphology, different time of spawning and different spawning sites and depths within the lake. Thus, they likely occupy different lake habitats and subsequent different diets, despite some habitat overlap likely occurs. Littoral whitefish in Lake Norsjø was reported by Jensen (1954) being the largest of these morphs, typically above 350–400 g. It spawns close to shore in shallow waters in November, and primarily feed on benthic organisms. Smaller fish (< 350–400 g) normally represents the two other morphs, the stream and winter whitefish, both preferring a planktonic diet as crustaceans. The stream whitefish was

reported to spawn in October–November in River Bøelva and River Sauerelva, north in Lake Norsjø, while the winter whitefish spawn in February at depths between 15–70 m. In this thesis, I have not tried to distinguish between the three morphs of whitefish. Nonetheless, as only three of 101 whitefish in the material weighted more than 350 g, this might indicate that the majority of fish caught was stream or winter whitefish. However, it is also important to underline that the study referred to, Jensen (1954), was implemented more than 60 years ago, a period when a lot more whitefish fishing occurred. Thus, changes in populations strength, weight of different morphs, food status etc. might have changed significantly during these years.

More recent fish studies in Lake Norsjø reported that the winter whitefish morph feed on a mixture of zooplankton based pelagic and profundal benthic diet (Olk et al., 2016). While Jensen (1954) found that whitefish in Lake Norsjø did not eat fish, Olk et al. (2016) found fish to be a considerable part of the whitefish diet in this lake. Lydersen & Moreno (2016) studied fish in the northern parts of Lake Norsjø and found whitefish individuals that almost only fed on benthic organisms, but also individuals that almost only fed on zooplankton, indicating differing habitat use. Accordingly, they assumed presence of more than one morph in their fish material, as earlier described by Jensen (1954).

4.2 Phylum Acanthocephala

Individuals of the phylum Acanthocephala were found in high numbers in both perch and whitefish, but the determination of acanthocephalan species, also known as spiny- or thorny-headed worms, is uncertain.

In perch, having the highest number of acanthocephalans, *Acanthocephalus lucii* is the most abundant and most frequently reported species in Norway (Andersen, 1978; Halvorsen, 1971; Hartvigsen et al., 2002) and Europe (Carney and Dick, 1999). However, several other acanthocephalans have been found to infect perch, among others *Neoechinorhynchus rutili* (Carney & Dick, 1999; Halvorsen, 1971; Morozinska-Gogol, 2008). Neither *A. lucii* nor *N. rutili* are host specific, and are therefore found in various

freshwater fish species, including whitefish (Bykhovskaya-Pavlovskaya et al., 1964; Karvonen & Valtonen, 2004).

A. lucii is described as having a proboscis with 12–16 longitudinal rows of hooks with 7–9 hooks per row. It has a body somewhat expanded anteriorly, and with a length of 4–21 mm (Bykhovskaya-Pavlovskaya et al., 1964). The visible morphological characteristics of the acanthocephalans in perch in Lake Norsjø fit this species description, and no other acanthocephalan species have been found to have a higher resemblance. Accordingly, this species, *A. lucii*, is likely the acanthocephalan species found in perch in Lake Norsjø. Based on morphology, the acanthocephalan species in whitefish appeared to be another species. The soft body of the individuals found in whitefish in Lake Norsjø, made it difficult to press out the proboscis of the unattached individuals enough to expose and count the hooks. Some seemed to have considerable fewer hooks in each row than what normally found on *A. lucii*, but no individuals had as few and as small hooks as normally present in *N. rutili*. This might indicate that several acanthocephalan species are present in fish in Lake Norsjø, but it might also be a misinterpretation caused by insufficiently exposed proboscis. Despite different “structure” (soft/hard) of the acanthocephalans in perch and whitefish from Lake Norsjø, it theoretically might be the same species only expressing different morphology, as fish can both be paratenic and final hosts (Bykhovskaya-Pavlovskaya et al., 1964; Taraschewski, 2000). The species definition is therefore uncertain in both fish hosts in Lake Norsjø, as other possible species descriptions have not been sufficiently examined. More detailed studies of the morphology were not possible at USN, neither proper genetic analyses. Thus, the acanthocephalan parasites found in both perch and whitefish were only determined to the phylum, Acanthocephala.

As the acanthocephalans were found aggregated in very high numbers in only a few individuals of both fish species, while absent or few in most fishes, this explains the high intensities of acanthocephalans found in Lake Norsjø (Annex 2–5). This is in accordance with previous studies reporting overdispersed parasite infection patterns of acanthocephalans (Valtonen & Crompton, 1990). Acanthocephalans are short-lived, as several studies have reported life spans of about one year only (Chubb, 1982). Thus, they do not accumulate over time in the same manner as more long-lived parasites. The high

intensity of the acanthocephalan infection in fish in Lake Norsjø does likely reflect a relatively new recruitment of infection. Acanthocephalans are well known to manipulate their intermediate host into increased predation by the definitive host (Poulin & Thomas, 1999; Sparkes et al., 2004), which might be the main explanations for the high intensity of acanthocephalans in infected fish in Lake Norsjø.

In Lake Norsjø, significantly more acanthocephalans were found in perch than in whitefish. This might be explained by the differences in fish diet, with fish feeding on benthic organisms acquiring more benthic macroinvertebrates transmitted parasites than fish feeding on pelagic zooplankton (Knudsen et al., 2004; Stutz et al., 2014). Acanthocephalans have only one intermediate host in their life cycle, either amphipods, isopods or ostracods, all typically benthic organisms (Bykhovskaya-Pavlovskaya et al., 1964; Taraschewski, 2000). Accordingly, our parasite investigation supports that the perch diet is more based on benthic prey, typically more abundant in littoral lake areas, while the whitefish in Lake Norsjø have a more pelagic, zooplankton-based diet, causing the differences in acanthocephalan abundance.

Many of the acanthocephalan individuals found in both fish species had retracted proboscises and therefore not attached to the intestinal wall, as would be expected in a final host. While fish can serve as definitive host for many acanthocephalans, young immature acanthocephalans with retracted proboscises may indicate that the host is paratenic, and thus the parasite will not mature (Bykhovskaya-Pavlovskaya et al., 1964; Taraschewski, 2000). For example, *N. rutili* is reported being unable to reproduce in the broad whitefish (*Coregonus nasus*), as only a few of the many *N. rutili* individuals presented were attached and always below 2 mm in length, and whitefish therefore interpreted as an accidental host (Valtonen, 1979). As the morphology of the genital organs of this parasite was not studied in Lake Norsjø, mature status was not assessed. However, as some parasite individuals were attached and some not attached, this may indicate two or more different acanthocephalan species present in Lake Norsjø, with the attached species using the fish as host, and the unattached not infecting the fish, i.e. paratenic or accidental. In both cases it was difficult to get a correct count of hooks, regarding the attached individuals, because of difficulties with removing flesh attached

to the hooks on the proboscis, while in the unattached due to insufficiently exposed proboscis.

Some acanthocephalan species can however be almost unattached to the intestine. Both *A. lucii* and *N. rutili* are acanthocephalans with a shallow attachment, where only the anterior part of the proboscis is attached (Taraschewski, 2000). This could explain why many of the acanthocephalans in perch and whitefish in our fish material appeared to be unattached. Taraschewski (2000) also claimed that these acanthocephalans only were found intrainestinal and never extraintestinal, as they were not perforating the gut. However, in whitefish, some of the parasites were found attached to the outside of the intestine. These conflicting findings may support the speculation that the suspected species as mentioned above are incorrect, and/or that the acanthocephalans consist of more than one species. To avoid this, the acanthocephalans were treated as one group in the statistics.

The presence of seasonality and the timing of the cycles of acanthocephalan infection is reported to vary greatly between lakes (Andersen, 1978). This variation can be caused by e.g. different species of acanthocephalans and fish hosts, and differences within and between the lakes, like water temperatures, different intermediate hosts etc. (Chubb, 1982). A study of *A. lucii* reported highest prevalence from June to November (Andersen, 1978), while *N. rutili* was found with highest prevalence in the final host barbel (*Barbus barbus*) in February/March and lowest in July (Moravec & Scholz, 1993), although new recruitment of both parasite species occurred all year (Andersen, 1978; Moravec & Scholz, 1993). Thus, as the determination of acanthocephalan species in Lake Norsjø is uncertain, and the sampling only included May to September, the cause of the seasonality found in acanthocephalans in whitefish and perch of Lake Norsjø was not revealed.

In both fish species, the abundance of acanthocephalans was positive and significant correlated with fish length, although this effect was weak in perch. Similar observations are earlier reported by other scientists (Moravec & Scholz, 1993; Valtonen & Crompton, 1990), while other studies have reported highest parasite numbers in medium sized fish

(Andersen, 1978; Valtonen & Crompton, 1990). High abundance in medium sized fish, due to high mortality in heavily infected larger fish, might weaken the correlation between parasite load and fish length (Poulin, 2000). In general, an increase in endoparasite infection with fish length should be expected as larger and thus normally older fish have a need of more food and feed on more diverse prey, including ontogenetic shift to piscivory (Henriksen et al., 2016; Moravec & Scholz, 1993; Poulin, 2000; Valtonen et al., 2010; Zelmer & Arai, 1998).

4.3 Genus *Proteocephalus*

Proteocephalus spp. were found in both perch and whitefish in Lake Norsjø. In whitefish, *Proteocephalus exiguus* (syn. *Proteocephalus longicollis* and *Proteocephalus neglectus*) is the most common species. *P. exiguus* have been found to have several synonym species, and many formerly defined species are now considered invalid (Hanzelová et al., 1995; Hanzelová & Scholz, 1999; Scholz & Hanzelová, 1998). *P. exiguus* is thus reported to be a highly polymorphic species. It is considered not only the most frequent *Proteocephalus* species, but according to Scholz & Hanzelová (1998), the only species within this genus occurring in coregonid and salmonid fishes in Europe. Thus, *P. exiguus* is the most likely *Proteocephalus* species found in whitefish in Lake Norsjø.

As *P. exiguus* only occurs in coregonid and salmonid fishes in Europe, the *Proteocephalus* found in perch in Lake Norsjø is obviously another species. This was also supported by a different parasite morphology. In perch, *Proteocephalus percae* is the most abundant and most frequently reported species (Andersen, 1978; Carney & Dick, 1999; Halvorsen, 1971; Morozinska-Gogol, 2008). There is some debate regarding whether *P. percae* is strictly perch specific or not (Bykhovskaya-Pavlovskaya et al., 1964; Carney & Dick, 1999; Scholz & Hanzelová, 1998). Other species previously found in perch are *P. cernuae*, *P. torulosus* and *P. filicollis* (Carney & Dick, 1999; Morozinska-Gogol, 2008). However, the visible morphology characteristics of the individuals found in perch from Lake Norsjø fits the descriptions of scolex morphology of *P. percae*. These characteristics compared to Scholz et al. (1998), makes it likely that the predominant *Proteocephalus* species found in perch from Lake Norsjø is *P. percae*. The three “unusual” *Proteocephalus* sp. individuals

found in perch from Lake Norsjø, might be morphological variations as polymorphism in *Proteocephalus* species is common, and many characteristics have a high intraspecific variability (Scholz et al., 1998). Nevertheless, the unusual individuals might belong to another *Proteocephalus* species.

The morphometric characteristics visually studied were scolex size, form, neck width and size of suckers. However, we had not sufficient adequate detailing devices to look closer at other important morphology characteristics, as accurate measurements of width of the scolex, neck and suckers, presence of apical suckers, and more detailed morphology description of the strobila etc. Thus, there was not sufficient high-quality morphological data to conclude on species level, neither for whitefish nor perch. Thus, the presence of more than one *Proteocephalus* species cannot be excluded. Accordingly, the *Proteocephalus* parasites in whitefish and perch were only referred to as *Proteocephalus* sp.1 and *Proteocephalus* sp.2, respectively.

Proteocephalus spp. have an indirect life cycle consisting of only two hosts, copepods as the intermediate host and fish as the final host. Fish paratenic hosts are also known to sometimes have an important role in the life cycle of *Proteocephalus* (Scholz, 1999). The copepod host species changes through the year (Scholz, 1999). When the copepod intermediate hosts consume floating *Proteocephalus* eggs, the procercoids can develop. Whether the intermediate host gets infected from consuming floating eggs depends on several factors, like exposure time and water temperature, as well as variations in the copepod and parasite species present. The optimal temperature for development of several *Proteocephalus* procercoids, including *P. exiguus*, is reported to be about 20°C (Scholz, 1991, 1999). An exception from this is the procercoid development of *P. percae*, having perch as its definitive host, where complete development of procercoids have been reported to occur at 14°C, with inhabitation reported at both lower (5°C) and higher (20°C) temperatures (Wootten, 1974). Accordingly, water temperature may cause different seasonality of procercoids in the intermediate hosts of these *Proteocephalus* species.

The definitive hosts of *Proteocephalus* spp. are zooplanktivorous fish, and some *Proteocephalus* species are host specific (Scholz, 1999). Following ingestion of infected copepods, the procercoids mature in the definitive host. *P. exiguus* have been found to infect copepods from June to October, with highest prevalence both in copepods and fish in July and August (Anegg et al., 2015, Hanzelová et al., 1990). This was also found in whitefish in Lake Norsjø, where *Proteocephalus* sp.1 was more abundant in summer and autumn compared with spring. The seasonality of *Proteocephalus* sp.1 infection in Lake Norsjø is therefore most likely controlled by water temperature, as the parasites mature when the water temperatures reach a certain level (Scholz, 1999). Mean surface water temperature during summer in Lake Norsjø (ultimo July) was 22.3°C in 2018.

The seasonal changes in maturation of *P. percae* in perch is different from many other *Proteocephalus* species. Highest number of mature forms are reported to occur from March to May, when they become gravid. From June, egg release has occurred and *P. percae* is reported lost from the host, with only immature worms present until November (Andersen, 1978; Wootten, 1974). The seasonality found in perch of Lake Norsjø was in accordance with these studies, as *Proteocephalus* sp.2 was only found in spring. As the mean water temperature was 14.5°C in the spring, this also supports the development in this season. However, there are possibly other factors than temperature which are controlling the maturation of *P. percae*, like the spawning time of fish species (Wootten, 1974). Perch in Lake Norsjø primarily spawn during May.

While the prevalence of *Proteocephalus* sp.1 in whitefish was high (33.7 %), the *Proteocephalus* sp.2 prevalence in perch was low (8.5 %) compared with other studies (Andersen, 1978; Halvorsen, 1971). Six of the 34 infected whitefish contained from 19 to 108 *Proteocephalus* sp.1 individuals, constituting 73 % of the total *Proteocephalus* sp.1 count present in the 101 whitefish investigated. This typical overdispersion pattern is in accordance with previous studies (Zelmer & Arai, 1998). The significantly higher abundance in whitefish than in perch could be caused by differences in diet between the fish species, with whitefish feeding more on pelagic zooplankton and thus acquiring more parasites transmitted by copepods, like *Proteocephalus* spp., than the more littoral based perch (Knudsen et al., 2004; Stutz et al., 2014). However, both natural prevalence

differences between lakes and seasonal variations in lakes should be expected, and time of sampling might be crucial. As the fish sampling in Lake Norsjø started 28th of May, and this month is when *P. percae* becomes gravid and subsequently starts being lost from the host, we likely missed the *Proteocephalus* infection peak in perch in Lake Norsjø in 2018. After the parasites have released their eggs and the adult individuals are lost from the host, they are soon replaced by procercoids (Andersen, 1978; Wootten, 1974). In Lake Norsjø, only adult *Proteocephalus* sp.2 were found, and only in spring. Procercoids are too small to be detected by the naked eye, as fully developed procercoids only have a length of up to 730 µm (Scholz et al., 1999). The early maturation of the parasite has probably led to only immature forms being present in our summer and autumn samples, and thus too small to be detected by eye during analysis. The loss of this infection peak in perch might thus be the reason why significantly more *Proteocephalus* spp. individuals were found in whitefish than in perch in Lake Norsjø.

A significant increase of *Proteocephalus* spp. with increased fish length were revealed both by the whitefish model and the combined two fish species model. *Proteocephalus* spp. have previously been found to increase both with length and age of fish (Zelmer & Arai, 1998). The explanation for this is similar as described in the previous chapter about acanthocephalans, i.e. need of more food and feeding on more diverse prey, including ontogenetic shift to piscivory. As the number of both acanthocephalans and *Proteocephalus* sp.1 in whitefish was found to increase by length, and the parasites are transmitted by littoral benthic and pelagic zooplankton organisms respectively, indicates that the quantity of predation on both organism groups increase as the whitefish grow, rather than a shift in diet with increasing fish size.

No significant correlations were found between abundance of acanthocephalans and abundance of *Proteocephalus* sp. in neither perch nor whitefish. A negative correlation between *P. percae* and *A. lucii* in perch have earlier been reported, indicating interspecific competition (Andersen, 1978). However, our results did not reveal significant interspecific parasite competition.

Fulton's K (K_f) was used as a predictor in the whitefish model. For the *Proteocephalus* sp.1, there was lower parasite abundance with increasing condition factor. This could indicate that the presence of parasites has negative impact on fish growth, but may also be an effect of fish size *per se* as smaller fish often have lower condition and might feed more on infected copepods than larger fish. It must be mentioned that all premises for the use of K_f are not met, for example as all age classes are included, and it is not tested for K_f differences related to sex and time of spawning. Another assumption is that the whitefish has isometric growth.

4.4 Genus *Triaenophorus*

Triaenophorus spp. have an indirect life cycle consisting of three hosts, copepods, planktivorous fish and pike (Bykhovskaya-Pavlovskaya et al., 1964). It is common to find *Triaenophorus* spp. both in whitefish, perch, and other intermediate hosts, in lakes where they coexist with the final host pike (Anegg et al., 2015). Both *Triaenophorus* species were found in perch, while only *T. crassus* was found in whitefish. Both parasite species have previously been found in whitefish in Norway (Museth et al., 2017; Styrvold et al., 1981). Only *T. nodulosus* have been reported in perch in Norway (Hartvigsen et al., 2002), but *T. crassus* is reported in perch elsewhere (Morozinska-Gogol, 2008).

Triaenophorus spp. were found in all seasons and at all sampling sites in Lake Norsjø in 2018. Previous studies have found seasonality in egg release, but the seasonality in infection of fish hosts have been shown to vary considerably between lakes, as both water temperature and the *Triaenophorus* species are decisive factors for the variations in time (Amundsen & Kristoffersen, 1990; Anegg et al., 2015; Chubb, 1982).

T. crassus has mainly been found in intermediate host fish musculature, and *T. nodulosus* mainly encysted in the liver of the intermediate fish host in its plerocercoid stage. The adult stages are found in the intestine of pike (Bykhovskaya-Pavlovskaya et al., 1964). This might explain the very few individuals found in the intestine of perch and whitefish in Lake Norsjø, as those fish species are intermediate hosts. As the intermediate fish host eats proceroid infested copepods, the parasite develops into plerocercoids and travels

from the intestine to the liver or musculature, and thus seldom found in the intestine. This might be the explanation for the six unidentified cestodes found in perch. In these six cestodes, the hooks had likely not been formed yet, as hook development of plerocercoids might take place several months after infection of the second intermediate host (Dick & Rosen, 1982). This is further supported by that the most prevalent cestode in the material, the *Proteocephalus* spp., is reported forming a scolex that resembles the adult scolex already at the proceroid stage (Scholz, 1999). The unidentified parasites found in Lake Norsjø, are thus unlikely to be *Proteocephalus* spp., but more likely *Triaenophorus* spp.

To study the actual abundance and prevalence of *Triaenophorus* spp. would have demanded much more time in the laboratory with dissection of fish muscle and organs prior to microscopy. A such approach would likely revealed a much higher prevalence of *Triaenophorus* spp. and other parasites. For example, *T. crassus* infection in whitefish musculature have been found with a prevalence of 60.9 % in a lake in eastern Norway (Museth et al., 2017) and 85.7 % in a Finnish lake (Karvonen & Valtonen, 2004), while *T. nodulosus* infection in perch have been found with a prevalence ranging 11–100 % in lakes of South-Eastern Norway (Hartvigsen et al., 2002) and 94 % in a German lake (Brinker & Hamers, 2007). Thus, both parasites would probably have been found with much higher prevalence in Lake Norsjø with the investigation approach described above. *T. crassus* have been found to alter the swimming behaviour of infected copepods and consequently making them more susceptible for predation and with subsequent increased transmission and maturation potential (Pulkkinen et al., 2000). This is probably one of the main reasons for the high prevalence of *Triaenophorus* spp. found in many lakes.

4.5 Genus *Dibothriocephalus*

Three *Dibothriocephalus* species have frequently occurred in Europe, *D. ditremus*, *D. dendriticus* and *D. latus* (Andersen & Gibson, 1989), but due to sewage treatment, *D. latus* is now rarely found in Scandinavia (Dupouy-Camet & Peduzzi, 2004). The *Dibothriocephalus* individuals found in Lake Norsjø were only identified to genus as the

identification key specifies that it is not suitable for frozen material, as the freezing process affects the morphology (Andersen & Gibson, 1989).

Dibothriocephalus larvae are known to infect both perch and whitefish (Sobecka & Słomińska, 2007; Karvonen & Valtonen, 2004). It is unknown whether the individuals found in Lake Norsjø are *D. ditremus* or *D. dendriticus*. As the lengths of the larvae found in perch and whitefish differed in Lake Norsjø, this could indicate the presence of both species, as length is one important difference between them. However, the *Dibothriocephalus* species can have an extreme morphologic plasticity within its wide range of hosts (Andersen et al., 1987). This, and the abovementioned freezing effects, cannot be excluded as reasons for the morphological differences found. Accordingly, all individuals in this study are referred to as *Dibothriocephalus* spp.

Despite few *Dibothriocephalus* spp. were found in whitefish and perch of Lake Norsjø in 2018, the parasite was found in all three seasons and at all sampling sites. *Dibothriocephalus* spp. was the only allogenic parasite found, meaning that it transits between two types of ecosystems during their life cycle (aquatic and terrestrial, i.e. in birds). They have an indirect life cycle with copepods as first intermediate host, planktivorous fish as second, and piscivorous birds, occasionally fox, bear, cat, dog, man and other piscivorous warmblooded animals as final hosts (Andersen & Gibson, 1989). While other parasites, like the *Triaenophorus* spp., has a clear seasonality in their egg release, *Dibothriocephalus* spp. may be dispersed from birds all through the year (Amundsen & Kristoffersen, 1990). Seasonality is thus not expected.

4.6 Genus *Eubothrium*

It was not possible to get adequate details of the *Eubothrium* scolex to determine the species according to the literature key used (Andersen and Kennedy, 1983). The *Eubothrium* species are known to be difficult to determine based on morphology only (Andersen & Kennedy, 1983), but also by host specificity and distribution. The biological factors of host specificity and distribution suggest that the *Eubothrium* species in Lake Norsjø is *E. crassum*. This species has an indirect life cycle with a copepod intermediate

host, and is strictly host specific to its definitive host, brown trout. However, it is well known that perch can serve as an accidental or paratenic second intermediate host (Chubb, 1982; Hanzelová et al., 2002; Kennedy, 1978; Morozinska-Gogol, 2008; Sobecka & Słomińska, 2007). In the paratenic host, the parasite will not develop and mature, but can be a reservoir for the parasite if the fish is consumed by the definitive host. Thus, the low number of *E. crassum* often found in perch is likely because this parasite cannot deficiently establish in perch (Behrmann-Godel, 2013). As *E. crassum* in perch are reported as small and sexually immature (Hanzelová et al., 2002; Kennedy, 1978), this can explain the small size and low abundance found in perch in Lake Norsjø. Thus, they are likely a result of random acquisition because they have proper sympatric hosts (perch and brown trout) in the same lake, and likely with overlapping diet. However, because of challenges with studying morphology and uncertainties regarding host specificity and distribution, also this parasite is referred to as *Eubothrium* sp. in this investigation.

4.7 Class Cestoda

Four genera of cestodes, as discussed separately above, were found in Lake Norsjø in 2018, three species in whitefish and five species in perch. They are transmitted to fish by a copepod intermediate host, and some of them have a second intermediate host. The cestodes, also known as tapeworms, are present as proceroid in the copepod, as plerocercoids in the second intermediate host, and mature to adult in the final host, and piscivory is an important route of transmission (Henriksen et al., 2016).

According to Jensen (1954), the whitefish in Lake Norsjø at that time (more than 60 years ago) had few parasites, and only one unidentified cestode was found in the 78 whitefish investigated, in addition to a few cysts on abdominal organs. The parasite infection in perch was considered negligible and not further described in his report. In our data from 2018, 70 cestodes were found in perch and 370 in whitefish. As the lake previously was subject to substantial fishing, today's larger fish populations might explain this increase.

Several of the parasites were found aggregated in very high numbers in a few fish individuals, while they were absent or few in most individuals. This is in accordance with

other studies, revealing overdispersed patterns of cestode infection, as some species can accumulate in the host over time (Amundsen & Kristoffersen, 1990; Henriksen et al, 2016; Knudsen et al., 2004; Zelmer & Arai, 1998).

The abundance of cestodes were found to change by season. In perch, significantly fewer cestodes were found in summer and autumn than in spring (spring n=53, summer n=2, autumn n=15). However, *Proteocephalus* sp.2 constituted 53 % of these cestodes, while the remaining 47 % belongs to the four other cestode species (spring n=16, summer n=2, autumn n=15). Thus, the significantly fewer cestodes in summer and autumn reflects that all *Proteocephalus* sp.2 were found in spring. Regarding cestodes, the effect of season was larger in whitefish than in perch. As *Proteocephalus* sp.1 constituted 99 % of the cestodes in whitefish, this species is the main cause of the difference. The seasonality of *Proteocephalus* sp.1 in whitefish was different from the seasonality of cestodes in perch, with highest abundance of *Proteocephalus* sp.1 in summer and autumn. The very high percentage of *Proteocephalus* sp.1 in whitefish was the primary cause for the significantly higher abundance of cestodes in whitefish than in perch. The cestode fauna of perch was more diverse than in whitefish, likely because perch feeds across several trophic levels and habitats, and thus more exposed to more parasite species (Carney and Dick, 1999; Valtonen et al., 2010). However, other studies have found that fish with a narrower food choice can have more parasites and higher species richness than polyphagous fish like perch (Sobecka & Słomińska, 2007).

In our study, the number of cestodes were found to increase with increasing fish length, as also reported by others (Poulin, 2000). This can be explained by factors mentioned earlier, i.e. larger and older fish eat more, and more diverse prey than smaller fish. Unlike in acanthocephalans and *Proteocephalus* spp., the abundance also increases with a longer time feeding history in long-lived cestodes. While adult *Proteocephalus* spp. have a life span of about one year (Andersen, 1978; Chubb, 1982; Scholz, 1999; Wootten, 1974), *Eubothrium* spp. and plerocercoid *Dibothriocephalus* spp. and *Triaenophorus* spp. can have longevities of several years (Chubb, 1980, 1982; Mackiewicz, 1988). Cestodes surviving in their host for years means that the species can accumulate over a very long time period. However, as cestode infection also can reduce fish growth (Blanar et al.,

2005; Brinker & Hamers, 2007; Dörücü, 2000), this might weaken the positive correlation between parasite abundance and fish length, with a subsequent negative correlation as result.

Due to differences in copepod consumption by different morphs of whitefish, pelagic morphs have been found with higher prevalence of several cestodes than littoral morphs (Amundsen & Kristoffersen, 1990). Despite the whitefish morphs caught in Lake Norsjø was not determined or identified, the high prevalence of cestodes found in whitefish in Lake Norsjø in 2018 might indicate that most of the whitefish caught belongs to the two pelagic morphs, two of three morphs earlier documented in Lake Norsjø (Jensen, 1954). Our results also agreed with earlier studies documenting positive correlation between cestode infection and fish length in pelagic whitefish, not in benthic whitefish, indicating increased consume of infected copepods by age in pelagic whitefish morphs (Amundsen & Kristoffersen, 1990). Increased copepod consumption by age, combined with long lived cestodes are therefore the most likely causes for the positive correlation found between cestode infection and length of pelagic whitefish.

Regarding water quality, the abundance of both *T. crassus* and *T. nodulosus* have been found to be higher in perch and whitefish of oligotrophic lakes, as lake Norsjø (Brinker & Hamers, 2007; Lucký & Navrátil, 1984; Schähle et al., 2014). This is because lower concentrations of nutrients in oligotrophic lakes increase the relative amount of copepods compared with cladocerans, and thus higher probability for predation on infected copepods (Lucký & Navrátil, 1984). However, *Triaenophorus* spp. were not found in high numbers, but this is likely because no investigation was performed in muscles and other internal organs than the intestinal tract of our fish, where these species normally are found. Similar effects of oligotrophy might also be relevant for other cestodes being transmitted by copepods.

Higher abundance of cestodes were revealed in Lake Norsjø at site North than at site Middle, although only significant in perch and with a confidence interval including zero. At site South, lower abundance was found than at site Middle, but only significant regarding *Proteocephalus* sp.1 in whitefish. The size of perch (Table 6) at site North was

significantly larger than at site Middle and South. As size is often well correlated with age within a species, increased copepod consumption and more time to acquire infection cannot be excluded as cause of higher abundance in larger individuals, rather than different growth conditions between sites. The size of the whitefish did not differ significantly between the three sites (Table 6). Thus, differences in volume of copepod consumption and various time to acquire infection in whitefish cannot explain the lower parasite abundance at site South. Possible explanations might be local differences in cestode fauna, or that at site South, more littoral morphs of whitefish were caught, with a more benthic based diet and thus less exposed to copepod-transmitted parasites like *Proteocephalus* spp. (Knudsen et al., 2004; Stutz et al., 2014).

4.8 Genus *Salmincola*

Salmincola sp., using salmonids as hosts (Kabata, 1969), were only found on 21 whitefish. The structure of the appendages (Kabata, 1969) was studied in more detail by using a digital stereo microscope in addition to a light microscope. Based on morphology, the parasite was considered to be *Salmincola extensus* (formerly *Achtheres extensus*, revised according to Kabata, 1969). Although the morphological details discussed could be seen, it was difficult to verify this on the pictures taken.

As far as I know, *S. extensus* has never previously been reported in Norwegian fauna. The species *Salmincola extumescens* and *Salmincola coregonorum* (*Salmincola* sp. reported as “probably *S. coregonorum*”) have been reported on whitefish in Norway (Sterud, 1999; Styrvold et al., 1981). Both are morphologically, significantly different from *S. extensus*, i.e. shape of bulla and egg sacs, length of palp on maxilliped, and presence of spinulation on endopod of second antenna (Kabata, 1969). *S. extensus* is reported on whitefish in Finland (Karvonen & Valtonen, 2004) and in lakes and rivers in Russia draining to the White and Baltic Seas (Bykhovskaya-Pavlovskaya et al., 1964; Kabata, 1969). Ascribed to possible uncertainties in determination of this species, I prefer to identify this species to *Salmincola* sp. only.

The prevalence of *Salmincola* sp. in whitefish from Lake Norsjø was somewhat higher than what found in other studies of *S. extensus* in Finnish and Canadian lakes (Hursky & Pietrock, 2012; Karvonen & Valtonen, 2004). As there exists a water temperature and ice-cover dependent seasonality in egg production of *Salmincola* sp. (Amundsen et al., 1997; McGladdery & Johnston, 1988), sampling through the entire year might have revealed similar trends in parasite abundance in Lake Norsjø. *Salmincola* sp. has a direct life cycle, with free-swimming stages, and stages where it is attached to and matures on its host (Kabata & Cousens, 1973). Adult *Salmincola* sp. is permanently attached to its host, and random acquisition through transfer in the gillnets is thus not a problem, but it cannot be excluded that some individuals were lost from the host while removing fish from the gillnets.

4.9 Genus *Argulus*

Totally 30 individuals of the ectoparasite *Argulus coregoni* was found on whitefish in Lake Norsjø, while one individual was surprisingly found on a perch. *A. coregoni* is a fish louse with a direct life cycle and only one host, salmonid fishes (Bykhovskaya-Pavlovskaya et al., 1964). It has previously been found on whitefish in Norway (Styrvold et al., 1981), and although more often found on brown trout, the latin species name "*coregoni*" means whitefish as a host (Thorell, 1864). Another species, *Argulus foliaceus* has earlier been reported on perch in Norway (Økland, 1985, Hartvigsen et al., 2002), but this species was not found in Lake Norsjø. I have not succeeded in finding literature describing *A. coregoni* on perch, as it is not expected to be found on this host. However, *A. coregoni* has a relatively low host specificity, and the individual found on perch was small. Juvenile *A. coregoni* can attach to many different host species, but adult stages strictly prefer salmonid fishes. The host specificity increases at maturation due to higher oxygen sensitivity, reducing the range of suitable fish species (Mikheev et al, 2007). However, *A. coregoni* have been reported to occasionally attach and even complete its life cycle on other hosts than salmonids (Pasternak et al., 2004).

Argulus spp. can move on the surface of the fish skin and is attached by two suckers and hooks. The fish can also swim through the water to find a host or to lay eggs (Økland,

1985). Since *Argulus* spp. is not permanently attached to its host, it is probable that some individuals were lost due to the gillnet fishing method. Therefore, the actual abundance could be somewhat higher. This also means that the finding of *A. coregoni* on perch could be a result of parasite transfer from another fish to the perch while still in the gillnets, as both infected whitefish and Arctic charr were caught in the same gillnets. As only one individual was found on perch, this supports that it is a random acquisition of some sort.

All except one *A. coregoni* individual were found in our summer catches. This reflects that *A. coregoni* has its active period during summer and overwinters as eggs (Shimura, 1983, Mikheev et al., 2001). Thus, there might have been small larvae on the fish caught in spring, but too small to be detected by eye.

4.10 Phylum Nematoda

Parasites within the phylum Nematoda were not determined further. The life cycles of nematodes, also known as roundworms, are variable and species specific, as fish can serve both as intermediate, paratenic and definitive hosts (Bykhovskaya-Pavlovskaya et al., 1964; Yanong, 2017). In our material, it was not revealed whether the parasites found in perch and whitefish were mature.

The nematodes in whitefish might belong to several species, as the morphology appeared to be very variable. Several nematode species have previously been found with high prevalence in whitefish (Karvonen & Valtonen, 2004). *Camallanus lacustris* is most frequently reported in perch, including Norwegian lakes (Andersen, 1978; Carney & Dick, 1999; Hartvigsen et al., 2002). Often, this species is the only nematode found in perch, although not host specific (Andersen, 1978; Hartvigsen et al., 2002). It is not unlikely that *C. lacustris* also is the nematode found in perch in Lake Norsjø. As the morphology of the nematodes found in perch and whitefish of Lake Norsjø was not studied in detail, they are only defined to phylum level, Nematoda.

Nematodes are often found in the intestinal tract, but can be found in almost all parts and organs of the fish (Yanong, 2017). As this study only focused on the parasites of the intestine, and no other parts like muscle or other internal organs, higher abundance

might have been revealed with a different approach. All 14 nematodes, except one, were found at site North. As this sampling site stands out as the shallowest area, this might have caused more fish to feed on the intermediate hosts of nematodes there.

4.11 Class Trematoda

Also the class Trematoda was not determined in detail. All three individuals dissolved soon after withdrawn from the intestine. Several trematode species have been found to infect whitefish (Karvonen & Valtonen, 2004; Sterud, 1999). The low abundance of trematodes found in the fish from Lake Norsjø was likely a result of insufficient detailing and investigation time.

4.12 Pathogenicity

The influence on the fish from parasite infections varies. Species of the ectoparasite *Salmincola* spp. have been found to cause mortality at high infection rates (> 120 parasite individuals) (McGladdery & Johnston, 1988) and sublethal effects at lower infection (Sutherland & Wittrock, 1985; Vaughan & Coble, 1975). *Argulus* spp. can also cause skin lesion infections which might be lethal at high intensities (Hakalahti-Sirén et al., 2008; Menezes et al., 1990; Økland, 1985). However, the ectoparasite infections found in Lake Norsjø during 2018 were low and likely without severe consequences.

Acanthocephalan infections might cause damage in the intestine at the point of attachment, with increased damage by increasing intensity and with deeper proboscis penetration (Dezfuli et al., 2009; Taraschewski, 2000), but in general fish are reported to tolerate high intensities and deep penetrations without marked symptoms of disease (Taraschewski, 2000; Wanstall et al., 1986). Accordingly, the unattached parasites present in fish from Lake Norsjø do likely not cause severe negative effects on the fish. Nematodes, however, are well known to cause illness and mortality when the numbers increase, but the low nematode intensity found in Lake Norsjø, are comparable with that often found in healthy fish populations (Yanong, 2017).

Within the class Cestoda, the damage from infection varies considerably. *Proteocephalus* spp. infection is thought to be relatively harmless for the fish, but as for most parasites, effects on fish health is reported at high parasite intensities (Priemer, 1987, as cited in Aneegg et al., 2015; Sundnes, 2003). In the intestinal tract of the most infected fish from Lake Norsjø, the parasites seemed to block the intestine, likely with severe effects on fish health (Lucký & Navrátil, 1984). *Dibothriocephalus* spp. is known to cause damage to the fish host, both by reduced growth and increased mortality (Blanar et al., 2005; Dörücü, 2000; Rahkonen et al., 1996). In whitefish and rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*, revised according to Smith & Stearley, 1989), mortality has also been reported from infection by *T. crassus*, with only one to three parasites sufficient to kill the fish (Dick & Rosen, 1982; Rosen & Dick, 1984). The mortality occurs when the size of the plerocercoid increase, causing reduced fish condition, with haemorrhaging, muscle necrosis and reduced swimming activity. Infection with *T. nodulosus* also causes serious pathological alterations in perch, even at a low parasite load, causing reduced fish growth and health (Brinker & Hamers, 2007; Lucký & Navrátil, 1984). These three parasites were only found in few fish individuals in Lake Norsjø.

As fish damage in general increases with increased parasite intensity, and not all hosts experience marked damage from low infection intensity, the host can often be evaluated unharmed of the infection (Hoste, 2001). However, the actual cost for the host might be difficult to detect, as effects also can be other than direct physically observed effects (Leung & Poulin, 2008). In addition, continuous adaptations may occur to ensure both host and parasite survival, meaning that the association between symbionts are not static (Dimijian, 2000; Hoste, 2001; Leung & Poulin, 2008). Thus, the symbiont relationship might be seen as commensalism when few parasites are present, and as parasitism when sufficient number of parasites are present to cause harm. Often the symbiotic relationship exists somewhere between commensalism and parasitism on the continuum, depending upon the level of pathogenicity, but this relationship can change over time (Dimijian, 2000). Thus, adaptations might avoid severe detrimental effects on the host, and subsequent reduce mortality.

5 Conclusion

In 2018, parasites in 258 perch and 101 whitefish from Lake Norsjø were investigated. Totally 2113 parasite individuals were revealed. The most abundant parasites found in European whitefish and European perch were acanthocephalans and *Proteocephalus* spp., constituting 95 % of the total parasite material. The remaining 5 % were individuals of *Triaenophorus crassus*, *Dibothriocephalus* spp., nematodes, trematodes, *Salmincola* sp. and *Argulus coregoni* in whitefish and *Triaenophorus crassus*, *Triaenophorus nodulosus*, *Dibothriocephalus* spp., *Eubothrium* sp., Nematoda and *Argulus coregoni* in perch. Only three types of parasites were fully identified to species, while for several species, identification was evaluated and discussed.

Higher abundance of *Proteocephalus* spp. was revealed in whitefish than in perch, while higher abundance of acanthocephalans was found in perch. Cestode fauna was more diverse in perch than in whitefish. These differences between fish species indicate differences in diet, but other causes like parasite seasonality could not be excluded.

The most important parasite predictors were fish length and season. The abundance in five models; the three acanthocephalan models, *Proteocephalus* sp.1 in whitefish and cestodes in perch, all increased significantly by increasing fish length. This is likely caused by increased exposure to the parasites by age *per se*, but also because older fish are larger and thus eat more and have a more diverse diet. All seven models showed seasonality, which might correspond to various individual parasites' life cycles. Acanthocephalans were significantly less abundant in autumn than spring in both fish species, while in perch the parasite was significantly more abundant in summer than in spring. *Proteocephalus* sp.1 was significantly more abundant in summer and autumn than in spring in whitefish, while *Proteocephalus* sp.2 of perch was found only in spring.

The parasite intensities in whitefish and perch from Lake Norsjø were generally low and thus assessed relatively harmless. Knowledge about the parasite fauna could be increasingly useful in future ecological studies in Lake Norsjø.

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7 List of figures and tables

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8 Annexes

Annex 1. Statistical tests for model selection.

Annex 2. Whitefish macroparasite distribution in total and per season.

Annex 3. Whitefish macroparasite distribution in total and per sampling site.

Annex 4. Perch macroparasite distribution in total and per season.

Annex 5. Perch macroparasite distribution in total and per sampling site.

Annex 6. Water analyses from Lake Norsjø.

Annex 7. Ion water analyses from Lake Norsjø.

Annex 1. Statistical tests for model selection.

Tests of equidispersion, zero-inflation tests, Kolmogorov-Smirnov tests and outlier tests.

Test of the H_0 of equidispersion.

Model response variable		Dispersion	z-value	p-value
Fish species	Parasite species			
Whitefish	Acanthocephala	9.7	2.66	0.004
Whitefish	<i>Proteocephalus</i>	17.1	1.65	0.050
Perch	Acanthocephala	12.7	3.20	<0.001
Perch	Cestoda	1.9	1.64	0.050
Both	Acanthocephala	15.8	3.83	<0.001
Both	<i>Proteocephalus</i>	12.9	1.69	0.045
Both	Cestoda	13.5	1.76	0.039

Zero-inflation tests (ZI), Kolmogorov-Smirnov tests (KS) and outlier tests (Out) with the H_0 of a fitted model. Results are p-values.

Model response variable		ZI	KS	Out
Fish species	Parasite species			
Whitefish	Acanthocephala	0.938	0.289	0.740
Whitefish	<i>Proteocephalus</i>	0.614	0.501	0.485
Perch	Acanthocephala	0.307	0.124	0.164
Perch	Cestoda	0.884	0.791	1
Both	Acanthocephala	0.345	0.156	0.037
Both	<i>Proteocephalus</i>	0.735	0.586	0.159
Both	Cestoda	0.669	0.690	0.526

Annex 2. Whitefish macroparasite distribution in total and per season. Table showing the prevalence (percent infected), mean intensity (mean number of parasites on infected fish) and mean abundance (mean number of parasites on examined fish).

Whitefish, <i>Coregonus lavaretus</i>						
Species/Season	No. of fish		No. of parasites	Prevalence, % (95% CI)	Intensity ± SE	Abundance ± SE
	examined	infected				
Cestoda	101	36	370	35.6 (27.0–45.4)	10.3 ± 3.4	3.7 ± 1.3
spring	39	9	79	23 (13–39)	8.8 ± 5.6	2.0 ± 1.4
summer	39	17	190	44 (29–59)	11.2 ± 6.4	4.9 ± 2.9
autumn	23	10	101	43 (26–63)	10.1 ± 3.7	4.4 ± 1.9
<i>Proteocephalus</i> sp.1	101	34	367	33.7 (25.2–43.4)	10.8 ± 3.5	3.6 ± 1.3
spring	39	9	79	23 (13–39)	8.8 ± 5.6	2.0 ± 1.4
summer	39	16	188	41 (27–57)	12 ± 6.7	4.8 ± 2.8
autumn	23	9	100	39 (22–59)	11 ± 3.9	4.3 ± 1.9
Acanthocephala	101	28	329	27.7 (19.9–37.2)	11.8 ± 3.1	3.3 ± 1.0
spring	39	10	135	26 (15–41)	14 ± 4.1	3.5 ± 1.4
summer	39	15	181	39 (25–54)	12 ± 5.1	4.6 ± 2.2
autumn	23	3	13	13 (3.9–33)	4.3 ± 3.3	0.6 ± 0.5
<i>Argulus coregoni</i>	101	12	30	11.9 (6.8–19.8)	2.5 ± 0.7	0.3 ± 0.1
spring	39	0	0	0.0 (0.0–10)		0.0
summer	39	11	29	28 (16–44)	2.6 ± 0.8	0.7 ± 0.3
autumn	23	1	1	4.3 (0.0–23)	1.0	<0.1 ± <0.1
<i>Salmincola</i> sp.	101	21	29	20.8 (14.0–29.8)	1.4 ± 0.2	0.3 ± 0.1
spring	39	8	11	21 (11–36)	1.4 ± 0.2	0.3 ± 0.1
summer	39	8	9	21 (11–36)	1.1 ± 0.1	0.2 ± 0.1
autumn	23	5	9	22 (9.4–43)	1.8 ± 0.6	0.4 ± 0.2
Nematoda	101	4	8	4.0 (1.3–10.2)	2.0 ± 1.0	0.1 ± 0.1
spring	39	1	1	2.6 (0.0–15)	1.0	<0.1 ± <0.1
summer	39	0	0	0.0 (0.0–11)		0.0
autumn	23	3	7	13 (3.9–33)	2.3 ± 1.3	0.3 ± 0.2
Trematoda	101	1	3	1.0 (0.0–6.0)	3.0	<0.1 ± <0.1
spring	39	0	0	0.0 (0.0–11)		0.0
summer	39	0	0	0.0 (0.0–11)		0.0
autumn	23	1	3	4.3 (0.0–23)	3.0	0.1 ± 0.1
<i>Dibothriocephalus</i> spp.	101	2	2	2.0 (0.1–7.5)	1.0 ± <0.1	<0.1 ± <0.1
spring	39	0	0	0.0 (0.0–11)		0.0
summer	39	1	1	2.6 (0.0–15)	1.0	<0.1 ± <0.1
autumn	23	1	1	4.3 (0.0–23)	1.0	<0.1 ± <0.1
<i>Triaenophorus crassus</i>	101	1	1	1.0 (0.0–6.0)	1.0	<0.1 ± <0.1
spring	39	0	0	0.0 (0.0–11)		0.0
summer	39	1	1	2.6 (0.0–15)	1.0	<0.1 ± <0.1
autumn	23	0	0	0.0 (0.0–17)		0.0
SUM	101	69	769	68.3 (58.7–76.6)	11.1 ± 2.4	7.6 ± 1.7
sum spring	39	21	226	54 (37–68)	11 ± 4.0	5.8 ± 2.3
sum summer	39	32	409	82 (67–91)	13 ± 4.2	10.5 ± 3.5
sum autumn	23	16	134	70 (49–84)	8.4 ± 2.4	5.8 ± 1.9

Annex 3. Whitefish macroparasite distribution in total and per sampling site. Table showing the prevalence (percent infected), mean intensity (mean number of parasites on infected fish) and mean abundance (mean number of parasites on examined fish).

Whitefish, <i>Coregonus lavaretus</i>						
Species/Site	No. of fish		No. of parasites	Prevalence, % (95% CI)	Intensity ± SE	Abundance ± SE
	examined	infected				
Cestoda	101	36	370	35.6 (27.0–45.4)	10.3 ± 3.4	3.7 ± 1.3
North	67	23	293	34 (24–46)	13 ± 5.1	4.4 ± 1.9
Middle	24	10	69	42 (25–61)	6.9 ± 3.3	2.9 ± 1.5
South	10	3	8	30 (11–61)	2.7 ± 1.2	0.8 ± 0.5
<i>Proteocephalus</i> sp.1	101	34	367	33.7 (25.2–43.4)	10.8 ± 3.5	3.6 ± 1.3
North	67	23	292	34 (24–46)	13 ± 5.0	4.4 ± 1.9
Middle	24	9	68	38 (21–57)	8.0 ± 3.7	2.8 ± 1.5
South	10	2	7	20 (4.9–52)	4.0 ± 1.5	0.7 ± 0.5
Acanthocephala	101	28	329	27.7 (19.9–37.2)	11.8 ± 3.1	3.3 ± 1.0
North	67	20	149	30 (20–42)	7.0 ± 2.3	2.2 ± 0.8
Middle	24	3	116	13 (3.7–32)	39 ± 19.1	4.8 ± 3.3
South	10	5	64	50 (24–76)	13 ± 5.5	6.4 ± 3.4
<i>Argulus coregoni</i>	101	12	30	11.9 (6.8–19.8)	2.5 ± 0.7	0.3 ± 0.1
North	67	5	6	7.5 (2.9–17)	1.2 ± 0.2	0.1 ± 0.0
Middle	24	7	21	29 (15–49)	3.0 ± 1.2	0.9 ± 0.4
South	10	2	3	20 (4.9–52)	1.5 ± 0.5	0.3 ± 0.2
<i>Salmincola</i> sp.	101	21	29	20.8 (14.0–29.8)	1.4 ± 0.2	0.3 ± 0.1
North	67	15	19	22 (14–34)	1.3 ± 0.1	0.3 ± 0.1
Middle	24	5	9	21 (9.0–41)	1.8 ± 0.6	0.4 ± 0.2
South	10	1	1	10 (-0.1–43)	1.0	0.1 ± 0.1
Nematoda	101	4	8	4.0 (1.3–10.2)	2.0 ± 1.0	0.1 ± 0.1
North	67	4	8	6.0 (2.0–15)	2.0 ± 1.0	0.1 ± 0.1
Middle	24	0	0	0.0 (-2.4–17)		0.0
South	10	0	0	0.0 (-4.0–33)		0.0
Trematoda	101	1	3	1.0 (0.0–6.0)	3.0	<0.1 ± <0.1
North	67	0	0	0.0 (-1.0–6.7)		0.0
Middle	24	0	0	0.0 (-2.4–17)		0.0
South	10	1	3	10 (-0.1–43)	3.0	0.3 ± 0.3
<i>Dibothriocephalus</i> spp.	101	2	2	2.0 (0.1–7.5)	1.0 ± <0.1	<0.1 ± <0.1
North	67	0	0	0.0 (-1.0–6.7)		0.0
Middle	24	1	1	4.2 (-0.7–22)	1.0	<0.1 ± <0.1
South	10	1	1	10 (-0.1–43)	1.0	0.1 ± 0.1
<i>Triaenophorus crassus</i>	101	1	1	1.0 (0.0–6.0)	1.0	<0.1 ± <0.1
North	67	1	1	1.5 (-0.5–8.9)	1.0	<0.1 ± <0.1
Middle	24	0	0	0.0 (-2.4–17)		0.0
South	10	0	0	0.0 (-4.0–33)		0.0
SUM	101	69	769	68.3 (58.7–76.6)	11.1 ± 2.4	7.6 ± 1.7
sum North	67	47	475	70 (58–80)	10 ± 2.9	7.1 ± 2.1
sum Middle	24	15	215	63 (43–79)	14 ± 5.8	9.0 ± 3.8
sum South	10	7	79	70 (39–89)	11 ± 4.5	7.9 ± 3.5

Annex 4. Perch macroparasite distribution in total and per season. Table showing the prevalence (percent infected), mean intensity (mean number of parasites on infected fish) and mean abundance (mean number of parasites on examined fish).

Perch, <i>Perca fluviatilis</i>						
Species/Season	No. of fish examined	No. of fish infected	No. of parasites	Prevalence, % (95% CI)	Intensity \pm SE	Abundance \pm SE
Acanthocephala	258	189	1270	73.3 (67.5–78.3)	6.7 \pm 0.8	4.9 \pm 0.6
spring	78	54	309	69 (58–78)	5.7 \pm 1.2	4.0 \pm 0.9
summer	90	77	767	86 (77–91)	10 \pm 1.6	8.5 \pm 1.4
autumn	90	58	194	64 (54–74)	3.3 \pm 0.6	2.2 \pm 0.4
Cestoda	258	38	70	14.7 (10.9–19.6)	1.8 \pm 0.3	0.3 \pm 0.1
spring	78	25	53	32.1 (23–43)	2.1 \pm 0.5	0.7 \pm 0.2
summer	90	2	2	2.2 (0.2–8.3)	1.0 \pm <0.1	<0.1 \pm <0.1
autumn	90	11	15	12.2 (6.9–21)	1.4 \pm 0.2	0.2 \pm 0.1
<i>Proteocephalus</i> sp.2	258	22	37	8.5 (5.7–12.7)	1.7 \pm 0.3	0.1 \pm <0.1
spring	78	22	37	28 (19–39)	1.7 \pm 0.3	0.5 \pm 0.1
summer	90	0	0	0.0 (0.0–5.0)		0.0
autumn	90	0	0	0.0 (0.0–5.0)		0.0
<i>Triaenophorus nodulosus</i>	258	12	13	4.7 (2.6–8.1)	1.1 \pm 0.1	0.1 \pm <0.1
spring	78	1	2	1.3 (0.0–7.7)	2.0	<0.1 \pm <0.1
summer	90	2	2	2.2 (0.2–8.3)	1.0 \pm <0.1	<0.1 \pm <0.1
autumn	90	9	9	10 (5.2–18)	1.0 \pm <0.1	0.1 \pm <0.1
<i>Triaenophorus crassus</i>	258	1	9	0.4 (0.0–2.4)	9.0	<0.1 \pm <0.1
spring	78	1	9	1.3 (0.0–7.7)	9.0	0.1 \pm 0.1
summer	90	0	0	0.0 (0.0–5.0)		0.0
autumn	90	0	0	0.0 (0.0–5.0)		0.0
<i>Dibothriocephalus</i> spp.	258	5	7	1.9 (0.7–4.6)	1.4 \pm 0.2	<0.1 \pm <0.1
spring	78	1	2	1.3 (0.0–7.7)	2.0	<0.1 \pm <0.1
summer	90	0	0	0.0 (0.0–5.0)		0.0
autumn	90	4	5	4.4 (1.4–11)	1.3 \pm 0.3	0.1 \pm <0.1
Nematoda	258	3	6	1.2 (0.3–3.6)	2.0 \pm 1.0	<0.1 \pm <0.1
spring	78	1	1	1.3 (0.0–7.7)	1.0	<0.1 \pm <0.1
summer	90	0	0	0.0 (0.0–5.0)		0.0
autumn	90	2	5	2.2 (0.2–8.3)	2.5 \pm 1.5	0.1 \pm <0.1
<i>Eubothrium</i> sp.	258	3	4	1.2 (0.3–3.6)	1.3 \pm 0.3	<0.1 \pm <0.1
spring	78	2	3	2.6 (0.2–9.5)	1.5 \pm 0.5	<0.1 \pm <0.1
summer	90	0	0	0.0 (0.0–5.0)		0.0
autumn	90	1	1	1.1 (0.0–6.7)	1.0	<0.1 \pm <0.1
<i>Argulus coregoni</i>	258	1	1	0.4 (0.0–2.4)	1.0	<0.1 \pm <0.1
spring	78	0	0	0.0 (0.0–5.8)		0.0
summer	90	1	1	1.1 (0.0–6.7)	1.0	<0.1 \pm <0.1
autumn	90	0	0	0.0 (0.0–5.0)		0.0
SUM	258	200	1344	77.5 (72.0–82.2)	6.7 \pm 0.7	5.2 \pm 0.6
sum spring	78	61	361	78 (68–86)	5.9 \pm 1.1	4.6 \pm 0.9
sum summer	90	77	769	86 (77–91)	10 \pm 1.6	8.5 \pm 1.4
sum autumn	90	62	214	69 (59–78)	3.5 \pm 0.5	2.4 \pm 0.4

Annex 5. Perch macroparasite distribution in total and per sampling site. Table showing the prevalence (percent infected), mean intensity (mean number of parasites on infected fish) and mean abundance (mean number of parasites on examined fish).

Perch, <i>Perca fluviatilis</i>						
Species/Site	No. of fish		No. of	Prevalence, %	Intensity	Abundance
	examined	infected	parasites	(95% CI)	± SE	± SE
Acanthocephala	258	189	1270	73.3 (67.5–78.3)	6.7 ± 0.8	4.9 ± 0.6
North	81	61	376	75 (65–83)	6.2 ± 1.2	4.6 ± 0.9
Middle	87	66	608	76 (66–84)	9.0 ± 1.8	7.0 ± 1.4
South	90	62	286	69 (59–78)	4.6 ± 0.7	3.2 ± 0.6
Cestoda	258	38	70	14.7 (10.9–19.6)	1.8 ± 0.3	0.3 ± 0.1
North	81	20	34	32 (17–35)	1.7 ± 0.3	0.4 ± 0.1
Middle	87	12	17	2.2 (8.0–23)	1.4 ± 0.2	0.2 ± 0.1
South	90	6	19	12 (2.9–14)	3.2 ± 1.8	0.2 ± 0.1
<i>Proteocephalus</i> sp.2	258	22	37	8.5 (5.7–12.7)	1.7 ± 0.3	0.1 ± <0.1
North	81	10	21	12 (6.7–22)	2.1 ± 0.6	0.3 ± 0.1
Middle	87	7	10	8.0 (3.8–16)	1.4 ± 0.2	0.1 ± <0.1
South	90	5	6	5.6 (2.1–13)	1.2 ± 0.2	0.1 ± <0.1
<i>Triaenophorus nodulosus</i>	258	12	13	4.7 (2.6–8.1)	1.1 ± 0.1	0.1 ± <0.1
North	81	8	8	9.9 (4.9–19)	1.0 ± <0.1	0.1 ± <0.1
Middle	87	3	3	3.4 (0.8–10)	1.0 ± <0.1	<0.1 ± <0.1
South	90	1	2	1.0 (-0.4–6.7)	2.0	<0.1 ± <0.1
<i>Triaenophorus crassus</i>	258	1	9	0.4 (0.0–2.4)	9.0	<0.1 ± <0.1
North	81	0	0	0.0 (-0.9–5.6)		0.0
Middle	87	0	0	0.0 (-0.8–5.2)		0.0
South	90	1	9	1.1 (-0.4–6.7)	9.0	0.1 ± 0.1
<i>Dibothriocephalus</i> spp.	258	5	7	1.9 (0.7–4.6)	1.4 ± 0.2	<0.1 ± <0.1
North	81	3	4	3.7 (0.9–11)	1.3 ± 0.3	<0.1 ± <0.1
Middle	87	2	3	2.3 (0.2–8.6)	1.5 ± 0.5	<0.1 ± <0.1
South	90	0	0	0.0 (-0.8–5.0)		0.0
Nematoda	258	3	6	1.2 (0.3–3.6)	2.0 ± 1.0	<0.1 ± <0.1
North	81	2	5	2.5 (0.2–9.2)	2.5 ± 1.5	0.1 ± 0.1
Middle	87	1	1	1.1 (-0.4–7.0)	1.0	<0.1 ± <0.1
South	90	0	0	0.0 (-0.8–5.0)		0.0
<i>Eubothrium</i> sp.	258	3	4	1.2 (0.3–3.6)	1.3 ± 0.3	<0.1 ± <0.1
North	81	1	1	1.2 (-0.4–7.5)	1.0	<0.1 ± <0.1
Middle	87	1	1	1.1 (-0.4–7.0)	1.0	<0.1 ± <0.1
South	90	1	2	1.1 (-0.4–6.7)	2.0	<0.1 ± <0.1
<i>Argulus coregoni</i>	258	1	1	0.4 (0.0–2.4)	1.0	<0.1 ± <0.1
North	81	1	1	1.2 (-0.4–7.5)	1.0	<0.1 ± <0.1
Middle	87	0	0	0.0 (-0.8–5.2)		0.0
South	90	0	0	0.0 (-0.8–5.0)		0.0
SUM	258	200	1344	77.5 (72.0–82.2)	6.7 ± 0.7	5.2 ± 0.6
sum North	81	68	415	85 (74–91)	6.1 ± 1.1	5.1 ± 0.9
sum Middle	87	69	625	79 (70–87)	9.0 ± 1.7	7.2 ± 1.4
sum South	90	63	304	70 (60–79)	4.8 ± 0.8	3.4 ± 0.6

Annex 6. Water analyses from Lake Norsjø.

Temperature, pH, conductivity, alkalinity, turbidity, total nitrogen, total phosphorous and water colour.

Season	Site	Depth m	T °C	pH	Cond. mS/m	Alk. mmol/L	Turb. FNU	Tot-N µg/L	Tot-P µg/L	Colour mg Pt/L
Spring	North	1	15.0	6.03	1.85	0.0155	0.24	213.8	2.0	13.7
	North	20	4.8	5.85	1.89	0.0099	0.42	252.0	2.5	20.2
	Middle	1	15.4	6.39	1.87	0.0094	0.35	238.3	3.0	18.3
	Middle	20	5.4	6.52	1.82	0.0144	0.42	190.3	3.5	16.5
	South	1	13.0	6.69	1.92	0.0164	0.18	218.2	2.5	15.5
	South	20	6.8	6.49	1.81	0.0112	0.27	214.9	3.0	13.0
Summer	North	1	23.1	6.98	1.79	0.0131	0.15	199.5	<2.0	10.8
	North	20	7.4	6.54	1.80	0.0095	0.30	250.5	2.5	16.2
	Middle	1	22.2	6.68	1.68	0.0127	0.20	170.0	<2.0	9.6
	Middle	20	11.5	6.53	1.73	0.0094	0.23	188.0	<2.0	12.9
	South	1	21.5	6.82	1.67	0.0174	0.22	172.7	10.0	10.1
	South	20	9.6	6.54	1.80	0.0119	0.12	177.0	2.5	13.0
Autumn	North	1	16.9	6.86	1.66	0.0122	0.20	164.1	3.0	10.8
	North	20	15.7	6.62	1.73	0.0032	1.00	309.3	8.0	21.6
	Middle	1	16.6	6.77	1.62	0.0135	0.30	195.3	6.5	10.7
	Middle	20	14.2	6.73	1.64	0.0139	0.29	196.3	3.0	9.8
	South	1	16.6	6.68	1.70	0.0115	0.23	179.1	<2.0	9.4
	South	20	12.5	6.44	1.73	0.0091	0.25	183.1	<2.0	11.7

Annex 7. Ion water analyses from Lake Norsjø.

Season	Site	Depth m	Ca ²⁺ mg/L	Mg ²⁺ mg/L	Na ⁺ mg/L	K ⁺ mg/L	SO ₄ ²⁻ mg/L	Cl ⁻ mg/L	NO ₃ ⁻ µg/L	NH ₄ ⁺ µg/L
Spring	North	1	2.30	0.27	1.09	0.29	193.0	1.65	193.0	41.4
	North	20	2.24	0.28	1.22	0.23	95.38	1.80	95.4	
	Middle	1	2.26	0.29	1.23	0.23	103.2	1.80	103.1	
	Middle	20	2.27	0.27	1.13	0.22	61.28	1.70	61.3	
	South	1	2.41	0.29	1.18	0.23	62.12	1.69	62.1	
	South	20	2.31	0.28	1.17	0.27	103.8	1.75	103.8	
Summer	North	1	2.29	0.26	1.03	0.26	44.87	1.59	44.9	41.0
	North	20	2.26	0.26	1.14	0.22	92.93	1.69	92.9	
	Middle	1	2.22	0.24	0.92	0.23	43.98	1.40	44.0	49.2
	Middle	20	2.20	0.26	1.05	0.21	73.45	1.55	73.5	
	South	1	2.21	0.24	0.96	0.23	43.03	1.45	43.0	23.5
	South	20	2.28	0.27	1.09	0.21	83.12	1.65	83.1	
Autumn	North	1	2.18	0.24	1.00	0.21	55.64	1.45	55.6	
	North	20	2.13	0.29	1.02	0.29	98.12	1.60	98.1	31.5
	Middle	1	2.17	0.24	0.92	0.22	52.97	1.43	53.0	31.6
	Middle	20	2.19	0.24	0.92	0.23	67.75	1.61	67.8	24.7
	South	1	2.24	0.25	0.96	0.25	57.31	1.47	57.3	30.7
	South	20	2.20	0.26	1.01	0.24	74.63	1.54	74.6	10.6

Note. Blank cells were not analysed.