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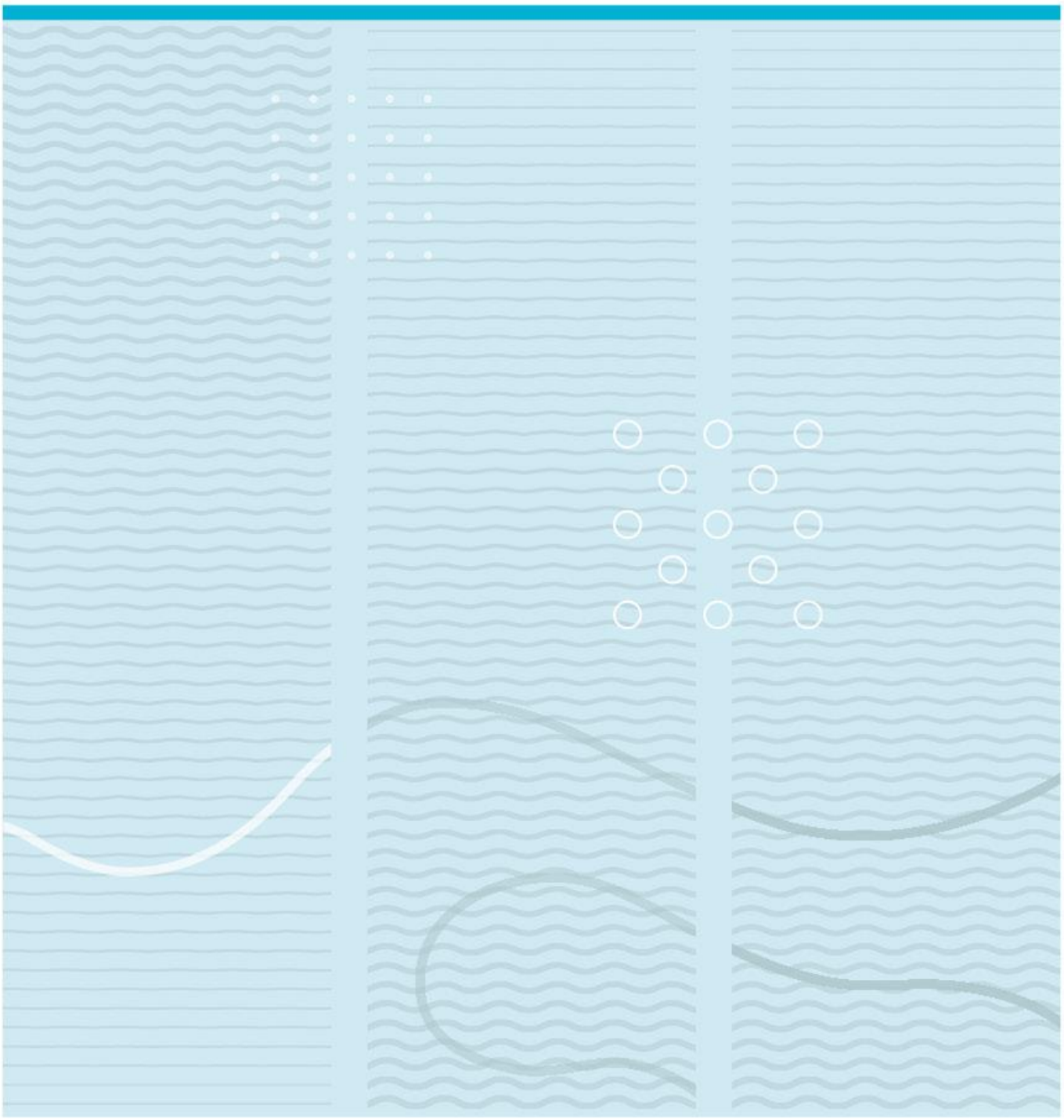
Seasonal and spatial variation in the macroparasite fauna of Arctic charr (*Salvelinus alpinus* L.) in Lake Norsjø, South-Eastern Norway



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This thesis is worth 60 study points

Abstract

Within freshwater systems, several factors contribute to aggregated distributions of parasites in fish. Niche segregation, individual feeding preferences, sex of the host, and water temperature are all examples of such factors. In this study, structural patterns of the macroparasite community of Arctic charr (*Salvelinus alpinus* L.*)* in Lake Norsjø, situated in South-Eastern Norway, was investigated.

Arctic charr was sampled from three locations within Lake Norsjø (North, Mid and South) three times (May, July, September) in 2018. Skin, gills, fins, intestinal tract, and coelom of the fish were examined macroscopically for ecto- and endoparasites. From 236 examined fish, seven parasite species were identified to species level. In addition, one parasite group was identified to genus level, and two groups to phylum level.

Generalised linear models were used to explore the effect of season, location, fish length and sex on the abundance of two individual parasite species, and two functional groups of parasites. Fish length was the most important predictor of infection in all models for endoparasites, where infection increased with increasing fish length. No such relationship was discovered for the ectoparasites. Two species of the class Cestoda displayed different abundance in fish from the three fishing periods. The fish from the locations Norsjø North and Mid had similar parasite infections, probably as a result of resembling habitats, fishing depth and fish size. The profundal location Norsjø South differed with considerably less endoparasite abundance, and smaller fish size. The pattern was opposite for the ectoparasites, with heavier infections in Norsjø South. According to the statistical models, the sex of the Arctic charr did not explain the differences in parasite infection for any of the parasite species or groups.

Contents

Preface

After five wonderful years of studying, it is with mixed feelings that I deliver this thesis as my final product within the Master programme “Freshwater Ecology” at the University of South-Eastern Norway. I would especially like to thank my project supervisors Professor Espen Lydersen from the University of South-Eastern Norway and Senior Research Scientist Tor Atle Mo from the Norwegian Institute of Nature Research, for facilitation, encouragement and very constructive feedback! All the field and laboratory work were done in collaboration with my fellow student Solveig Irene Dolven. Thank you for a great collaboration, the work would not have been half as fun without you! Moreover, thanks to Tone Jøran Oredalen, for nice days in both the field and laboratory.

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Bø I Telemark, 15.05.2019

Ann-Cecilie Henriksen

1 Introduction

Species dependent on living in and at the expense of other species can be considered a parasite. Parasitism is a common life strategy which contribute to 40 % of the species richness within an ecological community (Dobson et al., 2008). Despite their small size, parasites have important roles in the food web linkages within an ecosystem (Amundsen et al., 2009; Dobson et al., 2008; Lafferty et al., 2006; Marcogliese, 2004). For instance, by manipulating their host's behaviour, they can facilitate predation and further transmission within the food web (Hudson et al., 1992; Lafferty & Morris, 1996; Rogawa et al., 2018).

In freshwater systems, high abundance of parasites can decrease fish health, and subsequently reduce the recreational and commercial value of the fish (Ebrahimi et al., 2018; Hoffmann et al., 1986a). The distribution of fish parasites often occurs aggregated within hosts, resulting in large variations in abundance of infection (Henricson, 1977; Knudsen et al., 2004; Shaw & Dobson, 1995). Such variation indicates that infections of parasites do not occur randomly, and several factors can influence the infection rates (Shaw & Dobson, 1995). To understand parasite-fish relationships, researchers have been focusing on finding transferable factors and patterns within the discipline (Kennedy, 2009; Poulin, 2007; Poulin & Valtonen, 2002).

Parasites can be divided into micro- and macroparasites. As their names indicate, they differ in size, but also their lifecycle complexity (Hatcher & Dunn, 2011). Macroparasites are multicellular parasites, which have lifecycles with different life stages. They are often dependent on different hosts to reach maturity, from eggs, to intermediate hosts and to maturation in their definitive host (Hatcher & Dunn, 2011; Marcogliese, 2004). Going forward, all mentioning of parasites will strictly refer to macroparasites.

Fish parasites can be found both externally (ectoparasites) and internally (endoparasites) of their hosts. While most ectoparasites have a direct way of infection, some endoparasites have to enter the fish through consumption of other infected organisms. This is often referred to as trophic transmission, as the parasites are going up through the food web (Choisy et al., 2003; Hatcher & Dunn, 2011; Lafferty, 1999). Fish can serve as both intermediate and definitive hosts of these parasites, resulting in

some parasite species being mature, while others are immature in the fish. Trophic transmitted parasites of the class Cestoda that strictly uses fish as intermediate hosts, occur as plerocercoids, which is the last larval stage of their lifecycle. These can often be found encysted on the gastrointestinal tract or other internal organs like the spleen, milt, liver and kidney (Rodger, 1991). These long-lived parasites are waiting for the fish to be consumed by their definitive host, and thereby accumulate with increasing fish age and size (Halvorsen & Andersen, 1984; Rosen & Dick, 1984).

Seasonal variation in parasite abundance are often seen (Amundsen et al., 2003; Andersen, 1978; Borgstrøm, 1970; Kennedy, 1968; Kuhn et al., 2016; Poulin & Valtonen, 2002). These can be caused by changes in water temperature, which affect the development of ectoparasites (Amundsen et al., 1997; Hakalahti & Valtonen, 2003). For trophic transmitted parasites, prey choice, availability of infectious larvae, and release of mature worms with eggs varies with the seasons (Borgstrøm, 1970; Chubb, 1963; Kennedy, 1968; Knudsen et al., 2007; Pennycuick, 1971).

Male and female fish can display dissimilar abundances of trophic transmitted parasites. Any dissimilarities have been related to unequal fish size and food consumption, and thereby unequal risk of infection (Andersen, 1978; Borgstrøm, 1970). Similar patterns are proposed for ectoparasites, as larger fish have a greater risk of infection (Amundsen et al., 1997). Further, Kennedy (1968) suggest that female fish have lower parasite resistance during spawning season, when energy is invested in the production of roe.

Arctic charr (*Salvelinus alpinus* L.) can seasonally or permanently segregate within different niches of a lake, to utilize food resources (Amundsen et al., 2007; Hindar & Jonsson, 1982; Skulason & Smith, 1995). In time, the segregation can result in dissimilar diets, behaviour, life history, and morphological traits, known as polymorphism (Knudsen et al., 2009; Skoglund, 2015). Trophic transmitted parasites can give valuable information about dietary choices of Arctic charr over time, since they infect by using species-specific intermediate hosts from different habitats (Knudsen et al., 2004; Knudsen et al., 2009; Nilsen, 2006; Refsnes, 2014). In lakes where charr co-exists with brown trout (*Salmo trutta*), the charr often feed more in the pelagic areas, and thus have a diet with higher proportions of zooplankton (Hegge et al., 1989). As several parasite species use zooplankton from the subclass Copepoda as intermediate host,

copepod-transmitted parasites often exhibit high abundances in Arctic charr in these lakes (Henriksen et al., 2016; Knudsen et al., 2007; Nilsen, 2006). Some parasites are able to re-establish in a second intermediate host, resulting in higher parasite abundances in specialised piscivorous Arctic charr individuals (Henriksen et al., 2016). In addition, genetic variability and immune response might influence the parasite abundances within the individual hosts (Matthews et al., 2010; Stutz et al., 2014).

Abiotic factors can also influence the parasite community within a lake. Studies have shown that abiotic variables such as temperature, oxygen and pH affect the composition of parasite species (Anegg et al., 2014; Boyce, 1974; Karvonen et al., 2013; Pietrock & Marcogliese, 2003). For instance, acidified waterbodies would be uninhabitable for some benthic organisms that can host parasites (Karvonen & Valtonen, 2004). Further, available nutrients in waterbodies determine the availability of zooplankton, which frequently serve as intermediate hosts (Brinker & Hamers, 2007; Esch, 1971; Moser & Cowen, 1991).

In Lake Norsjø, situated in South-Eastern Norway, a fish-stock study implemented in the 1950s mention parasites in Arctic charr with one sentence: "*the Arctic charr is little infected with parasites*"(Jensen, 1954). Thus, no thorough investigations of the parasite fauna of Arctic charr have earlier been carried out in this lake. Accordingly, the aim of this study was to investigate which parasites use Arctic charr as a host in Lake Norsjø, and which short-time variations in infection might occur in both time and space across the lake.

Sampling of fish was executed at three different times during the summer season 2018, i.e. in May, July and September. As Lake Norsjø is large, it was fished at three locations to see if there were any geographical within-lake differences in the parasite infection of the fish. Water samples were taken at 1 m and 20 m to characterise the water type of Lake Norsjø and to see if this could help explain the parasitic findings. Two main questions were investigated:

1) Which parasite species uses the Arctic charr as a host in Lake Norsjø?

2) Does the abundance of the different parasite species vary with season, location, fish sex, and size?

2 Material and methods

2.1 Study area

Lake Norsjø is a large (55.48 km^2) lake in Telemark county, South-Eastern Norway (Vann-Nett, 2019). The lake is almost 30 km long, with an average width of about 3 km. It is located 15 meters above sea level (m a.s.l) and is a part of the Telemark watercourse. The catchment and area is 10 388 km^2 (NVE, 2019) respectively, and the lake volume is approximately 5.1 km^3. Maximum depth is 171 m, and mean depth 87 m. Theoretical residence time has been calculated to 0.61 years (Tjomsland et al., 1983).

Three main rivers enter Lake Norsjø, all draining higher lying mountain areas in north/west of the Telemark county. Both upstream and downstream the lake, there are dams for electrical power production. The lake itself is also dammed in the south end (Skotfoss), where the lake water is released into River Skienselva. The regulation height in Lake Norsjø is minor (< 1 m), and the lake is moderately impacted by agricultural, industrial and recreational activities.

Lake Norsjø hosts many fish species, and Jensen (1954) registered a total of 13 different species; Arctic charr, brown trout, pike *(Esox lucius),* perch (*Percae fluviatilis*), whitefish (*Coregonus lavaretus),* Atlantic salmon (*Salmo salar),* smelt (*Osmerus eperlanus*), eel (*Aunguilla anguilla*), crucian carp (*Carassius carassius*), river lamprey (*Lampetra fluviatilis*), minnow (*Phoxinus phoxinus*), tench (*Tinca tinca)* and three-spined sticklebacks (*Gasterosteus aculeatus*). We only caught brown trout, pike, perch, whitefish and smelt.

Three sampling locations were selected in the lake (Figure 2-1). The location named Norsjø North is in the Årnes bay, close to the inlets of both River Bøelva and River Sauarelva. Most of Årnes bay is shallow (0-10 m, maximum depth about 30 m), with typical wetland vegetation, and has been a nature reserve since 1994 (Regulaton on Nature Reserves, 1990). The location Norsjø Mid is in the mid-area of the lake, near the

village of Ulefoss, close to the outlet of River Eidselva. The lake at this site is generally somewhat deeper compared with Norsjø North, with depths up to 60 m.

The location Norsjø South is the southernmost part of the lake. In this region, the lake divides into two areas, Fjærekilen and Skotfoss. The Skotfoss area is relatively shallow (< 30 m), while Fjærekilen has some deeper areas (> 60 m). The lake drains into River Skienselva at Skotfoss.

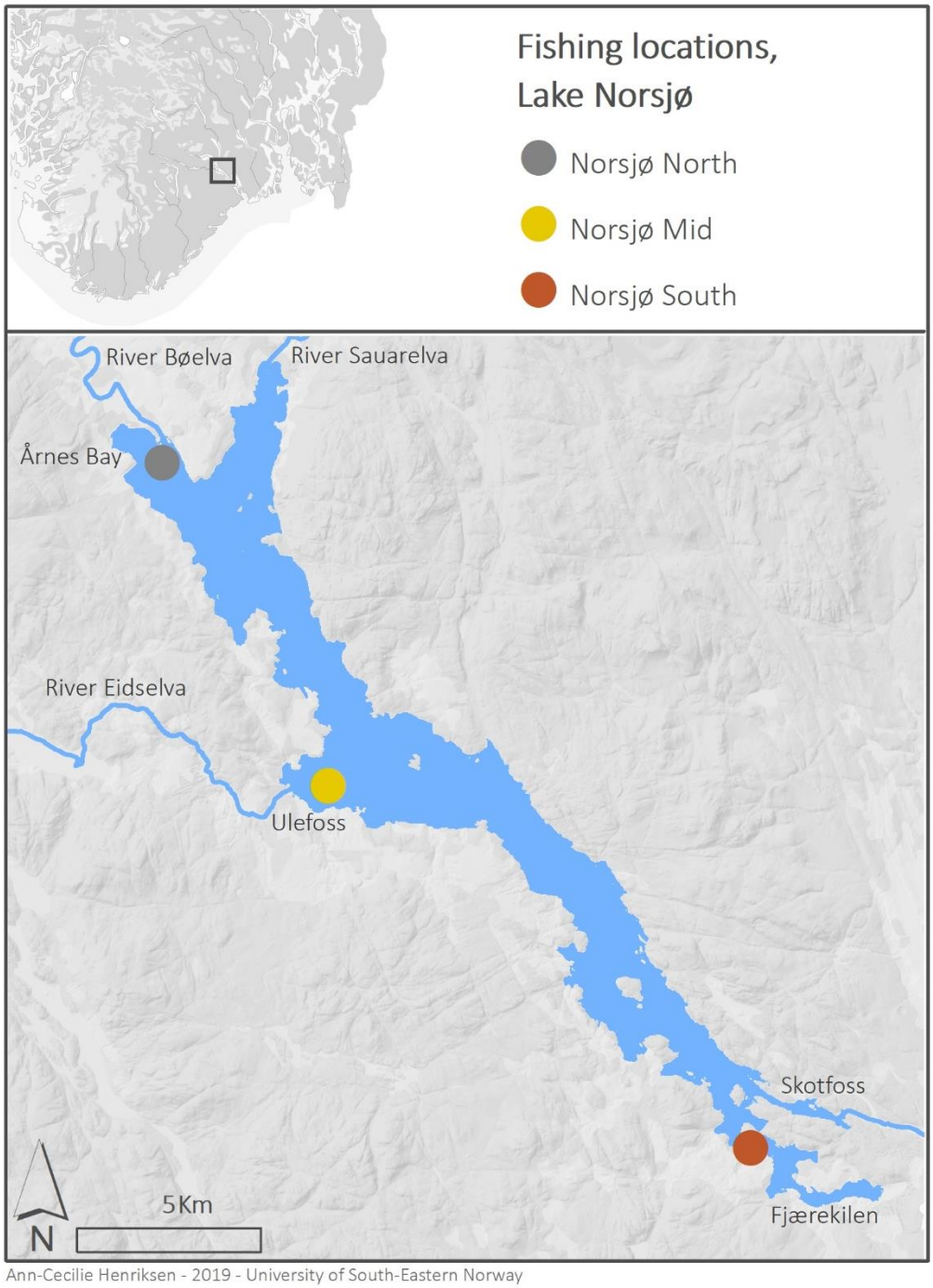


Figure 2-1. Map of Lake Norsjø with sampling locations. Created with the GIS program ArcMap version 10.6.1, using geo data from Geonorge (Geonorge, 2019).

2.2 Field sampling

The sampling was performed three times during 2018. The first sampling was in late May (spring), the second in late July (summer) and the third in the middle of September (fall). The sampling procedure were repeated at all three locations in all the seasons.

Water samples were taken at 1 and 20 m depth. The samples were collected in clean 1 L polyethylene bottles. They were washed 3 times with lake water prior to sampling, before stored in a dark cooling room at 4°C when back from the fieldwork.

For fishing, standard bottom-set gill nets (1.5 m x 30 m) were used, varying in mesh size from 13.5 mm to 45 mm. The nets were tied together to make 6 series of 8 nets and two series of nets were put out in every location (Figure 2-1). The nets were set in the morning, and collected the following day, giving a fishing period of approximately 24 hours. The nets were set from the shore, towards the deepest point in the area, thus covering various depths.

The fish weight was measured to the nearest gram using a digital weight, while total length (L_t) was measured to the nearest millimetre using a ruler. All ectoparasites from each fish were sampled in the field, and stored in small glass vials containing 96 % ethanol for later species identification. Thereafter all fish were frozen in individually labelled plastic bags for later sampling of endoparasites and subsequent examinations in the laboratory.

As sampling of the whole Arctic charr population is impossible, I aimed to catch 30 individuals from every location in all seasons, to have sufficient sample sizes for further statistical analyses. When catches exceeded 30 fish (in Norsjø North and occasionally Norsjø Mid), I randomly selected 30 fish to represent the fish catch.

Catches in Norsjø South were sometimes insufficient. To retrieve enough material from Norsjø South, fish was collected from grates of an industrial water intake at ≈ 50 m depth in Fjærekilen. These fish were treated similarly to the other fishes and defined as a part of the material from Norsjø South.

2.3 Analyses of water samples

All water samples were analysed at the laboratory at the University of South-Eastern Norway. Conductivity and pH were measured as soon as possible after sampling, while the remaining analyses were performed later. Methods used for the chemical analyses of major water chemical parameters are presented in the Table 2-1. The results from the analysis were compared and interpreted by the guidance document 02:2018 in accordance with the Norwegian Water Management Regulation (Direktoratsgruppen vanndirektivet, 2018).

Table 2-1. The parameters that the water samples from Lake Norsjø were analysed for, the equipment that was used, the method specified (internal or Norwegian standard), and the date the analyses took place.

Parameter	Equipment/Machine	Method	Date measured
pH	Mettler Toledo SevenCompact S210	Internal method	Spring/ summer: 2 days after sampling Fall: same day
Conductivity	WTW Cond 3110 TetraCon 325	NS-ISO 7888:1985	Spring/ summer: 2 days after sampling Fall: same day
Alkalinity	Mettler Toledo G20S Compact Titrator	Internal method	22.01.19
Turbidity	Turbiquant 1100 IR	Internal method	16.01.19
Ca^{2+}, $Mg^{2+,}$ Na^{+}, K^{+}, $SO_4^{2,}$ Cl^{-}, NO_3, NH_4^{+}	Dionex ICS-1100 Ion Chromatography System	Internal method	26.11.18
Tot-N	Certoclav-Tisch-Autoclav, FIAlyzer 1000 and AIM3200 Autosampler	NS 4743:1993	17.01.19
Tot-P	Certoclav-Tisch-Autoclav and Perkin Elmer Lambda 25 UV/VIS Spectrophotometer	NS 4725:1984	17.01.19
True colour	Perkin Elmer Lambda 25 UV/VIS Spectrophotometer	NS 4787:1988	16.01.19

2.4 Sampling of endoparasites

Fish were taken out of the freezer the day before, and left to thaw in the refrigerator overnight, before examinations in the laboratory. The fish was opened from gills to gut. All cysts on the intestinal tract and other tissue, containing plerocercoid cestodes, were registered. Some samples of the encysted parasites was identified, before removal of the organs.

The intestinal tract was placed in a petri dish with 9 % saline water and cut open from oesophagus to anus. All parasites located macroscopically was used for further identification and analyses. The located parasites were identified to the possible lowest taxonomical level by their morphological features using relevant literature (Section 2.5).

2.5 Parasite identification

Morphological identification was performed using a binocular loupe or microscope with 2-24 times magnification. To avoid overestimation of the cestodes, the number of present specimens was based on the number of heads (scolexes).

Bykhovskaya-Pavlovskaya et al. (1964) was used for species determination of members of the following genera: *Argulus*, *Triaenophorus, Eubothrium* and *Proteocephalus.* Specimens of the genus *Salmincola* were identified using Kabata (1969). Plerocercoid specimens of *Diphyllobothrium* were identified using Bykhovskaya-Pavlovskaya et al. (1964) and Andersen & Gibson (1989). Note that the key by Anderson & Gibson have some uncertainties when used on frozen parasite material, as morphological features may become less clear.

Because of morphological challenges, 1 Nematoda and 22 Acanthocephala specimens were not identified to species. They are however included in the total parasite counts.

2.6 Statistical analysis

The content of all cysts was not identified to species level, but subsamples showed that they contained the species: *Triaenophorus nodulosus*, *Diphyllobothrium ditremum* and *Diphyllobothrium dendriticum.* As all these parasites share the same characteristics in the intermediate host (Halvorsen & Andersen, 1984; Hoffmann et al., 1986b), they were pooled together as plerocercoids for statistical analyses. All copepod transmitted helminths were also pooled, to look for intra-lake patterns in copepod feeding (*Eubothrium salvelini, Proteocephalus* sp., *Triaenophorus crassus*, *T. nodulosus*, *D. ditremum* and *D. dendriticum*).

The gillnetted Arctic charr from Norsjø South (3 from the spring, 3 from the summer, and 1 from the fall) were removed from the data material prior to analysis. These were caught much closer to the surface than material collected from the industrial grates

(depth of ≈ 50 m) and were considerable larger, thus possibly representing another population.

Preliminary analyses revealed that the parasite count data was non-normal distributed and overdispersed. Hence, generalised linear modelling (GLM) was thought to be the best way of analysing the parasite distributions of Arctic charr from Lake Norsjø (O'Hara & Kotze, 2010; Wilson & Grenfell, 1997). Four models were made, the plerocercoids and copepod-transmitted parasites as grouped parasite data, while the ectoparasite species *Salmincola edwardsii* and the endoparasite *E. salvelini* were modelled individually.

Parasite intensity count for each individual fish was used as response variable in the models. The explanatory variables were as follow: location (3-levelled factor: Norsjø North, Mid and South), season (3-levelled factor: spring, summer, fall), length (numerical), weight (numerical) and sex (2-levelled factor: male, female). To avoid co-linearity, length was preferred as the parameter of fish size, and weight was removed. To look for different patterns within locations, the models included an interaction of location to season and length. To account for over dispersion, I used a "negative binomial distribution" in models for *E. salvelini,* plerocercoids and copepod-transmitted parasites. The distribution "Poisson" was used in the model for *S. edwardsii.* All data modelling was executed in the statistical program RStudio, version 1.1.4630 (RStudio Team, 2016). The function *glmmTMB* from the package glmmTMB was used to model the distributions of parasites (Brooks et al., 2017).

Models were validated by interpreting residuals, which were simulated with the function *simulateResiduals* from the package DHARMa (Hartig, 2019). The global models were simplified by using the function *dredging,* from the package MuMIn (Barton, 2018). The simplification (removal of variables) was based on the corrected Akaike information criterion, AICc (Hurvich & Tsai, 1993). Only candidate models with $\Delta AICc < 4$ were included in the model selection output (Appendix 1). Explanatory variables with 95 % confidence intervals (CI) spanning zero was considered uninformative. Figures and descriptive statistics were made in RStudio, with the package ggplot2 (Wickham, 2016).

Prevalence, mean abundance and intensity of infection were calculated for all parasite species. The terms were used in accordance with the descriptions in Bush et al. (1997). *Prevalence* is the portion of the sampled fish infected with one or more parasites, given in percentages. *Abundance* is the total number of a recorded parasite species within a single host, regardless of the host is infected or not. If stated as *mean abundance*, it is the total number of one parasites species, divided on all sampled hosts. *Intensity of infection* is the number of a parasite species found on a single infected host, given in range or mean.

3 Results

3.1 Water quality of Lake Norsjø

According to the analysed water samples from Lake Norsjø and the Norwegian quality guidance document for fresh waters, Veileder 02:2018 (Direktoratsgruppen vanndirektivet, 2018), the lake is characterised as very big, deep, (very) calcium poor and clear. In accordance with the parameters total phosphorous and nitrogen only, the lake is oligotrophic, which results in good ecologic state (Table 3-1). All chemical data are present in Appendix 2.

Surface temperature (1 m depth) in Lake Norsjø was recorded slightly higher in Norsjø North compared with Norsjø South. Surface water temperature varied from 13.0-15.4°C in the spring, 21.5-23.1°C in summer, and 16.6-16.9°C in fall (Table 3-2). At 20 m depth, all three stations had low spring temperatures (4.8-6.8°C), slightly higher temperatures (7.4-11.5°C) during summer, 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 3-1. Size (km^2), maximum depth (m) and mean water chemical parameters (spring, summer and fall) in Lake Norsjø during 2018. Based on the analysed water chemistry in 2018, the Water type of Lake Norsjø is assessed according to the Norwegian guidance document Veileder 02:2018.

Parameter	Lake Norsjø (mean value)	Water type
Depth (m)	87	Deep > 15
Size (km^2)	55.48	Very big > 50
Climate region(m a.s.l)	15	Lowland <200
Eco region	Telemark	(South) Eastern Norway
Alkalinity (mekv/l)	0.012	Very calcium poor
Calcium (mg/l)	2.24	Calcium poor
Turbidity (FNU)	0.3	Clear < 1.5
Colour (mg Pt/L)	13	Clear, 10-30
Total phosphorus (µg/L)	4.0	Very good ecologic state: 1-4
Total nitrogen (µg/L)	206	Good ecologic state: 200-400

Table 3-2. Water temperatures (°C) at 1 and 20 m, at locations Norsjø North, Mid and South, at spring (May), summer (July) and fall (September).

Location	Depth (m)	Spring (°C)	Summer (°C)	Fall (°C)
Norsjø North	1	15.0	23.1	16.9
Norsjø North	20	4.8	7.4	15.7
Norsjø Mid	1	15.4	22.2	16.6
Norsjø Mid	20	5.4	11.5	14.2
Norsjø South	1	13.0	21.5	16.6
Norsjø South	20	6.8	9.6	12.5

3.2 Arctic charr demography

A total of 236 Arctic charr were investigated. Seasonal sample size at the different locations ranged from 18 to 30 fish. Most fish were caught in Norsjø North, where 30 fish were collected during all the three seasons. The smallest sample size was from Norsjø South, with a total catch of 63 fish (Table 3-3).

The sex distribution in the total catch was relatively equal, i.e.114 females and 122 males. Average length of the fish were 233 mm (SD: ± 79 mm) and 167 g (SD: ± 176 g). The largest fish was caught in Norsjø North, and measured 500 mm and 1416 g. Fish from the South were smaller than fish from the other two locations (Table 3-4). The mean size was largest in the spring and decreases steadily throughout summer and fall.

Table 3-3. The number of Arctic charr caught in the different locations of Lake Norsjø in spring, summer and fall 2018.

Locations	Spring	Summer	Fall	Total
Norsjø North	30	30	30	90
Norsjø Mid	23	30	30	83
Norsjø South	27	18	18	63
Total	80	78	78	236

Table 3-4. Mean length (mm) and weight (g) of Arctic charr (n = 236) in Lake Norsjø 2018, and at the different locations and seasons.

Measure	North	Mid	South	Spring	Summer	Fall	Total
Mean length ± SD (mm)	279 ± 59	257 ± 56	139 ± 38	238 ± 89	235 ± 72	228 ± 73	233 ± 79
Range (mm)	146 - 500	153 - 438	88 - 252	88 - 500	99 - 415	88 - 398	88 - 500
Mean weight ± SD (g)	237 ± 178	196 ± 181	28 ± 28	185 - 216	163 ± 166	150 ± 135	167 ± 176
Range (g)	25 - 1416	28 - 981	5 - 122	6 - 1416	7 - 981	5 - 646	5 - 1416

3.3 Total parasite material

A total number of 5249 macroparasites were recorded in the 236 investigated fish, and the parasite identification resulted in seven different species. In addition, *Proteocephalus* sp. was recorded to genus, and Acanthocephala sp. and Nematoda sp. to phylum. Morphological features of the parasites specimens from these genus and phylum gave no indications that they were different species, and they are accordingly assumed the same.

Two ectoparasite species were identified, *S. edwardsii* and *Argulus coregoni*, which both uses Arctic charr as definitive (Table 3-5). Endoparasites were found in the intestinal tract, free in the coelom, encysted on the intestinal tissue or liver tissue. The following endoparasites were identified: *E. salvelini*, *Proteocephalus* sp., *T. nodulosus*, *T. crassus*, *D. ditremum*, *D. dendriticum*, Acanthocephala sp., and Nematoda sp.

In total, 96.2 % of the sampled fish were infected with one or more macroparasite specimens (Table 3-5). Endoparasites occurred more frequent than ectoparasites. Six fish had more than 100 parasites, and they accounted for 20 % of the total parasite material. The cysts of plerocercoids were the most frequent parasite stage. At the most, five different parasite species were recorded from one single host (the ectoparasite *S. edwardsii,* and the endoparasites: *E. salvelini, D. ditremum, D. dendriticum* and *T. nodulosus*).

The highest parasites abundance was recorded in the spring at Norsjø Mid, with 1061 parasites from 23 examined Arctic charr. Norsjø Mid also displayed the highest number of parasites during summer and fall (Figure 3-1). Even if the parasite counts were notably different between the locations, the prevalence of infection were high at all three locations. Norsjø Mid had the highest prevalence with 100 %, followed by Norsjø North (98.9 %) and Norsjø South (87.3 %) (Appendix 3). The intensity of parasite infection varied between the locations, with a mean of 33.1 (SD: ± 48.1, range: 1-373), 25.0 (SD: ± 19.2, range: 2-130) and 5.2 (SD: ± 5.8, range: 1-36) parasites, for Norsjø Mid, North and South respectively (Appendix 4). Tables of mean abundance, intensity and prevalence for all seasons and locations are enclosed in Appendix 3, 4, 5 and 6.

The distribution of the parasites between the male and female fish was relatively even. The most infected fish was female with 373 parasites, which were 213 parasites more than the second most infected (male).

Table 3-5. All parasites from Arctic charr (n = 236) from Lake Norsjø 2018, with way of transmission and life stage. Prevalence, mean abundance and intensity of infection is calculated both for the total number of parasites and for the individual parasite species/groups.

Parasite infection	Trans-mission	Life stage in Arctic charr	Prevalence (%)	Intensity range	Mean intensity ± SD	Mean abundance ± SD
Total			96.2	1 - 373	23.1 ± 33.4	23.1 ± 33.3
Copepod-transmitted parasites			94.5	1 - 373	23.3 ± 33.6	22.0 ± 33.1
Plerocercoids			94.5	1 - 372	21.4 ± 32.9	20.2 ± 32.4
A. coregoni	Direct	Adult	0.4	1	1.0 ± 0.0	0.004 ± 0.1
S. edwardsii	Direct	Adult	14.8	1 - 3	1.2 ± 0.4	0.2 ± 0.5
E. salvelini	Copepod	Adult	55.5	1 - 26	3.0 ± 3.5	1.6 ± 3.0
T. nodulosus	Copepod	Plerocercoid	37.3	1 - 14	1.9 ± 2.0	0.7 ± 1.5
T. crassus	Copepod	Plerocercoid	0.4	2	2.0 ± 0.0	0.01 ± 0.1
D. ditremum	Copepod	Plerocercoid	37.3	1 - 224	5.1 ± 23.7	1.9 ± 14.7
D. dendriticum	Copepod	Plerocercoid	12.3	1 - 3	1.3 ± 0.6	0.2 ± 0.5
Cysts	Copepod	Plerocercoid	87.7	1 - 156	19.9 ± 24.0	17.5 ± 23.4
Proteocephalus sp.	Copepod	Adult	5.5	1 - 9	2.4 ± 2.6	0.1 ± 0.8
Acanthocephala sp.			6.4	1 - 4	1.5 ± 0.9	0.1 ± 0.4
Nematoda sp.			0.4	1	1.0 ± 0.0	0.004 ± 0.1

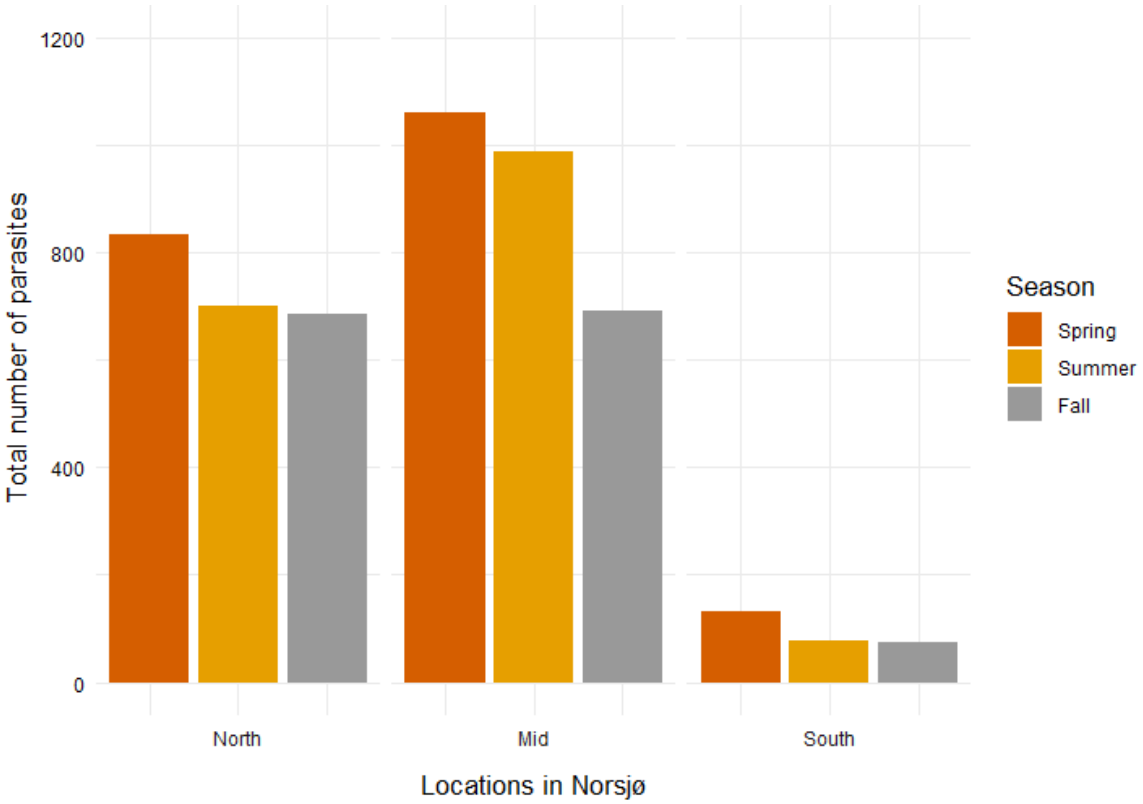


Figure 3-1. The sampling locations of Lake Norsjø (North, Mid and South) and the seasons (spring, summer and fall) distributions of the total number of parasites in Arctic charr in 2018. Norsjø North: n = 30 in all seasons. Mid: n = 23 in the spring, n = 30 in summer and fall. South: n = 27 in spring and n = 18 in summer and fall.

3.4 Copepod-transmitted parasites

The copepod-transmitted parasites use copepods as their intermediate host. In Lake Norsjø, *E. salvelini, Proteocephalus* sp., *D. ditremum, D. dendriticum, T. nodulosus* and *T. crassus* were found in Arctic charr within this parasite group. The two cestodes *E. salvelini* and *Proteocephalus* sp. use the Arctic charr as definitive host, while the remaining four parasites have other definitive hosts. In total, the prevalence of infected fish was 94.5 %. All fish from Norsjø Mid were infected (100 %), all but one fish in Norsjø North (98.9 %), while there were 12 uninfected fish in Norsjø South (80.9 %, Appendix 3).

The highest number of parasites were recorded in the spring, followed by the summer and the fall. However, season is not included in the model, as the selection process revealed that location and length were the most important explanatory variables. There

is a 62 % chance of this model best explaining the variance in the data, compared to the second best model with 22 % chance (Appendix 1). The model revealed less copepod-transmitted parasites in Norsjø South (Table 3-6). Length is the most certain explanatory variable, with a positive effect on the number of parasites (Table 3-6). The effect of length on the parasite number was largest in Norsjø Mid. In Arctic charr at length 150-250 mm, the infection was similar in all locations (Figure 3-2).

Table 3-6. Output from modelling of effects of location and fish length and the interaction between these variables, on the number of copepod-transmitted parasites in Arctic charr in Lake Norsjø 2018. Location Norsjø Mid was used as reference site (see also Appendix 1). Informative variables are marked with.*

				Confidence interval (95 %)	
Variable	Estimate (β)	Std. Error	z-value	Lower	Upper
(Intercept)	0.825	0.546	1.511	-0.246	1.897
Norsjø North	0.922	0.684	1.348	-0.419	2.264
Norsjø South	-2.257	0.726	-3.110	-3.679	-0.835*
Length	0.010	0.002	4.809	0.006	0.014*
Norsjø North x Length	-0.005	0.003	-1.972	-0.010	-2.94e-05*
Norsjø South x Length	0.008	0.004	2.174	0.001	0.016*

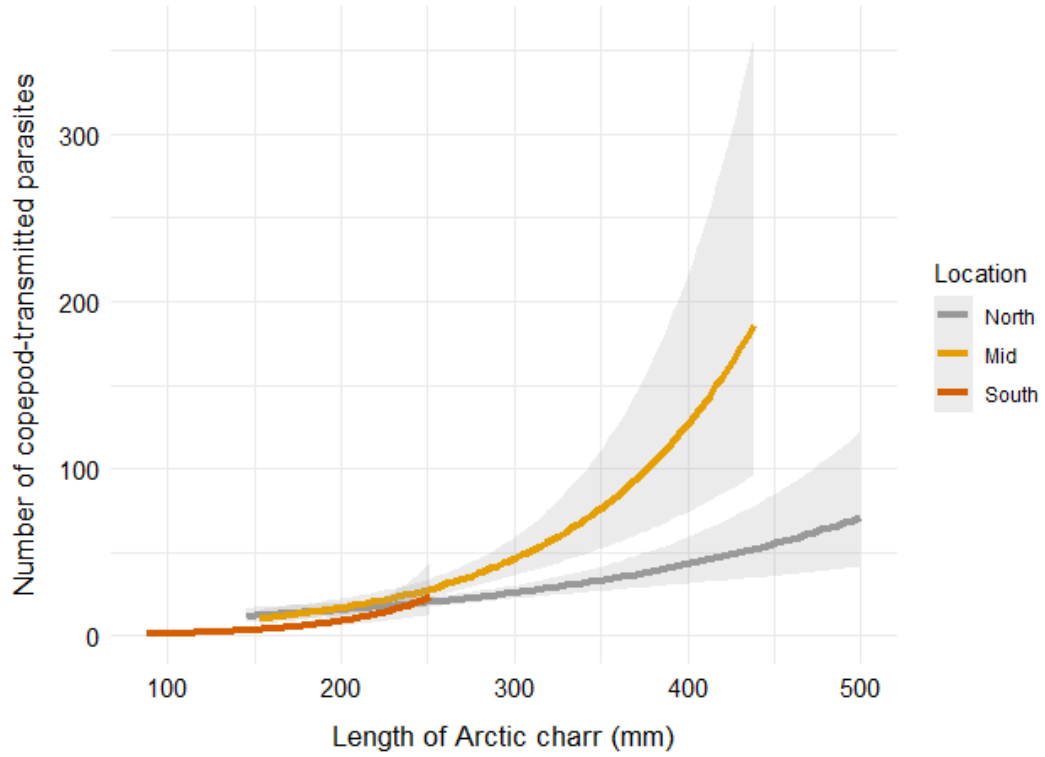
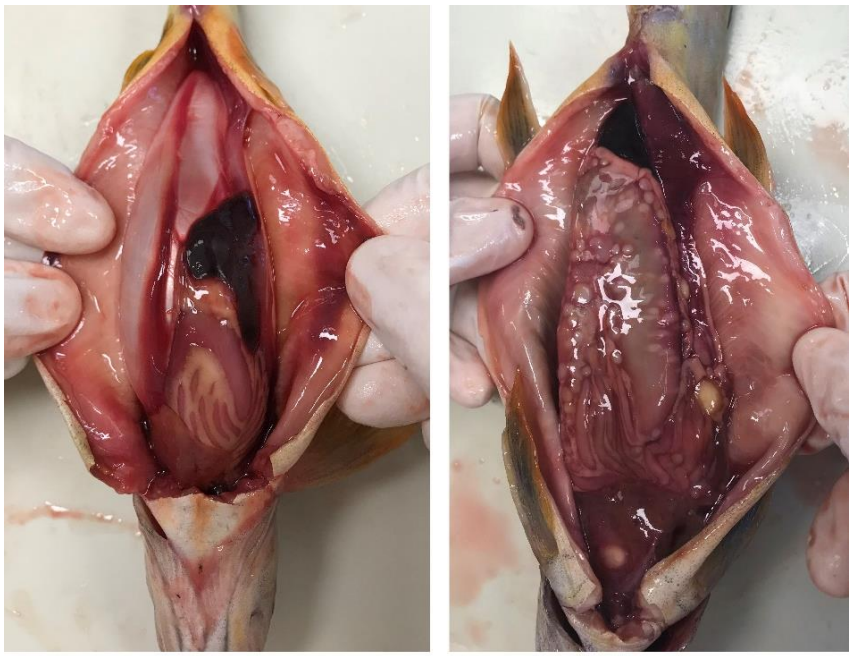


Figure 3-2. Modelled relationships between length of Arctic charr (mm) and number of copepod-transmitted parasites at different locations (North, Mid, South) in Lake Norsjø, 2018. The 95% confidence interval is marked with grey band.

3.5 Plerocercoids of cestodes

The plerocercoids consisted of *D. ditremum*, *D. dendriticum* and *T. nodulosus*. These species all occur in their larval form (plerocercoid) in Arctic charr, as they have other definitive hosts. Encysted plerocercoids were found mostly on the visceral side of the stomach wall, pyloric caeca and liver, while unencysted specimens were found in the abdominal cavity and occasionally within the intestinal tract (Figure 3-3, Figure 3-4).

In Lake Norsjø, 4776 plerocercoids were registered. The prevalence of encysted plerocercoids was 87.7 % (Table 3-5). In addition, unencysted specimens of plerocercoids were often located in the coelom or intestinal tract. Unencysted specimens of *D. ditremum* displayed a prevalence of 37.3 %, *D.dendriticum* 12.3 %, and *T. nodulosus* 37.3 % in the Arctic charr (Table 3-5). When combining all encysted and unencysted specimens, across all seasons, the total prevalence of infection by plerocercoids was 94.5 %. The highest intensity of infection was in the spring, with a mean of 24.9 (SD: ± 28.2, range: 1-159) plerocercoid specimens per infected fish, followed by the summer with 22 (SD: ± 44.6, range: 1-372) and fall with 17.4 (SD: ± 20.2, range: 1-123) (Appendix 5).



A B

Figure 3-3. Arctic charr from Lake Norsjø in 2018, with 4 encysted plerocercoids (A), and with 121 plerocercoids (B). The parasite-larvae are inside the white or yellow cysts on the fish stomach wall, pyloric caeca and liver.

Figure 3-4. T. nodulosus plerocercoid found unencysted in Arctic charr in Lake Norsjø in 2018 (2x magnification).

The single most infected fish individual was caught in Norsjø Mid in the summer, with an infection of 372 plerocercoids (148 encysted plerocercoids and 224 unencysted *D. ditremum).* All fish caught in this location were infected with one or more plerocercoid specimens at all seasons. The infection was also high in the other two locations, with infection prevalence of 98.9 % at Norsjø North, and 81.0 % at Norsjø South (Appendix 3).

As the plerocercoids makes up the larger part of the copepod-transmitted parasites (Section 3.4) in Lake Norsjø, the models share some of the trends. Length and locations, and their interaction, best explained the variation of plerocercoids in Arctic charr. Norsjø South stands out with a lower abundance of plerocercoids compared with the other two locations (Table 3-7). According to the model, fish length was the strongest explanatory variable for the number of plerocercoids, although the effect was small. There are fewer parasites in relation to fish weight in Norsjø North than in Norsjø Mid (Table 3-7). At ≈ 200 mm, several fish contracts higher infections of plerocercoids, with > 50 plerocercoid specimens (Figure 3-5).

Table 3-7. The effects of locations, fish length, and the interaction between the variables, on number of cestode plerocercoids in Arctic charr from Lake Norsjø 2018. The locations Norsjø North and Norsjø South were compared with Norsjø Mid, used as reference site in the model (see also Appendix 1). Informative variables are marked with.*

Variable	Estimate (β)	Std. Error	z value	Confidence interval (95 %) Lower	Upper
(Intercept)	0.637	0.589	1.082	-0.517	1.791
Norsjø North	1.137	0.730	1.557	-0.294	2.568
Norsjø South	-2.016	0.770	-2.620	-3.524	-0.508*
Length	0.010	0.002	4.632	0.006	0.015*
Norsjø North x Length	-0.006	0.003	-2.122	-0.011	-0.001*
Norsjø South x Length	0.007	0.004	1.769	-0.001	0.015

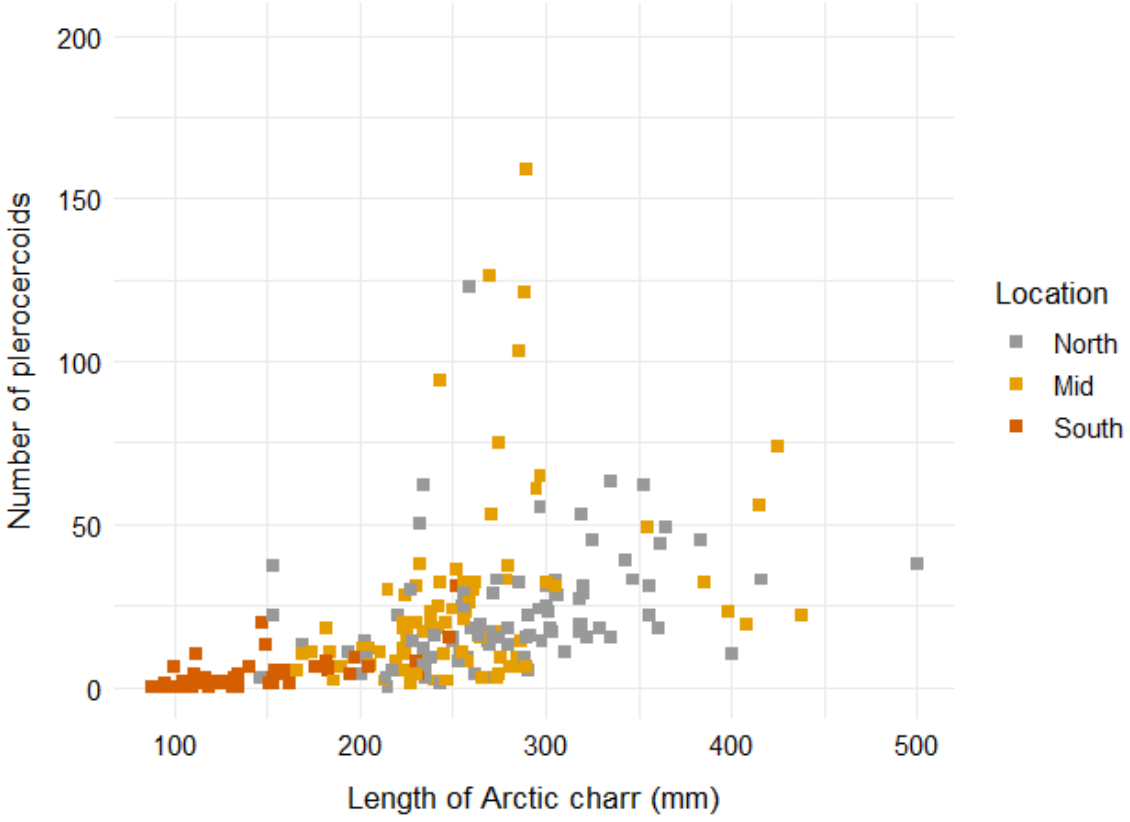


Figure 3-5. The length of Arctic charr (mm) in relation to number of plerocercoids from the different sampling locations (North, Mid and South) in Lake Norsjø 2018. One fish (275 mm) with 352 plerocercoids was omitted from the plot to improve visualisation.

3.6 *Eubothrium salvelini*

In total, 55.5 % of the investigated fish were infected with one or more specimens of *E. salvelini.* The mean intensity of infection was 3.0 (SD: ± 3.5, range: 1-26), and mean abundance 1.6 (SD: ± 3) parasites (Table 3-5). There were fewer infected fish in Norsjø South, with a prevalence of 15.9 %, while Norsjø North and Mid displayed a prevalence of 65.6 % and 74.7 %, respectively (Appendix 3). Regarding seasonal differences, the highest abundance of *E. salvelini* was revealed in the spring, and lowest in the summer (Figure 3-6).

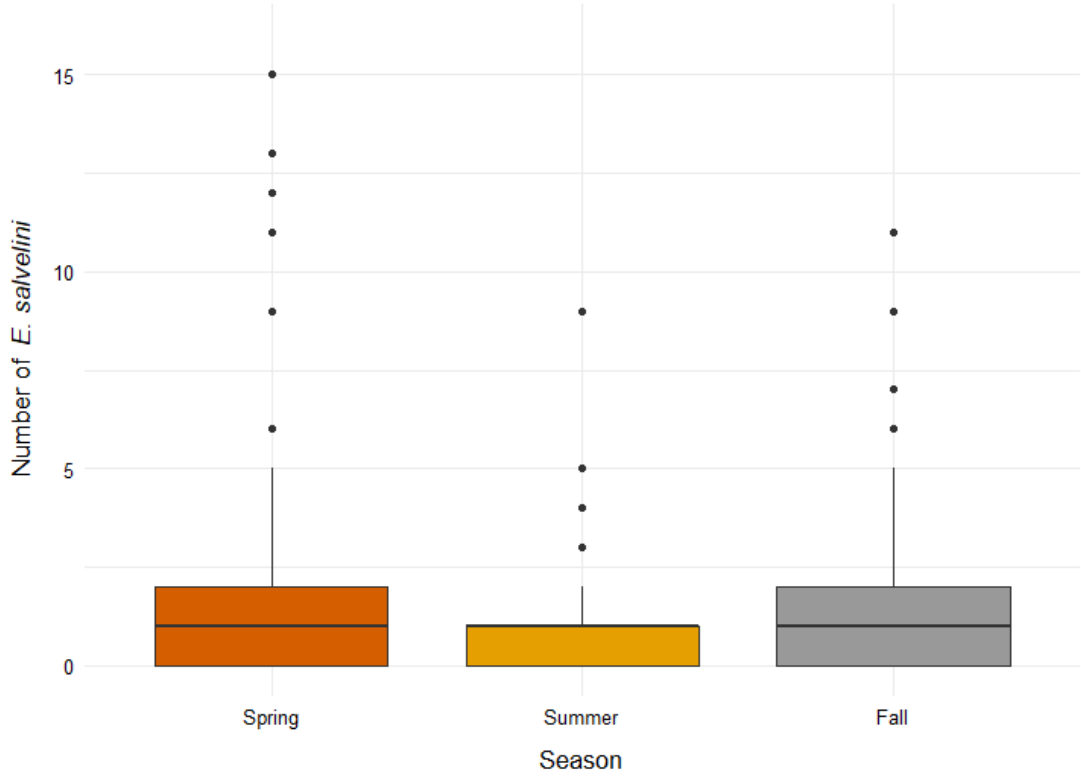


Figure 3-6. Seasonal distribution (spring, summer, fall) of the Number of E. salvelini, in Arctic charr from Lake Norsjø 2018. One outlier (26 parasites) from the spring was omitted from the plot to improve the visualisation.

The model revealed that fish length had a minor, positive effect on the number of *E. salvelini* (Table 3-8). Investigating this more thoroughly, Norsjø South was the only location with a certain increase of parasite infection with length. The model also revealed that season affected the degree of *E. salvelini* infection. Compared with spring (the season with the highest infections), summer had a lower degree of *E. salvelini*,

while fall exhibited no differences from spring (Table 3-8). Sex of the fish did not have any effect on the degree of parasite infection (Appendix 1).

Table 3-8. The effects of season, location (Norsjø) and fish length and interactions between length and location, on the number of E. salvelini (see also Appendix 1). The effects are compared with the reference site Norsjø Mid, at season spring. Informative variables are marked with.*

Variable	Estimate (β)	Std. Error	z-value	Confidence interval (95 %) Lower	Upper
(Intercept)	-0.903	0.583	-1.548	-2.046	0.240
Norsjø North	-0.778	0.908	-0.857	-2.557	1.001
Norsjø South	-4.222	1.290	-3.272	-6.751	-1.693*
Length	0.008	0.002	3.663	0.004	0.012*
Season Fall	-0.276	0.213	-1.294	-0.694	0.142
Season Summer	-0.563	0.218	-2.582	-0.991	-0.126*
Norsjø North x Length	0.001	0.003	0.282	-0.005	0.007
Norsjø South x Length	0.018	0.007	2.621	0.005	0.031*

3.7 *Salmincola edwardsii*

Totally, 41 specimens of the ectoparasite *S. edwardsii* (Figure 3-7) were found on Arctic charr in Lake Norsjø. Of the total fish material, the prevalence of infection by *S. edwardsii* was 14.8 % with a mean intensity of 1.2 (SD: ± 0.4, range: 1-3, Table 3-5). The prevalence of infection was highest in Norsjø South (22.2 %) compared with North (12.2 %) and Mid (12 %) (Appendix 3). Mean abundance was < 1 at all locations. *S. edwardsii* showed different attachment sites on the fish, as 78 % of the parasite specimens was attached on the fins/fin, base and 22 % on the gills/gill cavity (Figure 3-8).

Figure 3-7. The ectoparasite S. edwardsii from Arctic charr in Lake Norsjø in 2018 (2x magnification).

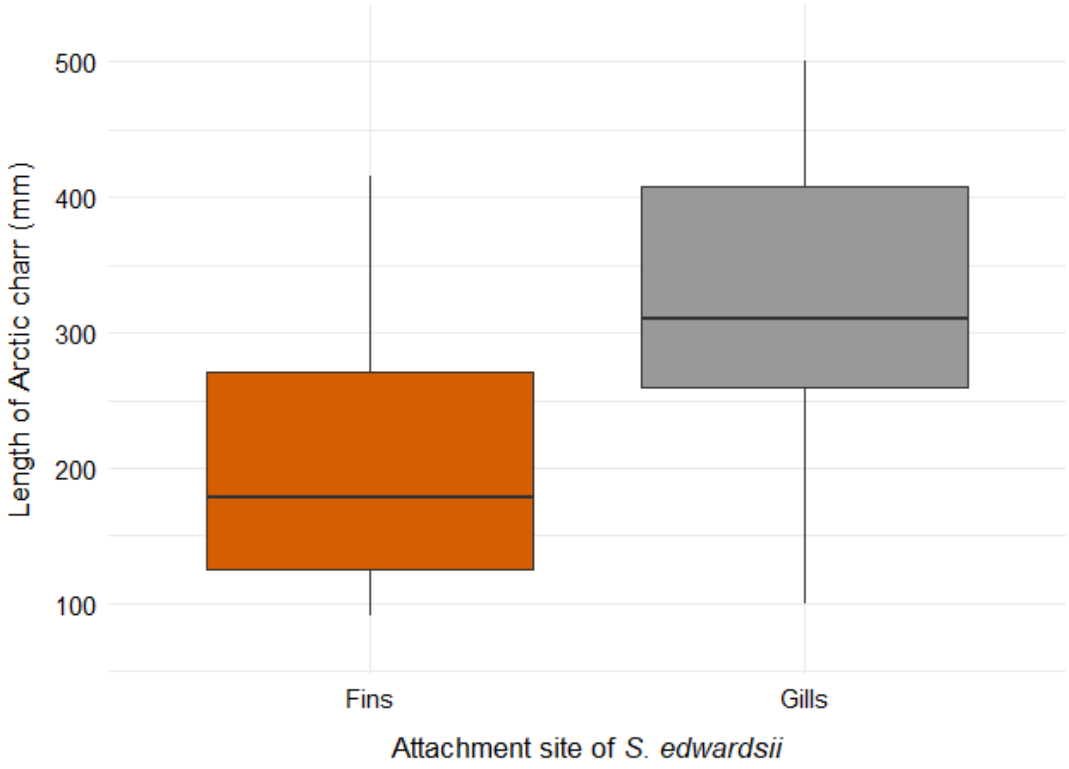


Figure 3-8. The Attachment sites (fins or gills) for the S. edwardsii, in relation to length of Arctic charr (mm). "Fins" includes parasites attached to the fins or to the fin base. "Gills" includes all parasites attached to the gill filaments or the operculum.

Neither season nor sex were considered important predictors to the abundance of *S. edwardsii* on Arctic charr. Based on the model selection, the variables length, location and the interaction between them, were the most suited to explain the variation in the data (Appendix 1). The model also showed that Norsjø South were the location with the highest abundance of *S. edwardsii* (Table 3-9). When treating all fish as one group, the fish length did not influence the infection. However, some minor length effects were revealed at the three different locations. In Norsjø South, there was a minor negative trend between fish length and degree of infection, while a corresponding minor positive trend was revealed in Norsjø Mid (Figure 3-9). No such trends were found in Norsjø North.

Table 3-9. Output from modelling of effects of locations and fish length and their interaction on the number of S. edwardsii from Arctic charr in Lake Norsjø, 2018 (see also Appendix 1). Informative variables are marked with.*

Variable	Estimate (β)	Std. Error	z-value	Confidence interval (95 %) Lower	Upper
(Intercept)	-3.221	1.268	-2.539	-5.707	-0.735*
Norsjø North	-1.845	1.749	-1.055	-5.272	1.583
Norsjø South	4.457	1.756	2.539	1.016	7.898*
Length	0.005	0.004	1.014	-0.004	0.013
Norsjø North x Length	0.006	0.006	1.034	-0.005	0.017
Norsjø South x Length	-0.024	0.011	-2.249	-0,046	-0.003*

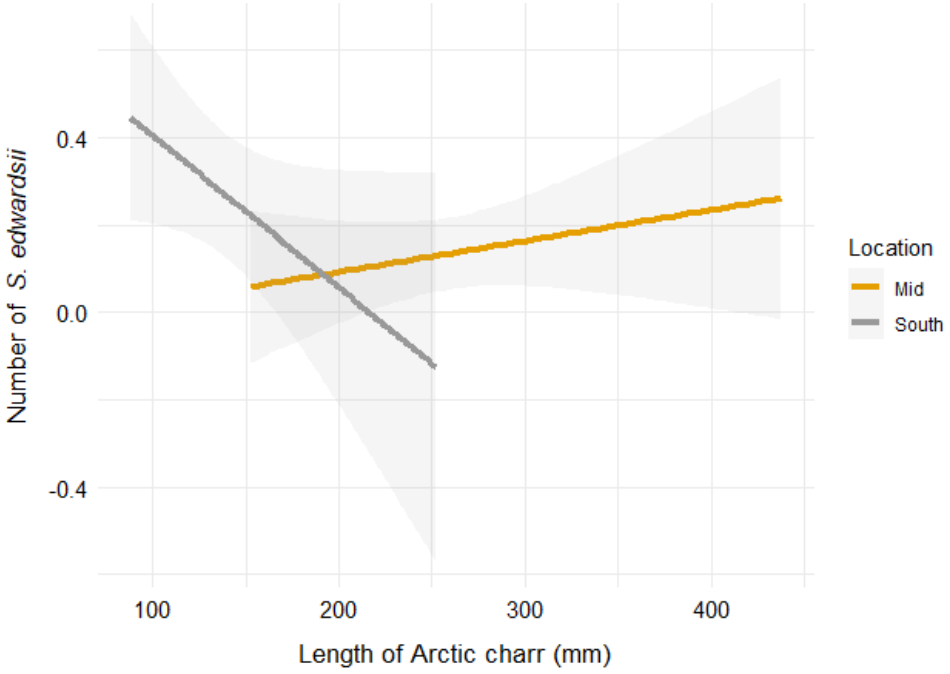


Figure 3-9. Linear relationship between length of Arctic charr (mm) and number of S. edwardsii at the locations Norsjø North and Mid 2018 (with 95 % confidence interval).

3.8 Non modelled parasite species

Some of the parasites in this study had insufficient numbers for individual statistical modelling. This involves specimens of *Proteocephalus* sp. (31), Acanthocephala sp. (22), *T .crassus* (2)*, A. coregoni* (1) and Nematoda sp. (1). The specimens of *Proteocephalus* sp. were very fragile, and when interacted with, they often dissolved.

None of the 31 specimens of *Proteocephalus* sp. were found in the spring. One specimen was found in the summer, while the remaining 30 were from fish in the fall. The parasites were present in 13 host individuals, giving a total prevalence of 5.5 %, with a mean intensity of 2.4 (SD: ± 2.6, range: 1-9, Table 3-5). None of the infected individuals derived from Norsjø South.

The 22 specimens of Acanthocephalans were found in the intestinal tract of 15 Arctic charrs. The total prevalence of infection was 6.4 %, and mean intensity 1.5 (SD: ± 0.9, range: 1-4) (Table 3-5). Two specimens of *T. crassus* were found in the intestinal tract of the largest fish caught in this investigation (500 mm and 1416 g).

Only one specimen of the ectoparasite *A. coregoni* was recorded in the total Arctic charr catch from Lake Norsjø in 2018 (n = 236). The infected fish was a female caught in summer, at Norsjø North. In addition, one specimen of an unidentified nematode species was revealed on a male fish caught in the fall in Norsjø North.

4 Discussion

When investigating Arctic charr from Lake Norsjø in 2018, I identified seven parasitic species, in addition to one group identified to genus and two to phylum. Arctic charr is known to utilize several niches of a lake, which gives different diets and exposure of parasite infection (Amundsen et al., 2007; Nilsen, 2006). This is demonstrated in the parasite patterns in Lake Norsjø, as the parasite abundance in the fish varied greatly between the locations (Figure 3-1).

Based on the levels of (total) phosphorus (4.0 µg/L) and nitrogen (206 µg/L), Lake Norsjø is considered an oligotrophic lake. Little is mentioned in the literature about Arctic charr parasitology in relation to the trophic status of a lake. However, studies of perch have shown that fish in oligotrophic waterbodies tends to have higher prevalence and intensity of *Triaenophorus* sp. (Brinker & Hamers, 2007; Lucký & Navrátil, 1984; Schähle et al., 2016). Suggesting that the trophic status of a lake will influence the food accessibility and diversity of zooplankton (Moser & Cowen, 1991). Copepods are known to tolerate lower values of nutrients than cladocerans (DeMott, 1989; Primicerio & Klemetsen, 1999). Hence, when a lake is oligotrophic, the infectious copepods will pose a larger part of the total zooplankton available. Since Arctic charr is proven to prey on both copepods and cladocerans (Klemetsen et al., 2003; Skoglund et al., 2013), this could be expected in Lake Norsjø, resulting in a high portion of copepod-transmitted parasites. The water samples also revealed that the lake is calcium poor (2.2 mg/l), which is linked to a lower diversity and abundance of intermediate hosts (Karvonen & Valtonen, 2004; Rukke, 2002).

The length of the fish had a positive effect on the abundance of copepod-transmitted parasites in Arctic charr in Lake Norsjø (Table 3-6). Generally, there are two main reasons for the increase of the parasites with larger fish: 1) long-living parasites accumulates with increasing fish age, and 2) larger fish consume more prey, which increase the probability of infection (Henriksen et al., 2016; Smith, 1973). The relationship of length and copepod-transmitted parasite numbers was less positive in Norsjø North than in Norsjø Mid (Table 3-6), indicating that the fish in the North have fewer parasites at a certain size. The shallow waters in Norsjø North can result in benthic prey being a larger part of the diet, and less copepods.

Fish from Norsjø Mid had the highest abundance of copepod-transmitted parasites, while fish from Norsjø South had the least (Table 3-6). As the fish from Norsjø South were the smallest (Table 3-4), few parasites could be an effect by the size of the fish, or by fewer copepods in their diet. For Norsjø South, the great depth of the location is important as it parasite infected copepods are found towards the surface (Anegg et al., 2014; Pulkkinen et al., 2000). Olk et al. (2016) performed a dietary analysis of Arctic charr from Norsjø South, and found copepods to be a small part of the diet (12 %), and only from August to February. Specimens of Chironimidae were the largest part of the diet (Olk et al., 2016). To the best of my knowledge, the benthic invertebrates Chironimides are not host for any of the parasites found in this study. In addition, the mean depth of Lake Norsjø is 87 m, and the water temperature was measured no deeper than 20 m, so temperatures towards 4°C are expected at deeper waters. Since temperature affect maturation of procercoids in copepods (Anegg et al., 2014), this is also a possible factor of the low parasite infections in fish from Norsjø South.

The plerocercoids consisted of three species: *D. ditremum*, *D. dendriticum* and *T. nodulosus*. All three uses copepods as first intermediate hosts, and fish as second intermediate host (Andersen et al., 1986). Specimens of *Diphyllobothrium* spp. have piscivorous birds or mammals as definitive host, while *T. nodulosus* matures in pike (Chubb, 1963; Hickey & Harris, 1947). Since the cysts contained three different species, it was difficult to characterise their individual species distribution. However, 451 unencysted specimens of *D. ditremum* were located in the total fish material. The infection of unencysted *D. dendriticum* was much lower, with only 37 specimens. It could of course be several specimens of *D. dendriticum* within the unidentified cysts, but the abundance of the unencysted *D. ditremum* was measurably higher. Henricson (1977) found an increase in the number of *D. ditremum* (11 %) located in the coelom when examining the fish more than one day after capture. The fish in the present study were frozen the same day as they were caught. Nevertheless, they could have been dead in the fishing nets for a maximum of 24 hours, plus some time on shore before freezing. Subsequently, the amount of free *D. ditremum* could be increased by the time between capture and freezing. Of *T. nodulosus*, 163 unencysted specimens were recorded, giving a total prevalence of 37.3 % (Table 3-5). This species is known to prefer

the fish liver as their microhabitat (Hoffmann et al., 1986b), and unencysted specimens were often found close to, or on the liver.

For the plerocercoids, fish length was the most certain predictor of the abundance. Specimens of *Triaenophorus* sp. might survive within the Arctic charr (intermediate host) for several years, which gives them the ability to accumulate with increasing fish size and age (Dick & Rosen, 1982; Hoffmann et al., 1986b; Rosen & Dick, 1984). This is a trait shared by the two species of *Diphyllobothrium* spp. detected in this study (Halvorsen & Andersen, 1984; Henriksen et al., 2016). In such, all the plerocercoid species have the same ability to accumulate with fish size, which could cause the positive effect of length on the abundance seen in this study (Table 3-7).

The eggs of mature *T. nodulosus* are released from the definitive host, pike, when it spawns in spring, and can thereafter be ingested by copepods (Marcogliese, 1995). Procercoids of *T. nodulosus*, which is the life stage before plerocercoid, are often detected in copepods 2-6 weeks after pike spawning, and are present approximately one month (Anegg et al., 2014; Lahnsteiner et al., 2009). Since the most common definitive host of *Diphyllobothrium* spp. are birds, parasite eggs can be released in the ice-free period. One could therefore expect an increase of all the plerocercoids throughout the growing season. However, no effect of season was seen in this study (Appendix 1). Seasonal patterns were also absent when investigating prevalence, mean abundance and intensity. The mean fish length was highest in the spring, followed by summer and fall (Table 3-4). Considering that fish length is the most certain explanation for the number of plerocercoids, the differences in the fish size can conceal any seasonal variations.

The distribution of parasites in Lake Norsjø occurred overdispersed, as often seen in former studies (Halvorsen & Andersen, 1984; Henricson, 1977; Knudsen et al., 2004; Shaw & Dobson, 1995). The highest aggregation was unveiled in six fish that harboured as much as 20 % of the endoparasites recorded in this study, with a mean of 170 parasites each. Their infection consisted mostly of copepod-transmitted parasites, especially the plerocercoids of *Diphyllobothrium* spp. One reason for such high aggregation could be individual feeding specialisation. Arctic charr has been seen to show long-term persistence in such specialisation (Knudsen et al., 2004; Knudsen et al.,

2009). Three-spined stickleback and European smelt are two of the possible second intermediate hosts of *Diphyllobothrium* spp. (Andersen et al., 1986; Andersen & Valtonen, 1992; Anikieva et al., 2017), and both of these small fish species inhabits Lake Norsjø (Jensen, 1954). Piscivorous behaviour of Arctic charr on these fish species, could explain the aggregation of *Diphyllobothrium* spp. seen in the present study, as *Diphyllobothrium* spp. are thought to re-establish in a second piscine intermediate host (Hammar, 2000; Henriksen et al., 2016). Though not registered in the present study, small fish were observed in the stomach content of several Arctic charr while locating parasites. Moreover, piscivorous behaviour of Arctic charr has previously been recorded in Lake Norsjø (Jensen, 1954; Lydersen & Vicente, 2016; Olk et al., 2016).

In Lake Norsjø, 55.9 % of the Arctic charr had an infection of the parasite *E. salvelini*. The parasite is specific to Arctic charr in Europe, and have a lifecycle of one intermediate host (copepod) and the Arctic charr as definitive host (Andersen & Kennedy, 1983). High abundances of the parasite have, among other effects, been reported to decrease the fish condition, possibly due to competition for nutrients (Hoffmann et al., 1986a). The infection rates of *E. salvelini* in the intermediate hosts are often low, with rates between 0.002 % and 0.001 % (Boyce, 1974; Hanzelová et al., 2002). If there are similar low infection of the copepods in Lake Norsjø, the high prevalence of *E. salvelini* in Arctic charr indicates heavy feeding on copepods. Although, it has been suggested that infection of *E. salvelini* in the copepods can alter the copepods behaviour, and make them more susceptible for predation by fish (Poulin et al., 1992).

The fish size and abundance of *E. salvelini* correlated positively in Lake Norsjø, which previous studies of the cestode support (Hoffmann et al., 1986a; Kuhn et al., 2016). Regardless of Norsjø South having a lower parasite count, the location displays the strongest relationship of length and abundance of *E. salvelini.* Hence, a higher parasite number with increasing fish size. Considering that copepods previously have been a small part of the diet in Norsjø South (Olk et al., 2016), it is more likely that the parasite have accumulate with increasing fish age (Hanzelová et al., 2002; Smith, 1973). In that case, the fish from Norsjø South could possibly be older than their small size indicate. In a recent study from Lake Norsjø, 77 Arctic charr from Norsjø South were age

determined. The age varied from 3 to 19 years, with an average of 9 (SD: ± 4) years (Olk et al., 2016). The size distribution of the age-determined fish was similar to the present study. On the other hand, profundal zones of lakes is known to harbour young Arctic charr that tries to avoid predation by larger fish (Amundsen et al., 2007; Refsnes, 2014). Age determination of the fish would therefore bring new insight into the relationship of length and abundance of *E. salvelini*.

The spring have the highest number of *E. salvelini* per infected fish, followed by the fall, while the lowest intensity of infection was in the summer (Appendix 5). Previous studies of *E. salvelini* report no differences in infection in different seasons (Hanzelová et al., 2002; Hernandez & Muzzall, 1998; Hoffmann et al., 1986a). This is connected to worms releasing their eggs continuously throughout the year (Hanzelová et al., 2002). However, some studies show a peak in egg shedding in the spring (Boyce, 1974; Hernandez & Muzzall, 1998; Kennedy, 1978). Heavy shedding of eggs (and worm death) in the spring could explain the low infection in the summer before new infections causes an increase in the fall. A theory also supported by the increase in prevalence from spring to fall (51.3 %, 56.4 % and 59.0 % for spring, summer and fall respectively, Appendix 3). Hence, there are more heavily infected fish in the spring, while the prevalence of *E. salvelini* increases from spring to fall, indicating new infections. The mean temperature in Lake Norsjø was 15.9°C during the summer and 15.4°C in the fall (Appendix 2). *E. salvelini* have shown higher growth rates in the intermediate host with increasing temperature, from 5° to 15°C (Boyce, 1974). The high temperatures in Lake Norsjø were probably facilitating the growth of the parasite in the copepods, and thereby new infections through the summer. Nevertheless, as *E. salvelini* can harm their host (Hoffmann et al., 1986a), it cannot be excluded that heavy infected fish die, and thereby reduce the infection.

Few specimens of the cestode *Proteocephalus* sp. was present in the Arctic charr, with only 5.5 % of the fish infected (Table 3-5). Nevertheless, with no infected fish in the spring, one in the summer, and 12 in the fall, there are indications of seasonality. Previous studies of *Proteocephalus* sp. seasonality in brown trout have shown a different pattern, with the lowest infection intensity in August/September (Hatleli, 2012; Lien & Borgstrøm, 1973). While, in a different lake, the highest infection rate of

Proteocephalus sp. procercoids in copepods were found in July and August (Anegg et al., 2014), which could result in more infected fish in the same period. If *Proteocephalus* sp. in other lakes show the same seasonality as in Lake Norsjø, their presence could easily be overlooked when using one sampling period. In addition, the number of present specimens were based on the number of scolexes. Thus, the fragile state of the parasites may have resulted in fewer scolexes removed from the pyloric caeca, and subsequently underrepresentation.

Two specimens of the cestode *T. crassus* were identified in the intestinal tract of one fish individual. This parasite uses pike as definitive host and is not considered an intestinal parasite, as it matures in the pike's musculature. The parasite has however been found in the musculature of *Salvelinus* spp. as a second intermediate host (Anegg et al., 2014; Schähle et al., 2016). Thus, the parasite specimens found in Arctic charr from Lake Norsjø had probably just entered the digestive system. As the musculature was not investigated in this study, *T. crassus* infection in other fish individuals is possible.

The ectoparasite *S. edwardsii* infected 14.8 % of all examined fish. This ectoparasite occurs mainly on fish from the genus *Salvelinus.* It has a direct way of infection with fish as its only host (Kabata, 1969). There were more specimens of *S. edwardsii* in Norsjø South than in the other two locations, and a negative relationship between the fish size and parasite numbers. This is indicating that smaller fish have more parasites. In the other two locations, there was no clear relationship between length and number of *S. edwardsii* (Table 3-9). The relatively high parasite abundance combined with the small fish size in Norsjø South could be the explanation (Table 3-4). Other studies of the ectoparasite have found a greater risk of infection with increasing fish size (Amundsen et al., 1997; Black et al., 1983). *S. edwardsii* often prefer attachment to the gill region of Arctic charr (Amundsen et al., 1997; Conley & Curtis, 1993). However, in Lake Norsjø, as much as 78 % of the recorded specimens occurred in other microhabitats. Previous studies show that *S. edwardsii* can be found attached to the fins/skin of small Arctic charr, especially at low infection intensities (Black et al., 1983; Conley & Curtis, 1993), which suits our findings well (Figure 3-8). Additionally, one reason for a high parasite infection in Norsjø South could be the great depth of the location (50 m). An

experiment by Poulin et al. (1990) revealed that the free-living stage of *S. edwardsii* (copepodids) spend most of their lifetime towards the bottom of the lake. The copepodids showed a sporadic upwards swimming motion, but the speed is not necessarily enough to keep them in the upper waterbody (Poulin et al., 1990). The upwards swimming motion can result in little resistance towards the natural water currents in the lake. In that case, the number of infectious copepodids could also increase in Norsjø South, which is close to the lake outlet (Figure 2-1).

Careful considerations of the results is important due to uncertainties during sampling. The two different fishing techniques used in this study may have influenced the fish sizes. Gillnetting can lead to an underrepresentation of small and young fish (Finstad et al., 2000; Henriksen et al., 2016) whereas the grates in the industrial water intake can collect fish from all sizes. While the smallest fish from Norsjø North and Norsjø Mid were 146 mm and 153 mm respectively, 42 fish measured beneath this size in the South (Table 3-4). Although poor nutritional conditions often results in small fish individuals to reside in the deep profundal zone in other lakes (Amundsen et al., 2007; Klemetsen et al., 2002; Siwertsson et al., 2016), the fishing method could amplify this pattern in Lake Norsjø.

In addition to selecting fish size, a reduction of ectoparasites by rough physical treatment when gillnetting is possible. Amundsen et al. (1997) used gillnetting when investigating the distribution of the ectoparasite *S. edwardsii*. They found 97.5 % of the parasites attached to the gills. In Lake Norsjø, only a small portion of the parasite had attached to the gills or gill cavity. The remaining parasites were found more exposed on the fins or the fin base (Figure 3-8). It is therefore a potential underrepresentation of *S. edwardsii* from the locations Norsjø North and Norsjø Mid, where gillnetting were the only fishing method. In addition, only one specimen of the ectoparasite *A. coregoni* was found (in the summer), from 236 sampled Arctic charr. *A. coregoni* overwinter as eggs and does not begin hatching before water temperatures reaches 10° C (Hakalahti & Valtonen, 2003; Mikheev et al., 2001). When performing the spring sampling, the water had a mean temperature of 14.5°C at 1 m, and 5.7°C at 20 meters (Appendix 2). Assumable, the hatching was just beginning and it would be unlikely to find the parasite. Nonetheless, it is surprising that only one specimen was recorded through the

summer and fall. Even if the gillnetting can reduce numbers of *A.coregoni* by rough treatment, no specimens were found in Norsjø South, where there were no gillnetting. It is therefore possible that *A.coregoni* uses another fish species than Arctic charr as the preferred host in Lake Norsjø.

5 Conclusion

The investigations of Arctic charr macroparasites in 2018 revealed seven different species in Lake Norsjø: *A. coregoni*, *D. ditremum*, *D. dendriticum*, *E. salvelini*, *T. crassus*, *T. nodulosus* and *S. edwardsii*. In addition, *Proteocephalus* sp. was recorded to genus, and *Acanthocephala* and *Nematoda* to phylum. As the encysted plerocercoids were the most numerous parasites present in the Arctic charr, future research in Lake Norsjø should focus on species identification of these parasites.

For the trophic transmitted endoparasites in Lake Norsjø, the most important predictor for parasite abundance is fish length and location. The location Norsjø South differed significantly from the other two in parasite abundances and fish size, which indicates several populations of Arctic charr in Lake Norsjø. Investigations of the age structure and spawning time of Arctic charr would reveal more about these possible populations.

Seasonal differences was only seen for two species. As the present study simply represent a snapshot of parasite patterns in Lake Norsjø, longer time series of investigations would be appropriate regarding both seasonal and long-term variations.

The musculature-living parasite *T. crassus* were recorded in the intestines of one fish. It would be interesting to investigate the presence of this parasite in the fish musculature, especially concerning the worth of Arctic charr from Lake Norsjø for human consumption. When considering commercial and recreational value of freshwater fish, investigations of the parasite communities is perhaps an underrepresented part of the management.

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Appendix

Appendix 1. The global models were simplified with the function "dredging" in the package MuMIn in RStudio. The model with the delta value 0 is the best fit to the data, and the model selected for the results. All categorical variables marked with "+" is included in the top model, as well as numerical variables with numerical values. The variables are length, location (Norsjø), season, sex and the interactions "Norsjø x length" and "Norsjø x season". The weight shows the likeliness of the model to be the best fit. All models with Δ < 4 is included in the table.

Response variable (parasite count)	Cond (Int)	Disp (Int)	Lng	Lct	Ssn	Sex	Lct x Lng	Lct x Ssn	df	logLik	AICc	delta	weight
S. edwardsii	-3.22	+	0.005	+			+		6	-108.73	229.8	0	0.74
	-3.22	+	0.004	+		+	+		7	-108.72	231.9	2.09	0.26
E. salvelini	-0.90	+	0.008	+	+		+		9	-354.15	727.1	0	0.46
	-0.87	+	0.008	+	+	+	+		10	-353.70	728.4	1.27	0.24
	-1.18	+	0.008	+			+		7	-357.40	729.3	2.19	0.16
	-1.31	+	0.009	+	+				7	-358.23	731.0	3.86	0.07
	-1.20	+	0.009	+	+	+			8	-357.17	731.0	3.87	0.07
Plero-cercoids	0.64	+	0.01	+			+		7	-860.03	1734.6	0	0.57
	0.64	+	0.01	+		+	+		8	-860.03	1736.7	2.14	0.20
	0.79	+	0.01	+	+		+		9	-859.19	1737.2	2.62	0.15
	1.13	+	0.01	+	+		+	+	13	-855.41	1738.5	3.89	0.08
Copepod-trans-mitted parasites	0.82	+	0.01	+			+		7	-873.37	1761.2	0	0.62
	0.83	+	0.01	+		+	+		8	-873.37	1763.4	2.14	0.22
	0.97	+	0.01	+	+		+		9	-872.56	1763.9	2.68	0.16

Appendix 2. Results from analysis of water samples from Lake Norsjø in 2018. The samples were taken at two different depths (1 m and 20 m) in three different locations (Lct) of Lake Norsjø (North (N), Mid(M) and South(S)). The samplings were done once in the spring (May), summer (July) and fall (September). N.a. = < 50 µg NH_4^+-N/L.

Nr	Lct	Date	Depth (m)	T °C	pH	Cond. (mS/m)	Alk. Mmol/L	Turb (FNU)	Ca^{2+} (mg/L)	Mg^{2+} (mg/L)	Na^+ (mg/L)	K^+ (mg/L)	SO_4^{2-} (mg/L)	Cl^- (mg/L)	NO_3^--N (µg/L)	NH_4^+-N (µg/L)	Tot-N (µg/L)	Tot-P (µg/L)	Colour mg Pt/L
1	N	28.05	1	15	6.03	1.85	0.02	0.24	2.30	0.27	1.09	0.29	192.95	1.65	193.00	41.4	213.75	2.0	13.70
2	N	28.05	20	4.8	5.85	1.89	0.01	0.42	2.24	0.28	1.22	0.23	95.38	1.80	95.40	N.a.	252.04	2.5	20.20
3	M	28.05	1	15.4	6.39	1.87	0.01	0.35	2.26	0.29	1.23	0.23	103.15	1.80	103.10	N.a.	238.30	3.0	18.30
4	M	28.05	20	5.4	6.52	1.82	0.01	0.42	2.27	0.27	1.13	0.22	61.28	1.70	61.30	N.a.	190.34	3.5	16.50
5	S	28.05	1	13	6.69	1.92	0.02	0.18	2.41	0.29	1.18	0.23	62.12	1.69	62.10	N.a.	218.20	2.5	15.50
6	S	28.05	20	6.8	6.49	1.81	0.01	0.27	2.31	0.28	1.17	0.27	103.76	1.75	103.80	N.a.	214.93	3.0	13.00
7	N	30.07	1	23.1	6.98	1.79	0.01	0.15	2.29	0.26	1.03	0.26	44.87	1.59	44.90	41.0	199.52	< 2.0	10.80
8	N	30.07	20	7.4	6.54	1.80	0.01	0.30	2.26	0.26	1.14	0.22	92.93	1.69	92.90	N.a.	250.46	2.5	16.20
9	M	30.07	1	22.2	6.68	1.68	0.01	0.20	2.22	0.24	0.92	0.23	43.98	1.40	44.00	49.2	169.98	< 2.0	9.60
10	M	30.07	20	11.5	6.53	1.73	0.01	0.23	2.20	0.26	1.05	0.21	73.45	1.55	73.50	N.a.	187.95	< 2.0	12.90
11	S	30.07	1	21.5	6.82	1.67	0.02	0.22	2.21	0.24	0.96	0.23	43.03	1.45	43.00	23.5	172.74	10.0	10.10
12	S	30.07	20	9.6	6.54	1.80	0.01	0.12	2.28	0.27	1.09	0.21	83.12	1.65	83.10	N.a.	176.97	2.5	13.00
13	N	10.09	1	16.9	6.86	1.66	0.01	0.20	2.18	0.24	1.00	0.21	55.64	1.45	55.60	N.a.	164.12	3.0	10.80
14	N	10.09	20	15.7	6.62	1.73	0.01	1.00	2.13	0.29	1.02	0.29	98.12	1.60	98.10	31.5	309.33	8.0	21.60
15	M	10.09	1	16.6	6.77	1.62	0.01	0.30	2.17	0.24	0.92	0.22	52.97	1.43	53.00	31.6	195.33	6.5	10.70
16	M	10.09	20	14.2	6.73	1.64	0.01	0.29	2.19	0.24	0.92	0.23	67.75	1.61	67.80	24.7	196.28	3.0	9.80
17	S	10.09	1	16.6	6.68	1.70	0.01	0.23	2.24	0.25	0.96	0.25	57.31	1.47	57.30	30.7	179.07	< 2.0	9.40
18	S	10.09	20	12.5	6.44	1.73	0.01	0.25	2.20	0.26	1.01	0.24	74.63	1.54	74.60	10.6	183.10	< 2.0	11.70

Appendix 3. Prevalence of infection of parasites (%) on Arctic charr from Lake Norsjø 2018. The data is grouped by sampling location (Norsjø North, Mid and South) and season (spring, summer and fall).

Parasite infection	North	Mid	South	Spring	Summer	Fall
Total	98.9	100	87.3	93.6	98.7	96.2
Copepod-transmitted parasites	98.9	100	80.9	91.3	97.4	94.9
Plerocercoids	98.9	100	81.0	91.3	97.4	94.9
A.coregoni	1.1	0	0	0	1.3	0
S. edwardsii	12.2	12.0	22.2	18.8	12.8	12.8
E. salvelini	65.6	74.7	15.9	51.3	56.4	59.0
T.nodulosus (plerocercoid)	47.8	30.1	31.7	32.5	39.7	39.7
T.crassus (plerocercoid)	1.1	0	0	1.3	0	0
D.ditremum (plerocercoid)	45.6	53	4.8	33.8	37.2	41.0
D.dendriticum (plerocercoid)	12.2	18.1	4.8	12.5	17.9	6.4
Cysts (plerocercoid)	98.9	96.4	61.9	85	91	87.2
Proteocephalus sp.	5.6	9.6	0	0	1.3	15.4
Acanthocephala sp.	6.7	3.6	9.5	98.8	3.8	9.0
Nematoda sp.	1.1	0	0	0	0	1.3

Appendix 4. The mean and range of the infection intensity by parasites on Arctic charr from Lake Norsjø 2018. The data is grouped by the sampling locations (Norsjø North. Mid and South).

Parasite infection	North		Mid		South	
	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
Total	2 - 130	25.0 ± 19.2	1 - 373	33.1 ± 48.1	1 - 36	5.2 ± 5.8
Copepod-transmitted parasites	1-127	24.5 ± 19.1	1 - 373	33.1 ± 48.1	1 - 36	4.9 ± 5.9
Plerocercoids	1 - 123	22.8 ± 18.0	1 - 372	30.3 ± 47.9	1 - 31	4.6 ± 5.3
A.coregoni	1	1.0 ± 0.0	-	-	-	-
S. edwardsii	1-2	1.2 ± 0.4	1 - 2	1.1 ± 0.3	1 - 3	1.2 ± 0.3
E. salvelini	1-13	2.7 ± 2.9	1 - 26	3.4 ± 4.1	1 - 6	2.0 ± 1.8
T.nodulosus (plerocercoid)	1-14	2.0 ± 2.3	1 - 12	2.0 ± 2.3	1 - 3	1.2 ± 0.5
T.crassus (plerocercoid)	2	2.0 ± 0.0	-	-	-	-
D.ditremum (plerocercoid)	1-23	2.5 ± 3.6	1 - 224	7.8 ± 33.0	1 - 2	1.3 ± 0.5
D.dendriticum (plerocercoid)	1-2	1.2 ± 0.4	1 - 3	1.3 ± 0.7	1 - 2	1.3 ± 0.5
Cysts (plerocercoid)	2-114	20.7 ± 16.8	1 - 156	26.3 ± 32.0	1 - 31	5.1 ± 5.8
Proteocephalus sp.	1-4	1.6 ± 12	1 - 9	2.9 ± 3.0	-	-
Acanthocephala sp.	1-2	1.2 ± 0.4	1	1.0 ± 0.0	1 - 4	2.0 ± 1.2
Nematoda sp.	1	1.0 ± 0.0	-	-	-	-

Appendix 5. The mean and range of the infection intensity by parasites on Arctic charr in Lake Norsjø 2018. The data is grouped by the different sampling season spring (May), summer (July), and fall (September).

Parasite infection	Spring		Summer		Fall	
	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
Total	1 - 160	27.0 ± 29.2	1 - 373	22.9 ± 44.6	1 - 130	19.4 ± 21.3
Copepod-transmitted parasites	1 - 160	27.4 ± 29.4	1 - 373	23.3 ± 44.8	1 - 127	19.4 ± 21.0
Plerocercoids	1 - 159	24.9 ± 28.2	1 - 372	22.0 ± 44.6	1 - 123	17.4 ± 20.2
A.coregoni	-	-	1	1.0 ± 0.0	-	-
S. edwardsii	1 - 2	1.1 ± 0.3	1 - 3	1.2 ± 0.6	1 - 2	1.2 ± 0.4
E. salvelini	1 - 26	4.4 ± 5.1	1 - 9	2.1 ± 1.9	1 - 11	2.5 ± 2.4
T.nodulosus (plerocercoid)	1 - 14	2.2 ± 2.7	1 - 12	1.8 ± 2.1	1 - 4	1.6 ± 0.9
T.crassus (plerocercoid)	2	2.0 ± 0.0	-	-	-	-
D.ditremum (plerocercoid)	1 - 15	2.6 ± 2.7	1 - 224	10.7 ± 40.5	1 - 10	2.3 ± 2.1
D.dendriticum (plerocercoid)	1 - 3	1.4 ± 0.7	1 - 3	1.2 ± 0.6	1	1.0 ± 0.0
Cysts (plerocercoid)	1 - 156	24.6 ± 27.6	1 - 148	18.2 ± 23.7	1 - 114	17.0 ± 19.4
Proteocephalus sp.	-	-	1	1.0 ± 0.0	1 - 9	2.5 ± 2.6
Acanthocephala sp.	1 - 3	1.6 - 0.8	1 - 4	2.0 ± 1.4	1 - 2	1.1 ± 0.3
Nematoda sp.	-	-	-	-	1	1.0 ± 0.0

Appendix 6. Mean abundance of parasite infection of Arctic charr from Lake Norsjø 2018. The data is grouped by the sampling seasons (spring, summer and fall) and the three sampling locations (Norsjø North, Mid and South).

Parasite infection	North	Mid	South	Spring	Summer	Fall
Total	24.7 ± 19.3	33.1 ± 48.1	4.5 ± 5.7	25.4 ± 29.0	22.6 ± 44.4	18.7 ± 21.2
Copepod-transmitted parasites	24.4 ± 19.1	33.1 ± 48.1	4.0 ± 5.7	25.0 ± 29.1	22.6 ± 44.4	18.4 ± 21.1
Plerocercoids	22.5 ± 18.1	30.3 ± 47.9	3.7 ± 5.1	22.7 ± 27.8	21.5 ± 44.2	16.5 ± 20.1
A.coregoni	0.01 ± 0.1	-	-	-	0.01 ± 0.1	-
S. edwardsii	0.1 ± 0.4	0.1 ± 0.4	0.3 ± 0.6	0.2 ± 0.5	0.2 ± 0.5	0.2 ± 0.4
E. salvelini	1.8 ± 2.7	2.5 ± 3.9	0.3 ± 1.0	2.3 ±4.3	1.2 ± 1.8	1.5 ± 2.2
T.nodulosus (plerocercoid)	1.0 ± 1.9	0.6 ± 1.6	0.4 ± 0.6	0.7 ± 1.9	0.7 ± 1.6	0.6 ± 1.0
T.crassus (plerocercoid)	0.02 ± 0.2	-	-	0.03 ± 0.2	-	-
D.ditremum (plerocercoid)	1.1 ± 2.7	4.1 ± 24.4	0.1 ± 0.3	0.9 ± 2.0	4.0 ± 25.2	0.9 ± 1.7
D.dendriticum (plerocercoid)	0.1 ± 0.4	0.2 ± 0.6	0.1 ± 0.3	0.2 ± 0.5	0.2 ± 0.6	0.1 ± 0.2
Cysts (plerocercoid)	20.3 ± 16.8	25.3 ± 31.8	3.2 ± 5.2	21.0 ± 26.9	16.6 ± 23.2	14.9 ± 19.0
Proteocephalus sp.	0.1 ± 0.5	0.3 ± 1.3	-	-	0.01 ± 0.1	0.4 ± 1.4
Acanthocephala sp.	0.1 ± 0.3	0.04 ± 0.2	0.2 ± 0.7	0.1 ± 0.4	0.1 ± 0.5	0.1 ± 0.3
Nematoda sp.	0.01 ± 0.1	-	-	-	-	1.3 ± 0.1