

Parallelism in parasite infections in two populations of polymorphic Arctic charr (*Salvelinus alpinus* L.) in northern Norway

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Summary

Parasitism is a ubiquitous life strategy that enhances local biodiversity and food web linkages. The composition and structure of a component community can vary widely across host populations of the same host species. Revealing the causes and consequences of geographical variation in parasite community composition is of great importance in order to determine parasites role in an ecosystem. Divergence in parasite infections among sympatric polymorphic Arctic charr is commonly associated with divergence in food and habitat preferences, and offers a great opportunity to test the factors determining parasite community composition. By contrasting the sympatric living morphs in Fjellfrøsvatn, and in Skogsfjordvatn, I aimed at assessing if the observed differences in feeding and habitat characteristics among the morphs, both within and across lakes, are reflected in their parasite community composition. The study revealed large intra-lake differences in parasite community between the sympatric morphs within and across lakes. The LO-morphs found in the littoral-pelagic habitat had higher parasite diversity than the PB-morphs occupying the profundal habitat. Morphs in the littoral-pelagic zone had also higher intensities of parasites transmitted through copepods and littoral amphipods, whereas morphs in the profundal had higher intensity of parasites transmitted through benthic amphipods. The highest parasite diversity was found in the piscivorous PP-morph residing in the profundal zone in Skogsfjordvatn. This morph also had highest parasite loadings, apparently accumulating parasites by predated upon the PB-morph, juvenile individuals from the LO-morph and sticklebacks. The study also revealed a parallelism in parasite species composition between the LO-and PB-morphs that occurred in both lakes. These similarities reflect the similar diet and habitat characteristics of the morphs, as well as the exposure to similar abiotic conditions in their respective habitats.

Introduction

Parasitism is an ubiquitous life strategy that considerably enhances local biodiversity and food web linkages, affecting host behavior and even regulating host abundance (Dobson et al. 2008). As parasites might have strong effects on their hosts, it is of great importance to characterize the determinants of parasite species diversity (Poulin and Morand 2000). However, to this date there is little understanding regarding the causes of geographical variation in parasite community composition, abundance and diversity (Poulin 2007). Revealing the causes and consequences of such variation in community composition is central to foster the understanding of evolutionary and ecological processes, such as speciation, as well as the dispersal and persistence of species (Levin 1992, Karvonen and Seehausen 2012).

Parasite communities are best defined at the individual and population levels (Henríquez and González 2014). The former refers to all parasites species found within a host individual (Bush et al. 1997). These communities, called infra-communities, are often short lived, with maximum lifespan equal to the host life span. Infra-communities are in constant turnover, with deceased parasites replaced by newer ones, which are recruited from the local species pool (Poulin 1997). The latter type of parasite community is the component community. The composition of a component community is influenced by the local availability of parasite species, thus including all parasite species exploiting the host population at one point in time (Bush et al. 1997). Parasite species may be added to this community following host migration from one locality to another (Poulin 2007).

Fish parasite communities are highly complex, being dynamic ecological systems that results from both evolutionary and ecological processes acting together at multiple levels (Alarcos and Timi 2012). Accordingly, no single host population is infected with all species of parasites known to exploit the host species simultaneously (Poulin 1997). Therefore, the composition and structure of a component community can vary widely across host populations of the same host species (Poulin et al. 2011). Variations may be due to both abiotic and biotic factors (Karvonen et al. 2013a). Abiotic factors account, for example, for geographical distances between host populations (Bell and Burt 1991), water temperature (Karvonen et al. 2013a) and lake morphometrics (Bell and Burt 1991). Biotic factors include host's age and immunological competence (Khan 2012), the rate at which the host can be colonized by parasites (Holmes and Price 1986), phylogenetic distance between host

populations (Holmes 1987), as well as host-species body size (Poulin and Leung 2011). Host ecology is considered to be one of the most important determinants of parasite composition (Kennedy 1978, Bush et al. 1990, Poulin 1995, Locke et al. 2014). For example, greater parasite diversity in hosts has been observed at higher trophic levels and in hosts with broad diets and access to more diverse prey (Chen et al. 2008). Piscivorous fish usually have higher diversity and loadings of parasites (Valtonen et al. 2010), especially of helminth species (Bell and Burt 1991), as parasites accumulate in predators through the food chain (Valtonen and Julkunen 1995). Some parasites are also able to re-establish in predatory fish, like e.g. salmonids feeding on sticklebacks (Bérubé and Curtis 1984, Sandlund et al. 1992). Finally, parasite species richness often correlates positively with body size (Bell and Burt 1991, Poulin 1995, Valtonen et al. 2010).

Many parasites of freshwater fish have complex life cycles, being transmitted from one host to another by consumption of infected hosts (Amundsen et al. 2009). Such trophically transmitted parasites usually have species specific intermediate host (Henrich et al. 2013). Dietary preferences towards a specific intermediate hosts may determine infection levels of a certain parasite in a host individual (Bush et al. 1990, Bell and Burt 1991). Some of the trophically transmitted parasite species might have a long life-span within its host (Black and Lankester 1980, 1981, Poulin et al. 1992), which thus may provide long-term information about each host individual habitat and feeding utilization. Parasites may therefore be used as markers to detect ecological differences between individuals of a host species, such as e.g. resource segregation (Knudsen et al. 2008, Karvonen et al. 2013b). This has been done for several freshwater fish species such as the yellow perch (*Perca flavescens*) (Bertrand et al. 2011), brook charr (*Salvelinus fontinalis*) (Bertrand et al. 2008), white fish (*Coregonus lavaretus*) (Knudsen et al. 2003, Karvonen et al. 2013b), three-spined sticklebacks (*Gasterosteus aculeatus*) (Maccoll 2009) and especially Arctic charr (*Salvelinus alpinus*) (Henricson and Nyman 1976, Frandsen et al. 1989, Dorucu et al. 1995, Knudsen et al. 1996, 1997, 2008).

Divergence in parasite infections among sympatric polymorphic species is commonly associated with divergence in food regimes and habitat, and this offers a great opportunity to test the factors determining parasite community composition (Karvonen and Seehausen 2012). When an ecotype or a morph represents a distinct dietary and habitat preference, the parasite community should retain similarities with similar ecotypes/morphs from other regions. Thus,

these parasite communities would be determined by biotic factors related to host ecology. Conversely, distinct morphs living in sympatry should also show some similarities regarding their parasite communities due to abiotic factors controlling them, like e.g. the short geographical distances between the host populations. Some of the best example of phenotypic variability in vertebrates comes from fish. Among them, the salmonid Arctic charr exhibits the greatest phenotypic variability, both within and across localities (Smith & Skulason, 1996), and it often occurs as several different morphs within the same lake (Klemetsen 2010). These sympatric living morphs differ in various biological parameters like coloration, ontogenetic niche shifts, growth pattern, age and size at sexual maturity, migratory behavior, diet and habitat use and parasite infection (Frandsen et al. 1989, Skulason and Smith 1995, Dorucu et al. 1995, Klemetsen et al. 1997, Byrne et al. 2000, Klemetsen 2002). Well-known examples of lakes holding sympatric morphs of Arctic charr, show that distinct morphs segregates in the upper water layers between the pelagic and littoral zone in respect to feeding ecology and habitat preference (Sandlund et al. 1992, Adams et al. 1998), as in Thingvallavatn in Iceland and Loch Rannoch in Scotland. The morphs in the upper water layers feed on zooplankton, surface insect and insect pupae, whereas the morphs in the littoral habitat feed on molluscs and insect larvae. Normally a piscivore niche is also exploited, where a piscivorous morph inhabits the pelagic zone, feeding on small fish like e.g. sticklebacks or juvenile individuals of charr (Malmquist et al. 1992, Sandlund et al. 1992, Adams et al. 1998).

In contrast to the above examples, lake Fjellfrøsvatn located in Northern-Norway, holds two genetically distinct morphs of Arctic charr that segregates in habitat and feeding ecology between the littoral-pelagic and profundal zones (Klemetsen et al. 1997, Klemetsen 2002, Knudsen et al. 2006). One of the morphs spawns in the littoral zone and mainly utilizes the littoral and pelagic habitat, feeding on zooplankton and littoral preys (*Gammarus* sp., gastropods and larval insect). It is called the littoral spawning omnivore morph (hereafter referred to as the LO-morph). The other morph is a small-sized morph that consistently resides in the profundal zone, spawn there in February-March, and feed upon profundal soft-bottom resources. It is called the profundal spawning benthivore morph (hereafter referred to as the PB-morph). These morphs are both temporally and spatially isolated in reproduction, and differ in life-history traits and morphology (Klemetsen et al. 1997).

Recently, a polymorphic population of Arctic charr was discovered in another north Norwegian lake, Skogsfjordvatn. There are three distinct morphs in the lake, diverging in

feeding ecology, habitat utilization, life-history traits and time and place of spawning (Skoglund 2013, Smalås et al. 2013). One of the morphs occupies the littoral-pelagic habitat feeding on zooplankton and zoobenthos (R. Knudsen, unpublished data) and spawns in shallow water in September (Smalås et al. 2013), resembling monomorphic populations of Arctic charr found elsewhere in northern Norway as well as the LO-morph in Fjellfrøsvatn. It is therefore also referred to as the littoral spawning omnivore morph (the LO-morph) (Skoglund 2013, Smalås et al. 2013). The LO-morphs in Fjellfrøsvatn and Skogsfjordvatn have similar habitat and diet characteristics, both residing and feeding predominantly in the littoral-and pelagic habitats, and utilizing a wide ecological niche. The two other morphs are found in the deep profundal zone (>20 m depth). One is a small-sized charr that feeds on soft bottom benthos similar to the PB-morph in Fjellfrøsvatn and is thus similarly referred to as the profundal spawning benthivore morph (or the PB-morph) (Skoglund 2013). This morph spawns in December at a young age (Smalås et al. 2013). The PB-morphs in Fjellfrøsvatn and Skogsfjordvatn also have similar habitat and diet characteristics, both being restricted to the profundal habitat. They are specialized on a few prey types found in the profundal zone, and thus have a narrow niche (Amundsen et al. 2008, R. Knudsen, unpublished data). The other morph found in the profundal zone in Skogsfjordvatn, is a large piscivore charr that feeds on the PB-morph, juvenile charr of the LO-morph, and three-spined sticklebacks (R. Knudsen, unpublished data). This morph spawns in the profundal zone mainly in November, and is called the profundal spawning piscivore morph (hereafter referred to as the PP-morph) (Smalås et al. 2013).

By contrasting the fish morphs in Fjellfrøsvatn and Skogsfjordvatn, I aimed at assessing if the observed differences in resource utilization in respect to feeding and habitat characteristics among the sympatric morphs, both within and across lakes, are reflected in their parasite community composition. As morphs with a wide niche are found to exhibit a higher parasite diversity compared to morphs that are restricted to more specific resources (Chen et al. 2008), I hypothesized that 1) the LO-morphs utilizing the littoral-pelagic habitat should harbor a more diverse parasite fauna than the profundal dwelling PB-morphs. Conversely, because of their narrow niche, 2) the parasite fauna of the PB-morphs was hypothesized to have the lowest parasite diversity among the studied morphs, whereas 3) the piscivore, long-lived and large PP-morph was hypothesized to have the highest parasite diversity. I further hypothesized that 4) the parasite communities of the morphs should also reflect the utilization of intermediate hosts restricted to their habitat, e.g. LO-morphs having a higher infection of

e.g. limnetic copepod- and littoral amphipod-transmitted parasites compared to the PB-morphs, whereas they have a higher infection of benthic copepod-transmitted parasites. Finally, due to similar ecological characteristics, 5) parasite communities were hypothesized to show some degree of similarity between the same morphs from distinct geographical locations (different lakes), reflecting strong biotic factors controlling them.

This study represents the first report of the parasite fauna of a profundal, piscivorous charr morph.

2. Materials and methods

2.1 The study lakes

This study was carried out in two dimictic, oligotrophic lakes, both located in subarctic Norway (fig. 1). The lakes are usually ice covered from December to May.

Fjellfrøsvatn (69° 05'N, 19° 20'E) is situated at 125 m above sea level in the Målselv River System (Balsfjord in Troms county). The surface area is 6.5 km² with a circumference of 13.88 km and a maximum depth of 88 m. The littoral zone (<12 m) represent about one-third of the lake surface area. The shore regions are mostly sandy or stony with very little vegetation, but some beds with submerged *Nitella* sp. occur in the 5-12 m depth zone. Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) are the only fish present in the lake. Fjellfrøsvatn is situated in a mixed forest landscape dominated by Scots pine (*Pinus silvestris*) and birch (*Betula pubescens*) and the bird community around the lake is dominated by black-throated diver (*Gavia arctica*), red-throated diver (*Gavia stellata*), red-breasted merganser (*Mergus serrator*) and tufted duck (*Aythya fuligula*) (R. Knudsen, pers. comm).

Skogsfjordvatn (69° 56' N, 19° 10'E) is situated on Ringvassøy in Troms. The lake has a surface area of 13 km² and a circumference of 38 km, constituting the biggest lake on an island in Norway. The main basin has a predominant depth of about 60-65 m with well-developed littoral, pelagic and profundal habitats. The southern part of the lake is dominated by large deep-water areas (max. 100 m), whereas the northern parts of the lake is dominated by shallow areas with several small islands. Skogsfjordvatn is located only 19 m above sea level and is connected to a marine fjord by a 1.6 km long river (Skogsfjordelva). This has resulted in a fish community consisting of both freshwater-resident and anadromous salmonids-including Arctic charr, brown trout and Atlantic salmon (*Salmo salar*). In addition to this, there are also a population of three-spined stickleback (*Gasterosteus aculeatus*) and a very small population of the catadromous European eel (*Anguilla anguilla*). The lake is situated in a mixed forest landscape dominated by birch (*Betula pubescens*). The bird community around Skogsfjordvatn is dominated by the common gull (*Larus canus*), herring gull (*Larus argentatus*) and Arctic tern (*Sterna paradisaea*) (R. Knudsen & L. Dalsbø, pers. comm).

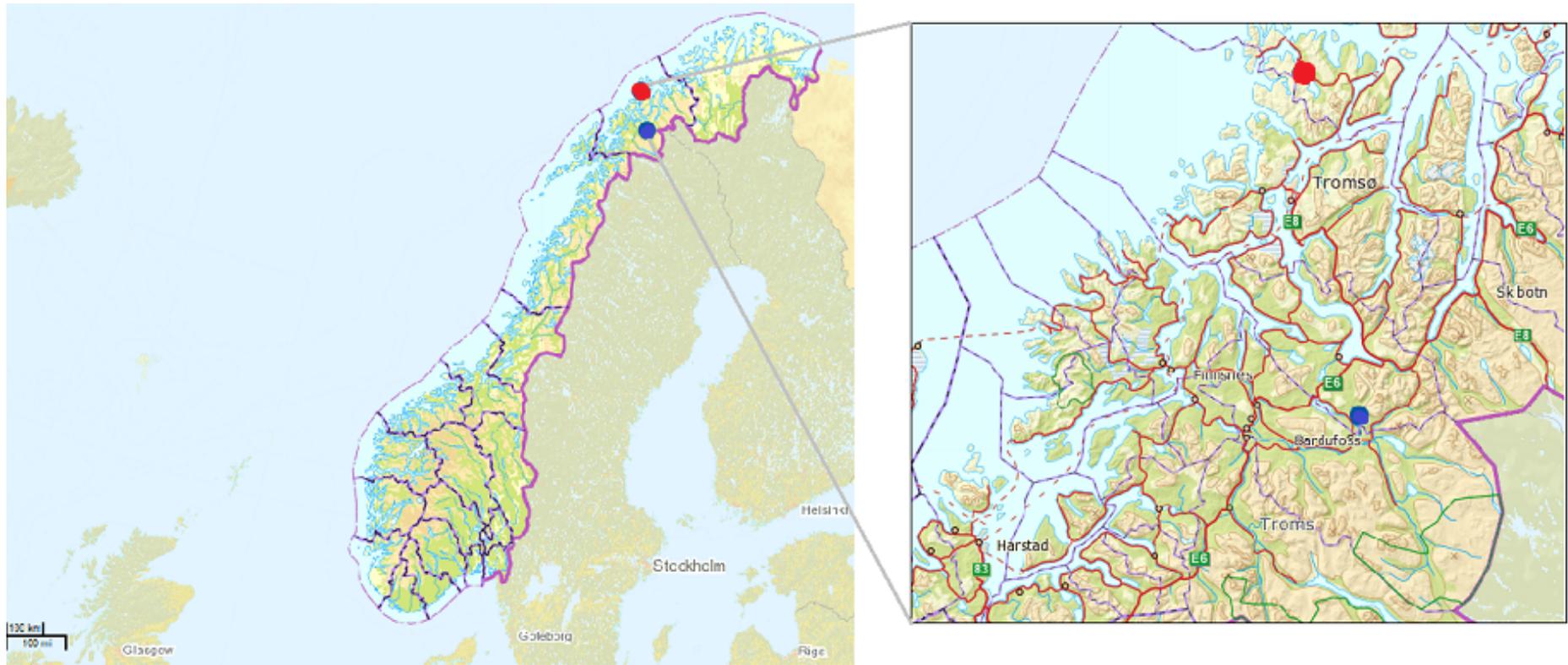


Figure 1. Skogsfjordvatn is situated ca. 70 km north of Tromsø (red dots) and Fjellfrøsvatn (blue dots) is situated ca. 115 km south of Tromsø.

2.2 Fish sampling

Arctic charr were sampled monthly from August to November (2012) in Skogsfjordvatn and from August to November (2010) and September (2012) in Fjellfrøsvatn. Fish were caught using gillnets in all main habitats (littoral, profundal, pelagic). Gillnets were set late in the evening and collected early the following day, giving each gillnet a fishing period of approximately 12 hours. Three different types of gillnets were used in this study in order to collect fish of different sizes in their respective habitats. Two of them were multi-meshed gillnets with a range of sizes. Survey benthic gillnets (OG) measuring 1.5 x 40 m are made up of eight panels, each 5 m long with bar mesh size 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm, whereas NORDIC gillnets measuring 1.5m x 30m are made up of twelve panels, each 2.5m long with bar mesh sizes ranging from 5-55 mm. The last type of gillnet that were used are referred to as standard gillnets (SG) measuring 1.5 x 30 m and with only a single mesh size. These benthic nets were set in the littoral habitat at in 0-12 m water depth and in the profundal habitat at 25-45 m depth. Pelagic charr were caught using survey floating nets (FGO) (measuring 6 x 40 m with bar mesh size 8, 10, 12.5 15, 18.5, 22, 26, 35 and 45 mm) that were placed at the surface in the pelagic habitat (with a minimum of 30 m water depth below).

Charr were sorted into different morphs associated to their external morphology, such as head and body shape/appearance and color. The LO-morph has a relatively small head compared to the body length, small eyes and red-orange spawning colors or silvery belly (immature), while the PB-morph has a relatively large, blunt head compared to its very small body size, large eyes and a yellow-green coloration with parr marks along the side of the body (Skoglund 2013, Smalås et al. 2013). The PP-morph has a slim, elongated body form, a large head with large teeth on the jaws, large eyes and a dark grey or black coloration with white spots (Skoglund 2013, Smalås et al. 2013).

Fish were measured (fork length, L_F) and weighed to the nearest gram. The gills were examined for gill-maggot (*Salmincola edwardsii*), which were enumerated when present. Furthermore, the otoliths were collected and stored in glasses filled with 96 % ethanol for later surface reading in order to estimate the age (Kristoffersen and Klemetsen 1991). The abdomen was cut open so that the sex and maturity status (1=non-spawning, 2=spawning, 3=spent spawners) of the fish could be stated. Nematodes occurring in the abdominal cavity, such as *Philonema oncorhynchi*, were enumerated. The ureter were examined for digeneans (*Phyllodistomum umblae*), which were noted as present or absent (Knudsen et al. 1997). The swim-bladder was removed and stored in a glass filled with 96 % ethanol for later examination for the nematode *Cystidicola farionis* that occurs in

Salvelinus spp. Furthermore, the stomach was cut off from the intestine and pyloric caeca. The intestines and pyloric caeca were carefully labeled and frozen down for later examination in the lab. The diet of Arctic charr was not analyzed in this study, but based on earlier findings (Knudsen et al. 1997, 2007, 2008, Klemetsen et al. 2003b). The stomach wall, visceral organs and potentially other organs infested with cysts of plerocercoids of *Diphyllbothrium* spp., or cyst located in the flesh of the fish, were put in a petri dish filled with digestion fluid (2 ml HCl, 5g pepsin and 9g NaCl in 1 liter water) and kept in room temperature (Knudsen and Klemetsen 1994). After a time interval of approximately 6 hours, larvae that had encysted themselves were picked out and preserved in glasses with 4 % formalin in 0.9 % saline solution. Some of the larvae needed more time to excyst, so the procedure was repeated after 12-16 hours. The species identification of *Diphyllbothrium* spp. was done later in the lab. Parasites located in the eyes of the charr (*Diplostomum* spp.) were not included in this study, due to the complexity of their identification and the limited time frame of this thesis work.

The total fish material (n=210) in this study includes fish of a wide age and length range (table 1).

Table 1. Overview of the total sample of Arctic charr from Fjellfrøsvatn and Skogsfjordvatn including sample size (n), mean length L_F (mm) \pm S.D with length range (min-max), and mean age \pm S.D with age range (min-max).

Lake	Morph	(n)	Mean L_F mm	Range (mm)	Mean age	Range (years)
Fjellfrøsvatn	F-PB	31	91.8 \pm 9.5	75-119	3.6 \pm 1.1	1-5.0
	F-LO	91	250.8 \pm 62.2	125-415	5.7 \pm 2.0	2-13.0
		122				
Skogsfjordvatn	S-PB	29	117.6 \pm 15.1	94-142	4.6 \pm 1.7	2-8.0
	S-LO	32	234.6 \pm 20.8	180-271	5.9 \pm 1.4	4-8.0
	S-PP	27	282.3 \pm 48.3	206-375	7.0 \pm 2.0	4-11.0
		88				

2.3 Parasite identification

In the laboratory, after defreezing the samples, the intestine and pyloric caeca was cut open all the way from the anal end to the pylorus and pyloric caeca, and the content was carefully taken out and put in a glass filled with water. The glass was shaken for 10 seconds in order to mix the content and the mixture was filtered through a fine filter (180 μ m) so that parasites and hard parts could be separated from the mucus. Adult cestodes (*Cyathocephalus truncatus*, *Eubothrium salvelini*, *Proteocephalus* sp.) and digeneans (*Crepidostomum* spp.) could then be picked out carefully from a

petri-dish under a dissecting microscope (6.5 – 40 x magnification). The different species were identified down to the species or genus level based on their external morphology, and enumerated and stored on labeled glasses with 96 % ethanol.

Plerocercoids of *Diphyllobothrium* spp. were identified as either *Diphyllobothrium ditremum* or *Diphyllobothrium dendriticum* based on scolex and body shape characteristics (Andersen and Gibson 1989). *D. ditremum* are small (< 2.5 cm) with a smooth body surface that lacks any signs of segmentation. The scolex is extruded and has usually a more white coloration than the rest of the body. *D. dendriticum* are bigger (~10 cm) with a wrinkled body surface that appears to be segmented. The scolex is partly retracted and has the same coloration as the rest of the body. The *Crepidostomum* species found in these lakes are *Crepidostomum meteocus* and *Crepidostomum farionis*. Some of the parasite data from Fjellfrøsvatn used in this study was already processed and the identification of the two different species was not carried out, therefore they were grouped together as *Crepidostomum* spp. in the present study. An earlier study of these species in Skogsfjordvatn has shown that *C. farionis* is the only *Crepidostomum* species present in that lake (Kennedy 1978). *P. umblae* was just registered as present/absent in the ureter. It is therefore only represented in the prevalence data (fig.6). Eleven different parasite species were recorded from Arctic charr in the two lakes (table 2). Some of the nematodes were difficult to identify and were not included in the result presentation.

The parasite species that was expected to be found in the lakes, were based on findings from Kennedy (1978) in Skogsfjordvatn and Knudsen et al. (1997) in Fjellfrøsvatn. The swim-bladder nematode (*C. farionis*) has been registered in the LO-morph from Fjellfrøsvatn. Therefore, the fish from Fjellfrøsvatn were examined in this study, as well as thirty random Arctic charr from Skogsfjordvatn. The swim-bladder nematode was only found in the LO-morph in Fjellfrøsvatn, whereas it was not found in Skogsfjordvatn. It is also known that the nematode *Capillaria salvelini* occurs in the intestine in fish from Skogsfjordvatn (Kennedy 1978), but the life cycle of this parasite is unknown (Moravec 1994).

Most of the parasite in the present study are transmitted to the fish by species-specific intermediate hosts (table 2), such as pelagic copepods (*D. ditremum*, *D. dendriticum*, *Proteocephalus* sp. and *E. salvelini*), the amphipod *Gammarus lacustris* (*C. truncatus* and *C. farionis*) and insect larvae (*P. umblae* and *Crepidostomum* spp.). The only parasite species with a direct life cycle is the gill-maggot *S. edwardsii* (Hoffman 1998).

Table 2. Latin and Norwegian names, main transmission and fish host for the parasite species registered in Skogsfjordvatn and Fjellfrøsvatn.

Parasitespecies	Norwegian names	Class	Intermediate host	Fish host
<i>Crepidostomum spp.</i>	Tarmikter	D	<i>Gammarus</i> spp., Mayfly-nymph	Charr/Trout
<i>Phyllodistomum umblae</i>	Nyreikter	D	<i>Gammarus</i> spp., Stonefly-nymph	Charr/Trout
<i>Cyathocephalus truncatus</i>	Marflomark	C	<i>Gammarus lacustris</i>	Charr/Trout
<i>Eubothrium salvelini</i>	Røyemark	C	Copepoda	Charr
<i>Diphyllobothrium dendriticum</i>	Måke-mark	C	Copepods	Charr/Trout
<i>Diphyllobothrium ditremum</i>	Fiskeandmark	C	Copepods	Charr/Trout
<i>Proteocephalus sp.</i>		C	Copepoda	Charr/Trout
<i>Capillaria salvelini</i>		N	Unknown	Charr/Trout
<i>Cystidicola farionis</i>	Svømmeblæremark	N	<i>Gammarus lacustris</i>	Charr/Trout
<i>Philonema oncorhynchi</i>		N	Copepoda	Charr/Trout
<i>Salmincola edwardsii</i>	Gjellelus	A	-	Charr

D= Digenean, C= Cestode, N= Nematoda and A= Arthropoda

2.4 Central parasitological terms

The terms prevalence, mean intensity and abundance are used according to Bush et al. (1997). Prevalence of infection was calculated for each parasite species, whereas mean intensity and mean abundance were calculated for each parasite species, except for *P. umblae*.

Prevalence (expressed as percentage) is the proportion of a particular host species population infected with one or more individuals of a particular species of parasite (100x total number of host infected/total number of host examined).

Mean intensity is the average intensity of a particular species of parasite among the infected members of a particular host species (Total number of parasites of a given species/total number of infected host).

Mean abundance is the total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of hosts of that species examined (Total number

of parasites from a given species/total number host examined- including both infected and uninfected hosts).

2.5 Diversity

Species richness (the number of species per unit area) is the simplest way to measure diversity (Brown et al. 2007). This measure should not be used alone because of its sensitivity to the number of individuals and samples collected, and because it gives just as much weight to those species which have very few individuals as to those which have many individuals (Krebs 1989). Evenness is a measure of the relative abundance of the different species making up the richness of an area. Comprehensive measures of species diversity should include both evenness, as well as species richness (Krebs 1989). Heterogeneity is a concept of diversity that combines species richness and evenness. To describe heterogeneity, Simpson's reciprocal index was used. The use of $1/D$ instead of the original formulation of Simpson's index ($1-D$), ensures that an increase in the reciprocal index reflects an increase in diversity (the higher the value, the greater the diversity)(Magurran 1988). This index varies from 1 to s , where s is the total number of species in the sample. A high number indicates an even distribution of the species throughout the community, while a low number indicates that there are few species present or one of the species is dominating the community. This measure is the probability that two individuals chosen at random will be different species

$$1/D = 1 / \sum p_i^2$$

Where $1/D$ = Simpson's reciprocal index, P_i = proportion of species i in the community.

Evenness is measured: D/D_{\max}

Where D = observed index of species, D_{\max} =maximum possible index of diversity

The Simpson's index is heavily weighted towards the most dominant- and more common species (Krebs 1989). A commonly used diversity index which is more sensitive to the presence of rare species, is the Shannon-Wiener Index (H') (Krebs 1989)

$$H = - \sum_{i=1}^s p_i \log_2 p_i$$

Where H' = index of species diversity, s = number of species, p_i = Proportion of total sample belonging to i species. Evenness is based on the Shannon-Wiener function

$$J' = H'/H'_{\max}$$

J' = evenness measure (0-1), H' = Shannon-Wiener function, H'_{\max} = Maximum value of H' = \log_2

2.6 Similarity

A simple measure of similarity that is often used to measure similarities between communities (sites) is the Renkonen index of similarity (P) (Krebs 1989). This is a measure based on relative (proportional) abundances of individuals of composite species,

$$p_i = n_i / \sum n_i$$

It is very little affected by differences in sample size and diversity between areas and thus is one of the best indices of similarity (Krebs 1989). This index was used to calculate similarity between morphs within and across localities.

2.7 Data analysis

Empirical surveys have shown that parasite counts rarely follow normal distribution, as macro-parasites tend to be aggregated across their host populations, where most host individuals harbor low numbers of parasites, and a few are host to many parasites (Shaw and Dobson 1995). Due to the non-normality and non-homogeneity of the variances of the data set (Kolmogorov–Smirnov test, Shapiro-Wilk test; both $P < 0.001$), a Mann-Whitney U test and Kruskal-Wallis test were used to evaluate differences in medians in the distribution of each parasite species and the parasite species richness between morphs within one lake, and between similar morph across lakes (Krebs 1989, Townend 2002). Mann-Whitney U test is a technique to test whether the medians of two unmatched samples are different from each other, where the values of observations are converted into ranks (Fowler et al. 1998, Ennos 2007). A Kruskal-Wallis test was used for comparing more than two samples (in Skogsfjordvatn), whether they originate from the same distribution. For all tests $P < 0.05$ was considered statistically significant.

Software used for computing statistical analysis and creating graphs include MYSTAT 12 (student version of SYSTAT 12) and Microsoft Excel 2010.

3. Results

3.1 Parasite diversity

In total, ten different parasite species were recorded in Arctic charr in Fjellfrøsvatn. The highest parasite diversity was found in the LO-morph, which harbored all ten species. This was also supported by the Simpson's reciprocal index and Shannon-Wiener index, where the LO-morph showed the highest scores in Fjellfrøsvatn (table 3). Moreover, a maximum of nine different parasite species was found in one individual from the LO-morph in Fjellfrøsvatn, and over 50 % of the fish was infected with 3-5 species (fig. 2). In contrast, the PB-morph in Fjellfrøsvatn had a much lower parasite diversity. Only four out of the ten different parasite species present in the lake were observed in the PB-morph. The low parasite diversity is also supported by the Simpson's reciprocal index and Shannon-Wiener index, where the PB-morph had low scores (table 3). Furthermore, the highest number of parasite species present in one individual from the PB-morph was three, and 67 % of the fish from this population harbored only one or two parasite species each (fig. 2). Hence, the LO-morph had a significantly higher number of parasite species present compared to the PB-morph in Fjellfrøsvatn (Mann-Whitney *U* Test; $P < 0.01$).

In total, ten different parasite species were recorded in Arctic charr in Skogsfjordvatn. The highest parasite diversity was found in the PP-morph, which harbored eight different parasite species and had the highest score both for the Simpson's reciprocal and the Shannon-Wiener index (table 3). Furthermore, the highest number of parasite species recorded in one individual of the PP-morph, was six, and 60 % of the fish harbored between 4-5 different parasite species each (fig. 2). The LO-morph in Skogsfjordvatn harbored nine different parasite species, but had slightly lower parasite diversity than the PP-morph revealed by the Simpson's reciprocal and Shannon-Wiener indices (table 3). The highest number of parasite species in one individual from the LO-population in Skogsfjordvatn was five, and 72 % of the fish from this population harbored between 2-4 species each (fig. 2). In contrast, the PB-morph harbored the lowest parasite diversity in Skogsfjordvatn, with only five different parasites and relatively low scores for the Simpson and Shannon-Wiener indices (table 3). A maximum of four different parasite species was found in one individual, but 76 % of the PB-morph individuals harbored only one or two species each (fig. 2). The PP-morph had significantly higher numbers of different parasite species than both the LO-and the PB-morph in Skogsfjordvatn (Mann-Whitney *U* Test; $P < 0.001$), whereas the LO-morph had significantly higher

numbers of different parasite species than the PB-morph in Skogsfjordvatn (Mann-Whitney *U* Test; $P < 0.001$).

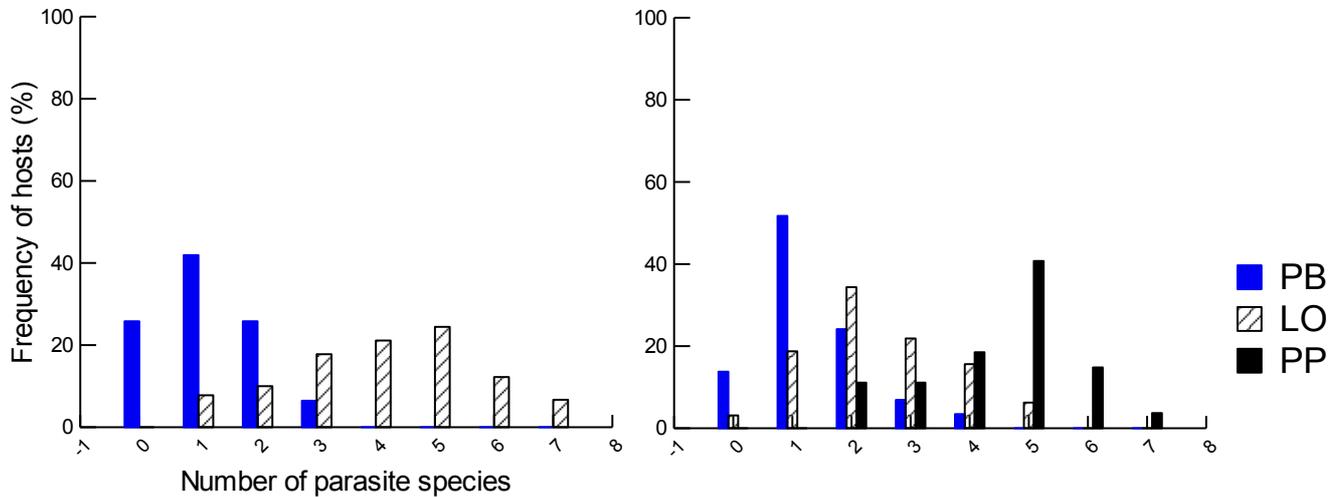


Figure 2. Distribution (%) of the number of parasite species per host from the PB-morph (blue bars), the LO-morph (striped bars) and the PP-morph (black bars) in Fjellfrøsvatn (left) and Skogsfjordvatn (right).

Table 3. Species richness, Simpson's reciprocal index and Shannon-Wiener index from all sympatric morphs (LO-, PB and PP-morphs) of Arctic charr from Fjellfrøsvatn and Skogsfjordvatn, with evenness given in the parentheses.

	FJELLFRØSVATN		SKOGSFJORDVATN		
	PB	LO	PB	LO	PP
Species richness	4	8*	5	8*	8
Simpson Index	1.47 (0.37)	2.49 (0.28)	2.44 (0.49)	3.43 (0.43)	3.77 (0.47)
Shannon-Wiener	0.81 (0.40)	1.72 (0.54)	1.60 (0.69)	2.08 (0.69)	2.22 (0.74)

**Phyllodistomum umblae* is not included in the species richness

3.2 Parasite community composition

The parasite community in the LO-morph from Fjellfrøsvatn was numerically dominated (57 %) by the swim-bladder nematode *C. farionis* (fig. 3). Furthermore, *Crepidostomum* spp. constituted 25 % of the community, whereas *E. salvelini* and *D. ditremum* constituted ca. 7 % each. In the LO-morph *Proteocephalus* sp. was nearly not present (0.3 %) and also gill-maggot, *C. truncatus* and *D. dendriticum* had low contributions to the total parasite community in this morph. In contrast to the LO-morph, the parasite community in the PB-morph in Fjellfrøsvatn was dominated by *Proteocephalus* sp. (80 %), whereas *Crepidostomum* spp. contributed 18 % and *E. salvelini* and *D. ditremum* approximately 1 % each.

The parasite community in the LO-morph in Skogsfjordvatn was composed of several parasite species, of which none strongly dominated the community (fig. 3). However, *Proteocephalus* sp. (38.7 %), *Crepidostomum* spp. (33.3 %) and *E. salvelini* (16.2 %) constituted nearly 90 % of the total parasite community of this morph. The parasite community in the PB-morph from this lake was in contrast dominated by *Crepidostomum* spp. (58 %). Furthermore, *Proteocephalus* sp. (24 %) was the second-most represented species, followed by *E. salvelini*. The PP-morph had the highest heterogeneity in respect to parasite community composition with *E. salvelini* (42 %) and *D. dendriticum* (24 %) as the most commonly represented species. *Proteocephalus* sp. and *Crepidostomum* spp. had a very low contribution to the parasite community in this morph compared to the other two morphs in Skogsfjordvatn.

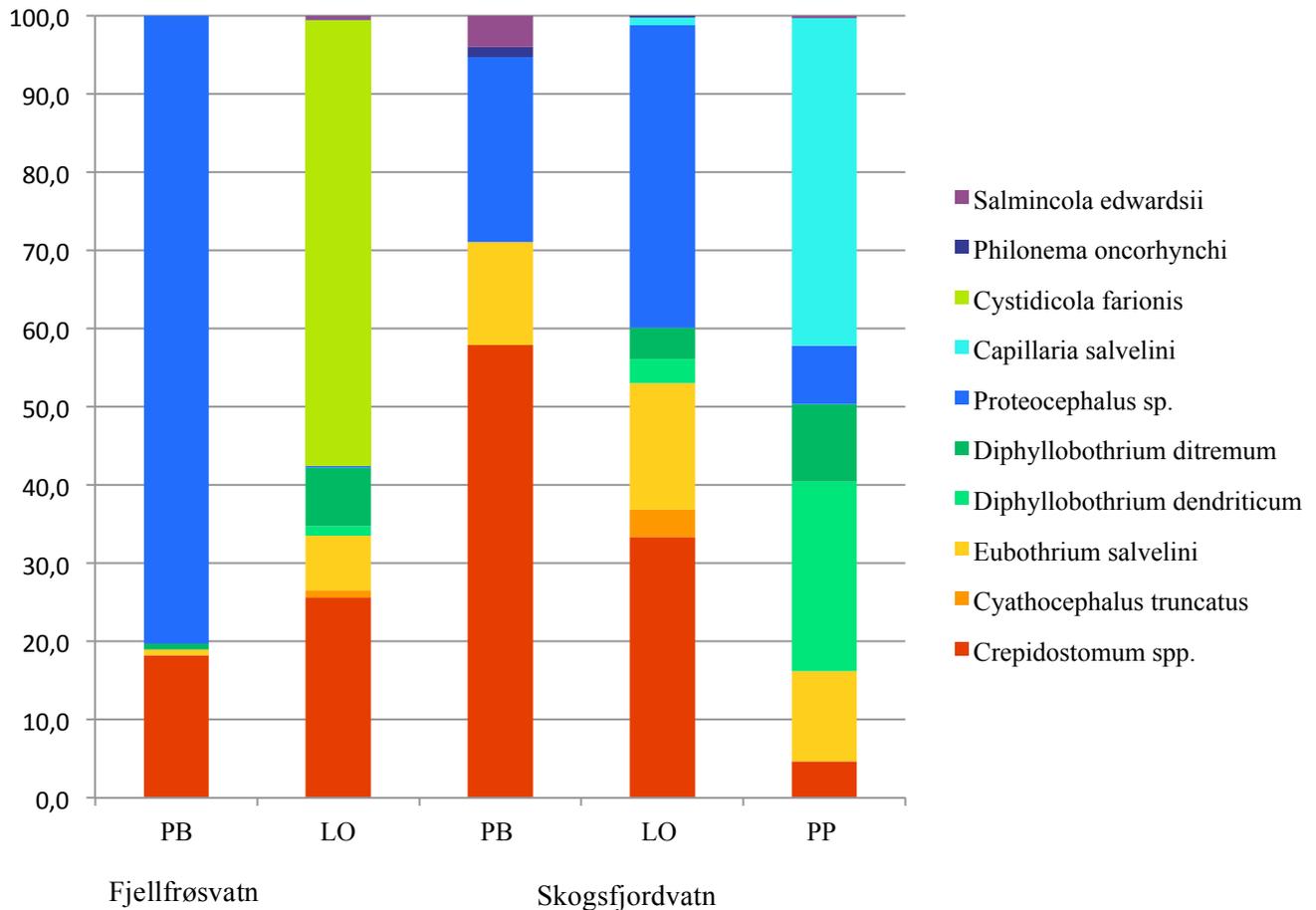


Figure 3. Species composition of the parasite community (%) in the PB- and LO-morphs from Fjellfrøsvatn (left) and in the PB-, LO- and PP-morphs in Skogsfjordvatn (right). Color-codes for the different parasite species is given at the right side.

3.3 Similarities in parasite communities

Altogether, the lowest percent similarity in parasite community was found between the PB- and LO-morph in Fjellfrøsvatn, with only 20 % overlap (fig. 4). In contrast, the PB- and LO-morph in Skogsfjordvatn showed a surprisingly high degree of similarity (70 %). The parasite communities of the PB- and PP-morphs in Skogsfjordvatn were in comparison very different, with only 24 % similarity (fig. 4). A slightly higher similarity (32 %) was found between the LO-morph and the PP-morph from the same lake. In respect to similarities between the corresponding morphs from the two lakes, a 39 % similarity was found in the parasite community of the LO-morphs, whereas the similarity was 43 % between the PB-morphs.

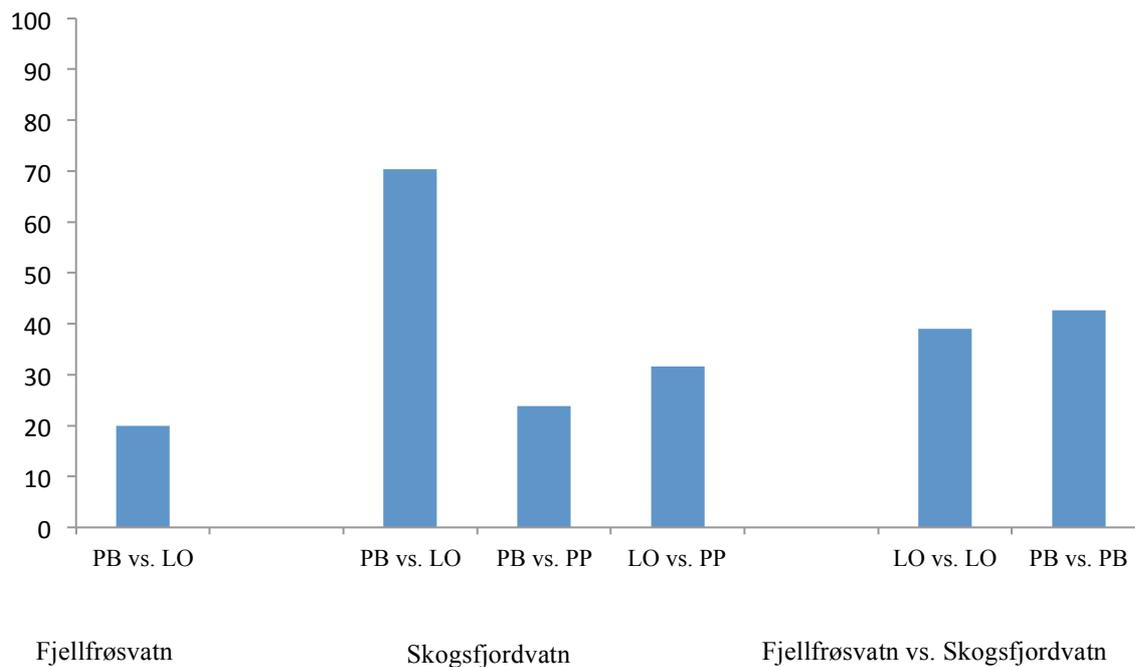


Figure 4. Percent similarity (% on the Y-axis) of parasite communities between different morphs within Fjellfrøsvatn (left) and Skogsfjordvatn (the middle) and between the LO-morphs and PB-morphs from both lakes (right).

3.4 Total parasite burden/loading

In total, 16 265 parasite individuals were recorded among the examined fish (n=122) of the two morphs in Fjellfrøsvatn, which gives a total mean parasite loading of 133.3 per individual.

Crepidostomum spp. and *C. farionis* constituted 82 % of the total loadings (table 1 in appendix).

Over 40 % of the fish from the LO-morph in Fjellfrøsvatn had 100-1000 parasites each (fig. 5). In contrast, 27 % of the fish had 1-15 parasites each. The highest number recorded in one individual from the LO-morph was 1357 parasites, while the lowest number was 2 parasites. The highest number of parasites recorded in one individual from the PB-morph in Fjellfrøsvatn was 27.

Furthermore, 65 % of the fish from this population had between one and ten parasites each (fig. 5). However, 26 % of the individuals from this population were totally free of parasites. The mean number of parasites per individual was significantly higher in the LO-morph than the PB-morph (Mann-Whitney *U* Test; $P < 0.01$).

Among the examined fish (n=88) of the three morphs in Skogsfjordvatn, a total of 1933 parasite specimens were recorded, which gives a total mean parasite loading of 22 per individual. Among these, the most numerous species were *C. salvelini* and *Proteocephalus* sp., which constituted 46 % of the total parasite loadings in the lake (table 1 in appendix). Nearly 50 % of the fish from the LO-

morph in this lake harbored only 1-5 parasites each (fig. 5). The highest parasite loading found in an individual from the LO-morph was 87 parasites, and only one fish was found without any parasites. In contrast, the highest number of parasites found in one individual from the PB-morph in Skogsfjordvatn was only 13. Similarly, over 70 % of the fish from the PB-morph was inhabited by only 1-5 parasite individuals, while 14 % of the fish from this morph were free of parasites. Hence, the mean number of parasites per individual was significantly higher in the LO-morph than in the PB-morph (Mann-Whitney *U* Test; $P < 0.01$). The most parasite rich morph in Skogsfjordvatn was the PP-morph, with a maximum loading of 230 parasites in one individual fish. Over 40 % of the fish from this population had between 16 and 30 parasites each (fig. 5), where the lowest parasite loading found in an individual was eight. The mean number of parasites per individual was significantly higher in the PP-morph than in the LO-morph, as well as in the PB-morph (Mann-Whitney *U* Test; $P < 0.01$).

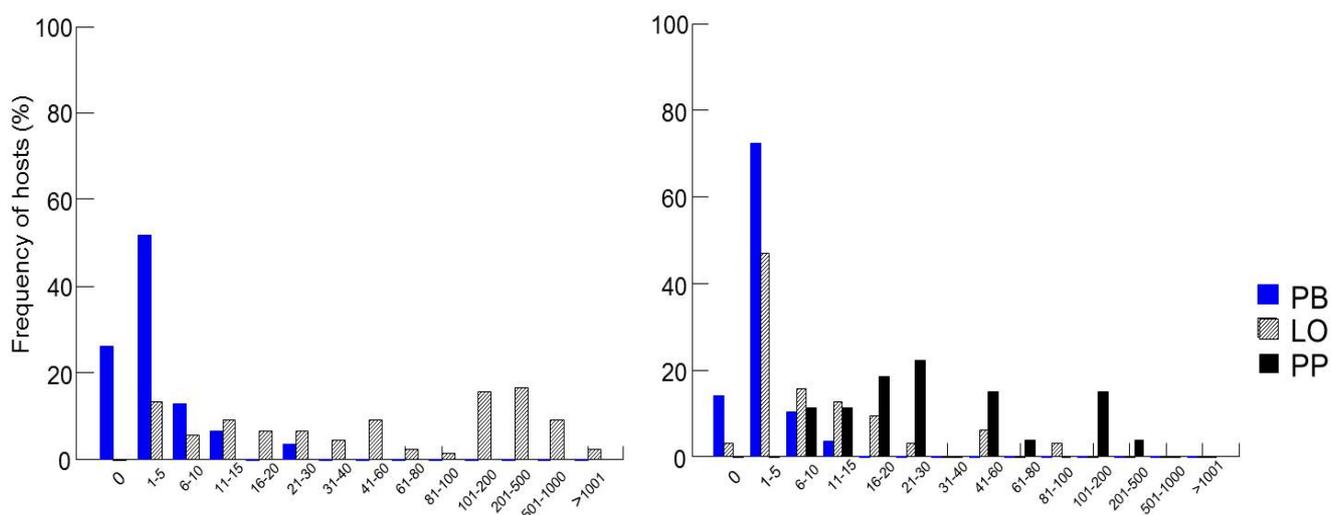


Figure 5. Frequency distribution of the total number of parasites per host (not dependent of species) in the PB-population (blue bars), LO-population (striped bars) and the PP-population (black bars) in Fjellfrøsvatn (left) and Skogsfjordvatn (right).

3.5 Prevalence of the parasite species

In Fjellfrøsvatn, 76 % the fish from the LO-morph were infected with *Crepidostomum* spp., while *P. umblae* (95 %) and *E. salvelini* (92 %) infected almost all of the fish in this population (fig. 6). The swim-bladder nematode *C. farionis* was only found in the LO-morph in Fjellfrøsvatn, with a prevalence of 77 %. The distribution of the two *Diphyllobothrium* species was uneven, were *D. ditremum* had a prevalence of 70 %, while *D. dendriticum* had a prevalence of 48 %. In contrast, *Proteocephalus* sp. (11 %), the gill-maggot (19 %) and *C. truncatus* (16 %) all showed a low prevalence in the LO-morph in Fjellfrøsvatn. Furthermore, *Proteocephalus* sp. (68 %) and *Crepidostomum* spp. (39 %) were the most prevalent parasite species the PB-morph in Fjellfrøsvatn, while *E. salvelini* and *D. ditremum* had an equally low prevalence (3 %). The individuals from the PB-morph in this lake were not infected with any nematodes.

The parasites with highest prevalence in the LO-morph from Skogsfjordvatn, was *Proteocephalus* sp. (75 %) and *P. umblae*. (85 %) (fig.6). The latter species, along with *C. truncatus* (19 %) was only found in the LO-morph among the sympatric morphs in Skogsfjordvatn. Furthermore, *Crepidostomum* spp. (56 %) and *E. salvelini* (44 %) were more prevalent than both *D. dendriticum* (22 %) and *D. ditremum* (19 %) in the LO-morph. The intestinal nematode *C. salvelini* was detected in some of the individuals from this morph (n=2), but only from bigger (> 240 mm) and older (> 6 years) fish caught in the pelagic habitat. The gill-maggot was not found on the LO-morph. Furthermore, *Crepidostomum* spp. (45 %) and *Proteocephalus* sp. (41 %), followed by *E. salvelini* (24 %), were the most prevalent parasites in the PB-morph in Skogsfjordvatn. Moreover, the gill-maggot (10 %) and *P. onchorhynchi* (3 %) showed low prevalence in the PB-morph. Furthermore, *E. salvelini* and *C. salvelini* (89 %) were the most prevalent parasites in the PP-morph in Skogsfjordvatn. The prevalence of *Diphyllobothrium* spp. (both of 63 %) was over twice as high in the PP-morph than the other morphs from this lake. The PP-morph had higher prevalence of *Proteocephalus* sp. (63 %) and *Crepidostomum* spp. (52 %) than the PB-morph, but lower than the LO-morph from the same lake.

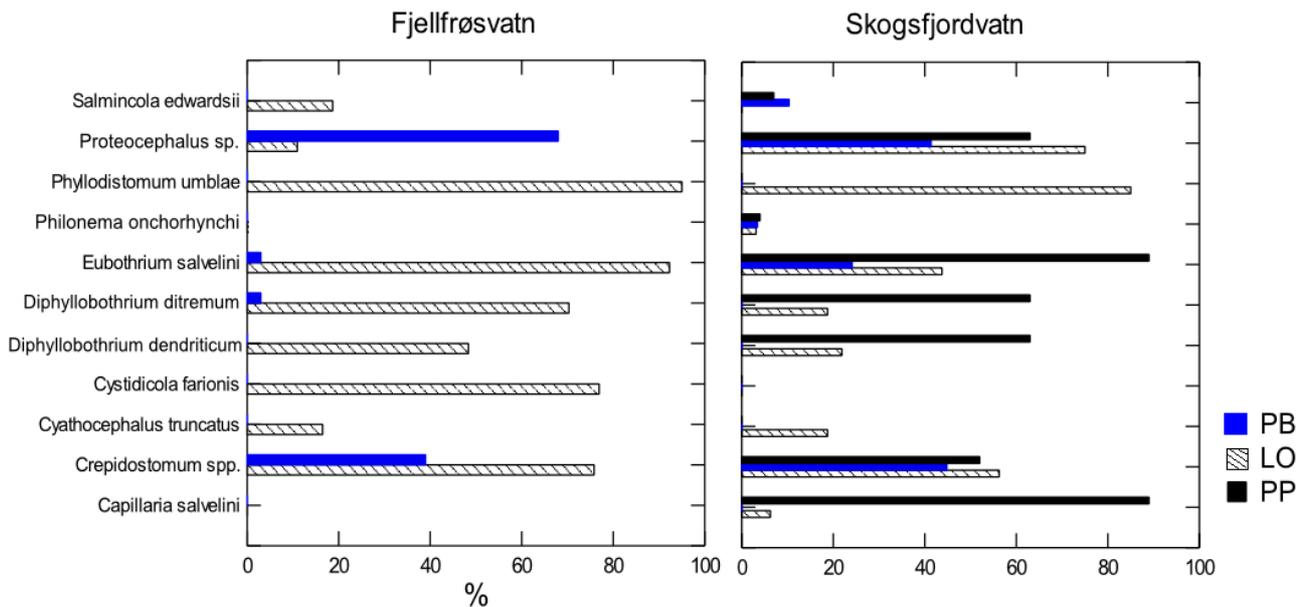


Figure 6. Prevalence (%) of the different parasite species found in the LO-morph (striped bars), PB-morph (blue bars) and PP-morph (black bars) in Fjellfrøsvatn and Skogsfjordvatn

3.6 Mean intensity and abundance

The mean intensity (see fig. A1 in appendix for all parasite species) and abundance (fig. 7) for most of the parasite followed generally the same trends (table A2 in appendix). The details of the differences in parasite infection between the morphs, based on a Mann-Whitney U test and Kruskal-Wallis test is given in table A3 in appendix.

The mean abundance (fig. 7) for the gill-maggot was in general very low in both lakes, but the highest levels were found in the LO-morph in Fjellfrøsvatn (fig. 7). The nematode *P. onchorhynchi* was not found in Fjellfrøsvatn, whereas the mean intensity and abundance of this parasite was equally low in the three morphs in Skogsfjordvatn (fig. 7). The LO-morphs in both lakes were the only morphs infected with the amphipod-transmitted parasite (*C. truncatus*), but there were not found significant differences in the infection of *C. truncatus* between them (see details in appendix). The PB-morph in Fjellfrøsvatn had significantly higher infection of *Proteocephalus sp.* than in the LO-morph (fig.7). In contrast, the LO-morph in Skogsfjordvatn had significantly higher infection of *Proteocephalus sp.* than in the PB-morph in Skogsfjordvatn (fig. 7). There were not found significant differences in infection of *Proteocephalus sp.* between the LO-and PP-morph in Skogsfjordvatn, whereas the PP-morph had significantly higher infection of this cestode compared to the PB-morph (fig. 7). The LO-morph in Skogsfjordvatn had significantly higher infection of

Proteocephalus sp. than in the LO-morph in Fjellfrøsvatn, whereas the PB-morph in Fjellfrøsvatn had significantly higher infection of *Proteocephalus* sp. than in the PB-morph in Skogsfjordvatn (fig. 7).

There were large differences in the infections of *Diphyllobothrium* spp. between the two morphs in Fjellfrøsvatn. In Fjellfrøsvatn, *D. dendriticum* was not found in the PB-morph, whereas *D. ditremum* was only found in one individual, thus the LO-morph had higher mean abundance of both species than in the PB-morph (fig. 7). The mean abundance of *Diphyllobothrium* spp. in Skogsfjordvatn was low for both the PB-and LO-morph (table A2 in appendix) and the PP-morph had significantly higher infection of both *Diphyllobothrium* species than in the other morphs in Skogsfjordvatn. The PP-morph had also higher infection of *D. dendriticum* than in the PB-and LO-morphs in Fjellfrøsvatn, whereas the LO-morph in Fjellfrøsvatn had higher infection of *D. ditremum* than in the PP-PB and LO-morph in Skogsfjordvatn (fig. 7).

Only one individual of the PB-morph in Fjellfrøsvatn was infected with *E. salvelini*, hence the low mean intensity and abundance (table A2 in appendix). For both lakes, the infection of *E. salvelini* was significantly higher in the LO-morphs than in the PB-morphs. The infection of *E. salvelini* was significantly higher in the PP-morph than in the LO-morph in Skogsfjordvatn. The LO-morph in Fjellfrøsvatn had significantly higher infection of *E. salvelini* than the LO-morph in Skogsfjordvatn (fig. 7), whereas the PB-morph in Skogsfjordvatn had significantly higher numbers of *E. salvelini* than in the PB-morph in Fjellfrøsvatn.

The infection for *Crepidostomum* spp. was significantly higher in the LO-morph than in the PB-morph in Fjellfrøsvatn. There were not found any significant differences in the infection between the morphs in Skogsfjordvatn, or between the PB-morphs in Fjellfrøsvatn and Skogsfjordvatn. The LO-morph in Fjellfrøsvatn had significantly higher numbers of *Crepidostomum* spp. than in the LO-morph in Skogsfjordvatn (fig. 7).

The PP-morph and LO-morph in Skogsfjordvatn was the only morphs infected *C. salvelini*, but the PP-morph had significantly higher numbers for *C. salvelini* than in the LO-morph (fig. 7). Only the LO-morph in Fjellfrøsvatn was infected with *C. farionis* and in general, the mean intensity and abundance were very high (table A2 in appendix).

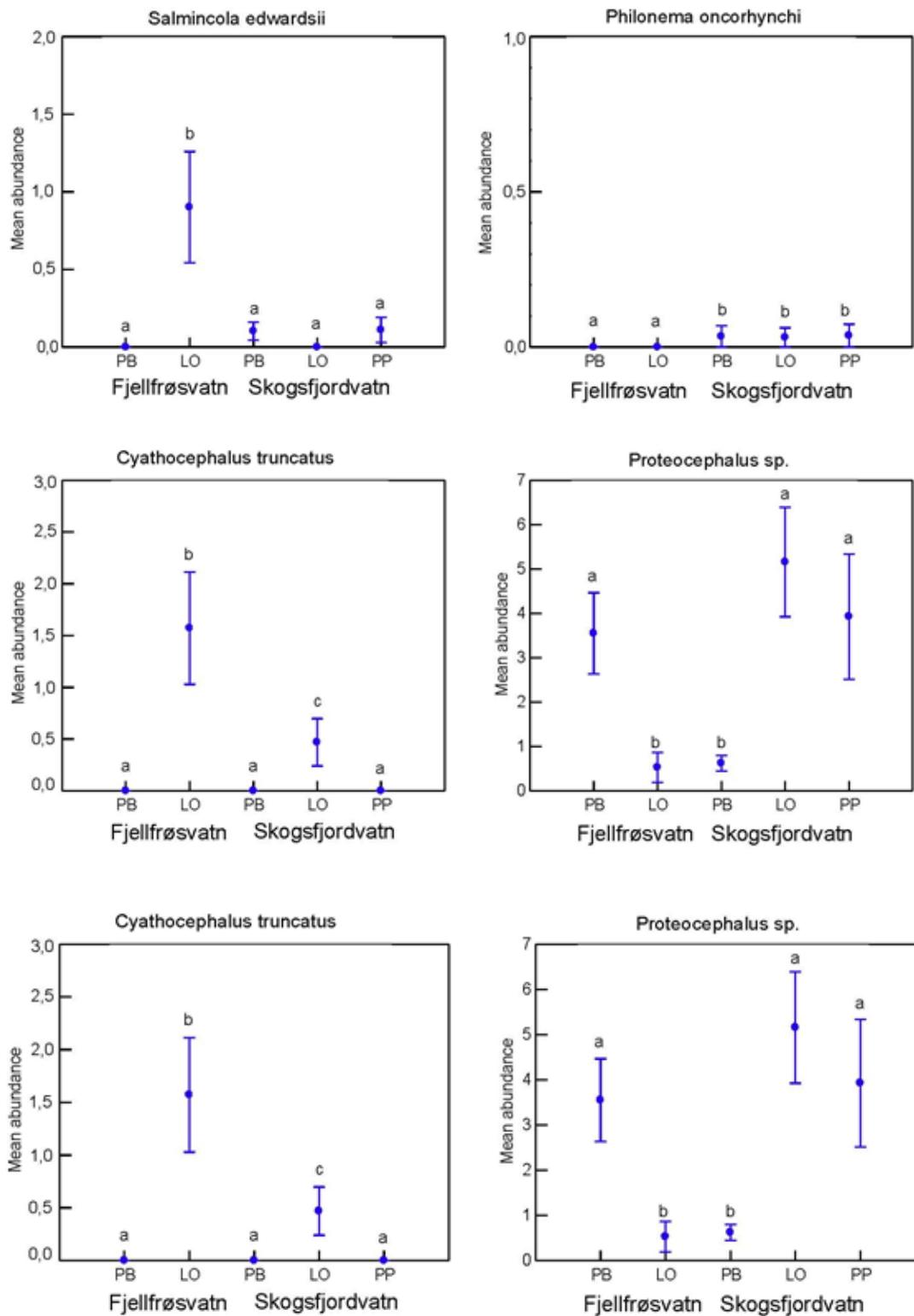


Figure 7. Mean abundance (\pm S.E) of different parasite species* in the Arctic charr morphs in Fjellfrøsvatn and Skogsfjordvatn. Unequal letters between morphs represent significant differences in infection between morphs (M-W U, $P < 0.05$), whereas equal letters represent no significant difference (M-W U, $P > 0.05$) **P. umblae* are not included

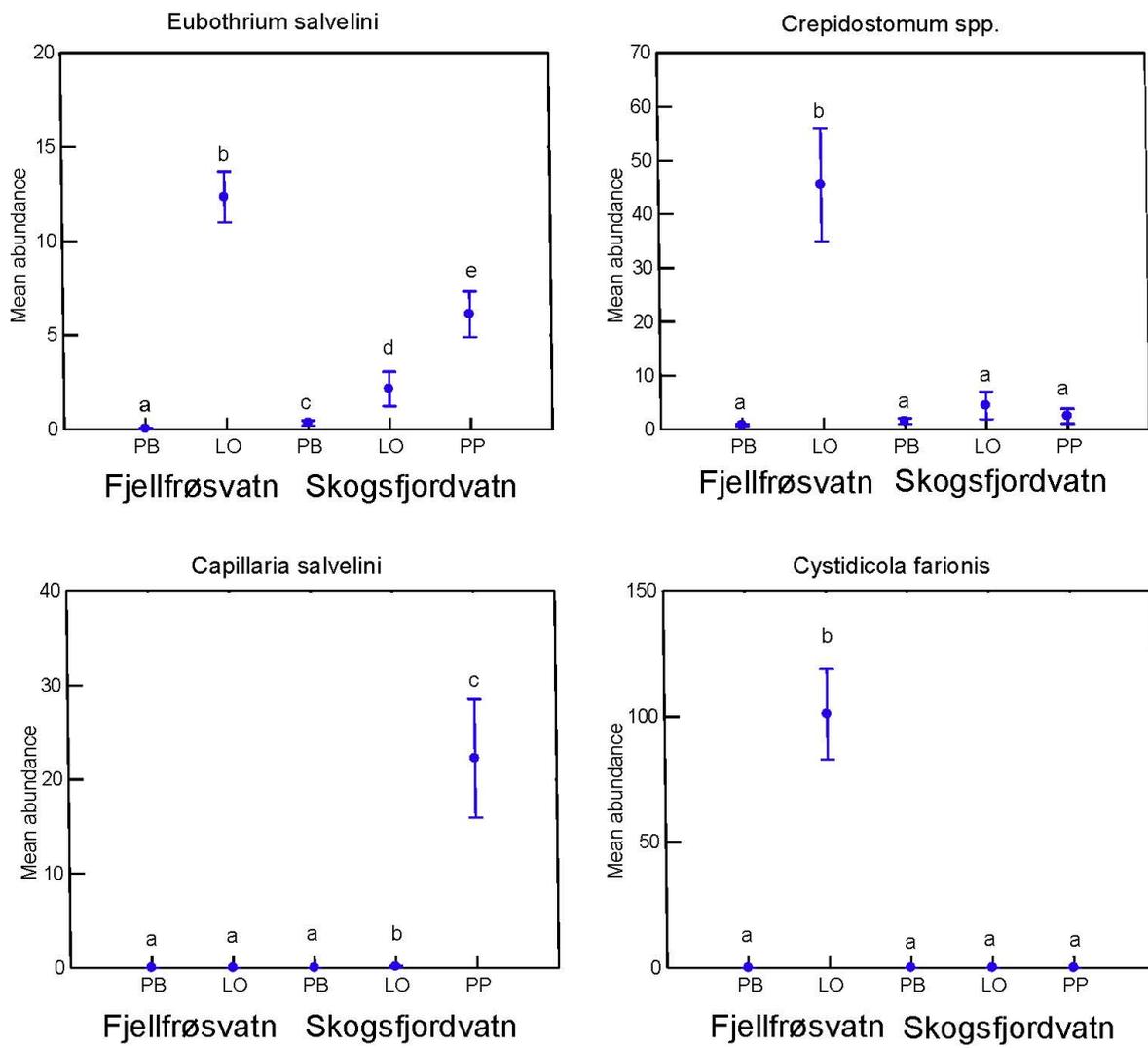


Figure 7. continued from last page. NOTE the scale differences on the Y-axis.

4. Discussion

As predicted, there were significant differences in parasite community composition between the sympatric morphs of Arctic charr, both within and across lakes. The parasite communities in general reflected the differences in resource utilization among the morphs.

The intra-lake differences in the parasite communities between the sympatric living morphs in Fjellfrøsvatn, and Skogsfjordvatn, indicate a spatial and temporal divergence in trophic ecology between the morphs, represented by the PB-morphs in both lakes specializing on a benthivore niche, the LO-morphs specializing on a zooplanktivore niche and the PP-morph specializing on a piscivore niche. These results are in accordance with similar studies of polymorphic Arctic charr, where the parasite community have been found to diverge between morphs utilizing the upper water layers and morphs utilizing the profundal habitats (Knudsen et al. 1997) and between sympatric morphs diverging along resource axes in the upper-water layers (Henricson and Nyman 1976, Frandsen et al. 1989, Dorucu et al. 1995). Differences in parasite communities between polymorphic populations of other postglacial fishes have also been reported in e.g. three-spined sticklebacks (Maccoll 2009), whitefish (Knudsen et al. 2003, Karvonen et al. 2013b) and brook charr (Bertrand et al. 2008).

Compared to most other lake systems holding sympatric morphs of Arctic charr, Skogsfjordvatn and Fjellfrøsvatn are special due to the presence of morphs in the deep profundal, especially the presence of two profundal morphs in Skogsfjordvatn, which is not observed elsewhere (Klemetsen 2010). The profundal piscivore morph (PP-morph) in Skogsfjordvatn represents the most unique form, and to my knowledge the parasite community of such a charr morph has not been studied before. Usually, piscivore behavior in Arctic charr occurs in lakes with suitable prey fish species and with low interspecific competition from other piscivore fish species (Jonsson and Jonsson 2001). Piscivore behavior in allopatric populations of charr is usually observed in larger individuals (> 20cm) (Amundsen 1994). Only a few polymorphic populations of Arctic charr have been reported to harbor morphs with piscivorous behavior (Snorrason et al. 1994, Adams et al. 1998, Klemetsen 2010), but in general, these morphs are located in the upper water layers where they feed on smaller fish mainly in the pelagic habitat (Sandlund et al. 1992). In Skogsfjordvatn, the occurrence of the PB-morph and juvenile individuals from the LO-morph in the profundal zone could have opened up for a piscivore niche utilization for the ancestors of the PP-morph (Smalås et al. 2013).

The parasite diversity was generally higher in Skogsfjordvatn than in Fjellfrøsvatn, where the component parasite communities of both the LO- and PB-morph in Skogsfjordvatn were more diverse than for the LO- and PB-morph in Fjellfrøsvatn. This may possibly be explained by the physical and geographical characteristics of the lakes. Kennedy (1978) found a positive correlation between the size of the lake and the total number of parasite species in the parasite communities of brown trout. A large lake (e.g. Skogsfjordvatn) is more likely to be colonized by a greater number of parasites species than a smaller lake (e.g. Fjellfrøsvatn). Furthermore, Kennedy (1978) compared parasite communities between three lakes on Bear Island with lakes on other Arctic and subarctic islands, as well as on the mainland, including Skogsfjordvatn, where he observed that lakes on coastal islands (e.g. Skogsfjordvatn) had higher parasite diversity than lakes on the inland (e.g. Fjellfrøsvatn).

In both lakes, the LO-morphs were found to be more diverse than the PB-morphs. The wide diet niche of the LO-morphs is known from several earlier studies (Klemetsen et al. 2003b, Amundsen et al. 2008, Knudsen et al. 2010, Eloranta et al. 2013), and the more diverse parasite community of the LO-morphs clearly support the hypothesis that morphs with a wide niche are more susceptible to parasite infections (Knudsen et al. 1997). The PB-morphs from both lakes had a narrow trophic niche compared to the LO-morphs, which apparently have resulted in the low diversity of trophically transmitted parasites as also found in earlier studies in Fjellfrøsvatn (Knudsen et al. 1997). The PP-morph was found to harbor the most diverse parasite community. The PP-morph probably accumulates parasites that are successfully transmitted from their prey fishes such as from the PB-morph and juvenile individuals from the LO-morph and three - spined sticklebacks. Predatory fishes seem commonly to accumulate a high variety of parasite species (Valtonen and Julkunen 1995). An important biotic factor that structures the parasite component community, is the habitat and dietary spectrum of the host species, which determines the amount of exposure to trophically transmitted parasites (Valtonen and Julkunen 1995).

Other factors proven to be important when structuring the parasite component community is the body size (Poulin 2000) and longevity of the host (Bell and Burt 1991). The PP-morph is the largest and most long-lived among the morphs in Skogsfjordvatn, whereas the PB-morphs are the smallest and have the shortest life-spans in both lakes (Klemetsen et al. 1997, Smalås et al. 2013). A more diverse parasite community can presumably be sustained in large-bodied host species as they provide a greater diversity of niches acquired through ontogeny and offer more space to parasites (Poulin 1995, Poulin and Leung 2011). Larger hosts also consume greater quantities of food and are thereby more likely to ingest prey that might be infected with parasites (Poulin 1997). Being long-lived

provides also a more permanent habitat for colonization and allowing for the accumulation of parasite species over time (Bell and Burt 1991). Hence, the fact that the PP-morph harbored the highest parasite diversity and the PB-morphs the lowest, suggests that host longevity and body size are important structuring forces for the host's parasite diversity.

As hypothesized, the parasite communities of the morphs were composed of parasite species transmitted through preys restricted to the habitat of the respective morphs. Copepod-transmitted cestodes were more common and found in higher intensities in the LO-morphs than in the PB-morphs in both Fjellfrøsvatn and Skogsfjordvatn. The LO-morph in both lakes feeds heavily on zooplankton (Skoglund et al. 2013). This explains the high intensities of copepod-transmitted parasites species, such as several cestodes (e.g. *E. salvelini*, *Diphyllbothrium* spp., *Proteocephalus* sp.) and the nematode *P. onchorhynchi*. The higher occurrence of copepod-transmitted parasites observed in the zooplanktivore morphs in the present study are in accordance with findings from other Arctic charr studies (Frandsen et al. 1989, Dorucu et al. 1995, Knudsen et al. 1997, 2003). Arctic charr can also be infected with both *D. ditremum* and *D. dendriticum* through consumption of prey fish such as three-spined stickleback, which is known to be a reservoir host for *Diphyllbothrium* spp. (Vik 1963, Halvorsen 1970, Bérubé and Curtis 1986) and also *E. salvelini* (Vik 1963). The higher abundance of *E. salvelini* in the PP-morph compared to the LO- and PB-morph in Skogsfjordvatn is explained by the diet of these morphs. The PP-morph feeds on sticklebacks (R. Knudsen pers.comm) which could be infected with juvenile *E. salvelini* (Vik 1963), and may therefore accumulate high numbers of this cestode. Nevertheless, the LO-morph in Fjellfrøsvatn had also a high abundance of *E. salvelini* even compared to the PP-morph in Skogsfjordvatn. This result suggest that the LO-morph in Fjellfrøsvatn get infections from higher feeding rates on copepods or prey fish (Eloranta et al. 2013) compared to the LO-morph in Skogsfjordvatn. Another explanation could be that copepods serving as intermediate hosts for this cestode are found in higher densities or have elevated infections of *E. salvelini* in Fjellfrøsvatn.

The LO-morphs in both lakes had high infections of *D. ditremum* than *D. dendriticum*, which is in accordance with findings from other studies of sub-arctic lakes (Henricson 1977, Sandlund et al. 1992, Knudsen et al. 1997). A tolerance to lower temperatures during its developing stages has been suggested as a factor explaining the higher abundance of *D. ditremum* in northern lakes (Halvorsen 1970). The differences in abundance of the two *Diphyllbothrium* species could also be connected with various degrees of pathogenicity, as it has been suggested that Arctic charr are able to sustain higher infections of *D. ditremum* than *D. dendriticum* (Kristoffersen 1993). Accordingly, the LO-morph in Fjellfrøsvatn had higher abundance of *D. dendriticum* and *D. ditremum* as the LO-morph

in Skogsfjordvatn. Such patterns could be related to differences in the availability of suitable hosts or the density of hosts. Firstly, the final host of *D. dendriticum* are gulls (*Laridae*), which are found in higher densities at Skogsfjordvatn than Fjellfrøsvatn due to its location near the sea. Thus, this contradicts somewhat the infection pattern of *D. dendriticum* between the lakes. The final hosts for *D. ditremum*, mergansers (*Mergus* spp.) and loons (*Gavia* spp.) (Kristoffersen 1993), are found in higher densities at Fjellfrøsvatn than at Skogsfjordvatn (R. Knudsen, pers. comm) and supports the higher infection of this parasite in Fjellfrøsvatn. Secondly, different exposure through zooplankton feeding activity could also explain these infection patterns. High infections of *D. ditremum* are often related to Arctic charr feeding on copepods in the pelagic habitat, whereas *D. dendriticum* is considered to be a more littoral oriented species (Henricson and Nyman 1976, Bérubé and Curtis 1984, Frandsen et al. 1989). Thus, different density of potential hosts (birds, fish or copepods) and local foraging habits of the charr morphs could explain the different infections levels of the *Diphyllobothrium* species between lakes. This is highlighted by the mean intensity and abundance of *D. dendriticum* in the PP-morph which was higher than in any of the other morphs, including the LO-morph in Fjellfrøsvatn. This is most likely related to the diet of the PP-morph that feeds upon charr and sticklebacks. It has been shown that plerocercoids of *D. dendriticum* are better to re-establish in piscivorous fish than *D. ditremum* (Halvorsen and Wissler 1973), and this likely explains the high infection levels of *D. dendriticum* in the PP-morph.

The nematode *P. onchorhynchi* is also transmitted through copepods and normally occurs in littoral-pelagic fish, but it has also been observed in relatively high numbers in piscivore fish (Frandsen et al. 1989). This supports the present study as the prevalence for this nematode was higher in the PP-morph compared with the LO- and PB-morphs in Skogsfjordvatn. This nematode has been reported from various anadromous salmonids (Moravec 1994). The presence of anadromous populations of Arctic charr, brown trout and Atlantic salmon, could explain why this nematode was found in Skogsfjordvatn and not in the landlocked Fjellfrøsvatn.

The LO-morph in Skogsfjordvatn had higher abundance of the intestinal cestode *Proteocephalus* sp. than the PB-morph. This is in accordance with findings from other studies, where fish from the pelagic habitat have high intensities of *Proteocephalus* sp. (Henricson and Nyman 1976, Frandsen et al. 1989). In Fjellfrøsvatn in contrast, *Proteocephalus* sp. dominated the parasite community of the PB-morph, whereas only 11 % of the LO-morph was infected, similar as found in earlier studies (Knudsen et al. 1997). This suggests different sources of infection between the lakes. Higher prevalence in the LO-morph could indicate that the most important intermediate host for *Proteocephalus* sp. in Skogsfjordvatn is limnetic copepods. In contrast, Knudsen et al. (1997)

suggested that *Proteocephalus* sp. in Fjellfrøsvatn most likely was transmitted through the benthic copepod *Acanthocyclops gigas* after detecting that the PB-morph fed much on this copepod compared to the LO-morph (Knudsen et al. 2006). On the other hand, also the PP-morph in Skogsfjordvatn had high prevalence, mean intensity and abundance of *Proteocephalus* sp. The larval stage of *Proteocephalus* sp. has been reported to be able to re-establish in piscivorous fish (Scholz 1999), which may explain why the PP-morph had higher infections of this cestode than the PB-morph. Due to the fact that *Proteocephalus* sp. never were identified down to species level in this study, it is unclear if there exist different species of *Proteocephalus* sp., which thus could use different copepod species as their main intermediate hosts. Proper identification of the *Proteocephalus* species in these sympatric forms needs to be carried out in the future in order to understand why such relatively large differences in infection pattern occur between the two lakes.

As hypothesized, the LO-morphs in both lakes were the only morphs that were infected with amphipod-transmitted parasites such as the cestode *C. truncatus* and the swim-bladder nematode *C. farionis* (Fjellfrøsvatn only). The occurrence of these two parasite species in the LO-morphs is related to differences between the morphs in exposure through their different diet- and habitat utilization, and in particular the heavy feeding on *Gammarus lacustris* by the LO-morph (see also Knudsen et al. 2004). The abundance of *C. truncatus* in the LO-morphs was in both lakes relatively low, which is also seen in other charr populations even though they have a high consumption of the intermediate host (Knudsen et al. 1997). This is due to the parasite's short life span (20-55 days) of the parasite, which thus is less frequent to accumulate in numbers in their fish host (Vik 1958). This species may also be deadly to the host even at low intensities (Berland 1999), resulting in constantly removal of highly infected individuals from the population. Infections of *C. farionis* tend to be locally stable at high levels in the fish host population (Black 1985, Giæver et al. 1991, Knudsen and Klemetsen 1994, Knudsen 1995), likely due to high consumption of *Gammarus* intermediate hosts (Smith and Lankester 1979). This nematode is in contrast long-lived (~ 2 years) and accumulate over time, especially in specialized amphipod-feeders, and may cause parasite-induced host mortality in the most heavily infected individuals (Knudsen et al. 2002). However, potential parasite induced host mortality seem to be lower for *C. farionis* than *C. truncatus*. Different pathogenicity and life-history patterns between these two parasite species may explain that individuals of the LO-morph in Fjellfrøsvatn were found to be highly infected with *C. farionis*, but still only had a few individuals of *C. truncatus*. Furthermore, *C. truncatus* was never found in the PB-morphs from both lakes or the PP-morph in Skogsfjordvatn, and *C. farionis* was never found in

the PB-morph in Fjellfrøsvatn. This is due to the fact that *Gammarus* sp. is rarely being ingested by the PB-and PP-morphs (Knudsen et al. 2006 R. Knudsen, unpublished data).

The prevalence, mean intensity and abundance of other parasites that utilize intermediate hosts restricted to the littoral-pelagic habitat, i.e. the trematodes *P. umblae* (only prevalence data available) and *Crepidostomum* spp., was higher in the LO-morphs than the PB-morphs in both lakes. *P. umblae* use stonefly larvae (*Plecoptera*) as the second intermediate host, an insect larva that has been found to be a common prey for morphs occupying the littoral habitat (Sandlund et al. 1992, Knudsen et al. 1997, Klemetsen et al. 2003b). The adult trematode *P. umblae* was never detected in any of the PB-morphs from the two lakes, which also is in accordance with earlier findings (Knudsen et al. 1997). This supports the conclusion that the PB-morphs are confined to the profundal zone throughout their life. In addition, the fact that *P. umblae* never was detected in the PP-morph in Skogsfjordvatn, indicates that the PP-morph rarely includes stonefly larvae in its diet.

The other adult trematodes *Crepidostomum* spp. constituted a larger portion of the parasite community composition in the LO-morph in Skogsfjordvatn than in Fjellfrøsvatn, but the mean intensity and abundance was much higher in the LO-morph in Fjellfrøsvatn. The large difference in mean intensity and abundance is an unexpected result. There were not carried out a proper identification of *Crepidostomum* spp. and they may have different first or second intermediate hosts. *Crepidostomum farionis* use *Pisidium* sp. as the first molluscan host, whereas *Crepidostomum metoecus* use *Radix peregra* (Hoffman 1998). Usually, *C. farionis* is more common in lakes because they can use both *Gammarus* sp. and mayfly-nymph as second intermediate host, compared to *C. metoecus* that seem only to be using *Gammarus* sp. Earlier studies have revealed that only *C. farionis* are present in Skogsfjordvatn (Kennedy 1978), whereas both *Crepidostomum* species are present in Fjellfrøsvatn (Knudsen et al. 1997).

Although the mean intensity and abundance of *Crepidostomum* spp. was higher in the LO-morphs than in the PB-morphs, they constituted a large portion of the parasite community composition in the PB-morphs, especially in Skogsfjordvatn. This is an unexpected result since the suggested second intermediate hosts for these trematodes live in the littoral habitat. Interestingly, all four charr morphs in Thingvallavatn were infected with *C. farionis*, even though neither of the second intermediate hosts (mayfly larvae or amphipods) were found in the lake (Frandsen et al. 1989). Their presence in Thingvallavatn suggested that 1) *Crepidostomum* spp. may only use one intermediate hosts (possibly just a mollusca) or 2) are able to use other insect larvae present in the lake as alternative second intermediate hosts (Kristmundsson and Richter 2009). The high stability

of *Crepidostomum* spp. infections in the PB-morph in Fjellfrøsvatn (Knudsen et al. 1997) combined with a diet dominated by *Pisidium* sp. and chironomid larvae during the last ~20 years (Knudsen et al. 2006, Amundsen et al. 2008), may indicate that the parasites can use one or both of these prey groups as intermediate host. This could also be the case for the observed pattern in Skogsfjordvatn. More research is needed in order to understand the processes behind the transmission of *Crepidostomum* spp. trematodes between different hosts, especially to the profundal PB-morphs.

The nematode *C. salvelini* was almost exclusively found in the PP-morph, constituting an important part of its parasite community composition. This nematode species is located in the intestine of mainly salmonid and cottid fishes (Moravec et al. 1987). The parasite was first described in Arctic charr by Polyanski in 1952 (Moravec 1994). In the late 1970's, *C. salvelini* was observed in the charr in Skogsfjordvatn (Kennedy 1978). The life cycle of *C. salvelini* is unknown, but it has been suggested that oligochaetes may serve as an intermediate host for this parasite (Threlfall and Hanek 1969). If so, the PB- and the juvenile PP-morph would be expected to exhibit the highest infection of this nematode through their feeding activity. However, as the largest and older individuals of the PP-morph had the highest infection, a piscivore behavior may suggestively be involved in the transmission process. As this nematode species have been observed in the flesh of fish (Moravec 1994), it is possible that the parasite is located in the flesh of small fish and therefore not detected in this study as the flesh was not examined for parasites. Nevertheless, the present results suggest that piscivory is central transmitting and accumulating this nematode between hosts, but further investigations is needed in order to find out more about the life cycle of *C. salvelini*.

The only parasite with a direct life cycle in this study is the gill-maggot *S. edwardsii*. In Fjellfrøsvatn, only the LO-morph was infected with this parasitic crustacean in contrast to Skogsfjordvatn, where the gill-maggot was only found on the PB- and PP-morph. The infective stage of *S. edwardsii* spend most of their time near the substrate at the bottom of the water column (Poulin et al. 1990). However, this can only explain part of these infection patterns observed as all morphs stay close to the bottom in either the profundal zone (PB-morphs and PP-morph) and in the littoral (LO-morphs). A large body size may explain why this ectoparasite was only found in the LO-morph, since it seems to be a positive correlation between host size and the number of parasites (Black 1982). Hence, the differences in infection between the morphs are most likely due to the small sample sizes, since the parasite several times has been observed on the LO-morph and PB-morph in Fjellfrøsvatn (Knudsen et al. 1997).

There were generally low similarities between LO-morphs (39 %) and between PB-morphs (43 %) across lakes. Furthermore, the low similarity (20 %) in the parasite community between the PB-morph and LO-morph in Fjellfrøsvatn could be related to a few species dominating each of their parasite communities. The parasite community of the LO-morph was dominated by *C. farionis*, whereas the parasite community of the PB-morph was dominated by *Proteocephalus* sp. In contrast, in Skogsfjordvatn, the similarity between the PB-and LO-morph was very high (70 %), and had a more heterogenic composition of parasite species such as *Crepidostomum* spp., *Proteocephalus* sp. and *E. salvelini*. These dissimilarities between and within lakes could mainly be due to local factors related to exposure (feeding habitats) and occurrence of suitable intermediate hosts. This is specially highlighted by the PP-morph that exhibit low percent similarity in parasite communities relative to the sympatric PB-and LO-morphs. This is probably caused by the diverged dietary niches observed and especially the highly specialized piscivore behavior of the PP-morph.

It appears to be some degree of predictability and parallelism in parasite diversity and species composition between the PB-morphs, as well as between the LO-morphs from the two localities in spite of low percent similarity between their parasite communities. The parasite species found regularly in the PB-morphs were trematodes (*Crepidostomum* spp.) and cestodes (e.g. *Proteocephalus* sp. and *E. salvelini*). In the LO-morphs, cestodes like e.g. *Diphyllobothrium* spp., *E. salvelini*, *C. truncatus* and the trematodes *Crepidostomum* spp. was regularly found, but in different intensities in the two lakes. This parallelism in species composition observed between the corresponding morphs across lakes could be explained by both biotic and abiotic factors. First, temperature is a key factor controlling parasite dynamics were it influence the rates of parasite establishment and development (Karvonen et al. 2013a). During the summer growth period, temperature decreases with increasing depth, leaving the shallow littoral zone and the upper water layers in the pelagic zone warmer than the deep, profundal zone (Wetzel 2001). Since sites with identical conditions are more likely to hold a similar species composition of the parasite community (Poulin 2010), the parasite communities of the PB-morphs are likely to be similar across lakes due to they both reside in the deep, cold profundal zone. The parasite communities are also likely to be similar for the LO-morph in both lakes, since they occur in the warmer littoral-pelagic zone in both lakes. This could explain the observed similarities in parasite species abundance in the corresponding morphs in Fjellfrøsvatn and Skogsfjordvatn. Secondly, biotic factors like e.g. exposure to parasites through similar host ecology observed across lakes, are probably important as most parasite species are transmitted to their host by the food-web. Both of the PB-morphs reside in the profundal throughout their life with a narrow dietary niche, while the LO-morphs mainly occur

in the littoral-pelagic habitat and are omnivore foragers (Klemetsen et al. 1997, Smalås et al. 2013). Based on similar host ecology, a certain degree of similarity in their parasite communities should therefore be expected as suggested from other studies (Bush et al. 1990, Alarcos and Timi 2012).

There were also some clear differences in species composition between morphs as the LO-morph in Fjellfrøsvatn was infected with the swim-bladder nematode *C. farionis* and the LO-morph in Skogsfjordvatn was infected with *C. salvelini* and *P. onchorhynchi*. Such site specific parasite occurrences between the lakes could be related to stochastic variance. Lakes are isolated ecosystems and often parasite species with low transmission and colonization rates are found. Colonization involves the establishment of a new parasite species in a host population (Bush et al. 2001). The dispersal of a parasite into a new habitat or geographic area like e.g. a lake, is a chance event and does not guarantee that the parasite will establish in the new environment or host (Bush et al. 2001). Secondly, the occurrence of site specific species could also be caused by their transmission rate. Similar for the site specific species in these lakes are that they are nematodes with an autogenic lifecycle (except for *C. salvelini* where the life cycle is unknown), where they use copepods as intermediate hosts and fish as final hosts. The transmission of fish parasites throughout freshwater localities is primarily due to the movements of the final hosts (Kennedy 2009). Species using birds as definitive hosts (allogenic species), like e.g. *Diphyllobothrium* spp., benefits naturally from greater passive dispersal among water bodies than species constrained to complete their life cycle in a water body, like these nematodes (Poulin et al. 2011). Skogsfjordvatn is connected to the sea and holds anadromous populations, which also could increase the transmission rates of freshwater parasites in this lake, compared to the landlocked Fjellfrøsvatn. These nematodes are not easily transmitted from one location to another, and may explain the difference in infection pattern observed in the lakes.

It has been suggested that parasitism could lead to polymorphism through ecological speciation (De Roij and MacColl 2012, Karvonen et al. 2013c, Bañuls et al. 2013). Such parasite-mediated divergent selection can operate in natural host population if parasite infection differs within or between host populations, a difference that remains constant over time, where infection imposes fitness consequences for the host (Karvonen and Seehausen 2012). Some of the best data of ecotypes that diverge in parasite infection comes from freshwater fish (Karvonen and Seehausen 2012), where the most well-known examples come from three-spine stickleback populations in the northern hemisphere (MacColl 2009, De Roij and MacColl 2012), and cichlid fishes in East African great lakes (Raeymaekers et al. 2013). Other good examples are whitefish and Arctic charr, with

large differences in parasite infections in ecotypes/morphs inhabiting the pelagic versus the benthic habitat and in ecotypes/morphs in the profundal versus the littoral-pelagic habitat. For morphs inhabiting the deep profundal, as shown in the PB-morph in the present study, the typical observation is that they have species-poor parasite communities with mild infections compared to morphs in the benthic or pelagic habitat (Knudsen et al. 1997). The profundal zone offers less favorable conditions for foraging than the littoral-pelagic habitat, forcing the PB-morphs to mature early at a small size (Klemetsen et al. 2003a, Smalås et al. 2013). This could indicate some sort of trade-off, where the PB-morph has occupied the unfavorable deep, cold profundal in order to escape or reduce their parasite burden. This idea is in accordance with Karvonen & Seehausen (2012) that asked the question “Do host divergence and the initiation of reproductive isolation follow divergence in parasite infections, or vice versa?” In contrast, the PP-morph from an identical environment has a contrasting life history strategy, a strategy that is seldom seen for Arctic charr. This morph utilize larger and more profitable prey (i.e. small fish) and invests more energy in somatic growth and postpones reproduction, which increase the fitness (Smalås et al. 2013). An increased size, high consumption of prey fish infected by a variety of parasites, combined with a high longevity that consequently will aggregate high parasite infection, as shown in the present study of the PP-morph. As a consequent of high parasite infections the host fitness would decrease, and a higher energy investment for a better immune system is needed (Eizaguirre and Lenz 2010 and the references therein). Thus, by their larger somatic growth through adopting a specialized but favorable feeding strategy, the PP-morph could be able to mobilizing a costly but better immune defense against parasites gained by their feeding activity. The relatively high parasite burden in the PP-morph compared with the low infections observed in the PB-morphs suggests that parasite infection is tightly associated with contrasting life-history strategies and divergent trophic niches in which parasite mediated divergent selection could be operating. Whether or not parasite mediated divergent selection has promoted the observed divergence of the sympatric morphs of Arctic charr in Skogsfjordvatn and Fjellfrøsvatn is an open question, and cannot be answered by the results of the present study. I agree with Karvonen & Seehausen (2012) that future research should investigate parasitism and host resistance at all stages of speciation, not just the early and late stages, in order to determine whether parasites influence the divergence process that causes ecological speciation.

Conclusion & further research

This study revealed large intra-lake differences in parasite community between the three Arctic charr morphs in Skogsfjordvatn and between the two morphs in Fjellfrøsvatn as hypothesized. The different parasite communities reflect the differences in habitat and diet utilization among the morphs. The LO-morphs that occupies the littoral-pelagic habitat had higher parasite diversity and higher intensities of parasites transmitted through littoral and pelagic intermediate hosts than the PB-morphs that occupy the profundal habitat that, in contrast, had higher intensities of parasites transmitted through profundal intermediate hosts.

The most novel findings were however related to the PP-morph, a piscivorous morph mainly residing in the profundal zone in Skogsfjordvatn. This morph had the highest parasite diversity, apparently accumulating parasites by predated upon the PB-morph, juvenile individuals from the LO-morph and sticklebacks. The differences in parasite community among the sympatric living morphs of Arctic charr in Skogsfjordvatn, supports the findings of Smalås et al. (2013) and Skoglund (2013) that the three morphs are specialized to exploit different habitats and diets.

The presence *Crepidostomum* spp. in both of the PB-morphs and *C. salvelini* in the PP-morph in Skogsfjordvatn, suggests that the transmission dynamics of these parasites in the deep-water morphs are not fully understood and further research is needed to understand their way of transmission.

Finally, the present study also revealed a parallelism in parasite species composition between the morphs that occurred in both lakes (the LO-and PB-morphs). The LO-and PB-morphs across lakes have similar diet and habitat characteristics, as well as being exposed to similar abiotic conditions. These similarities reflect the importance of both host ecology and abiotic factors as determinants in structuring a host's parasite community. The dissimilarities in the local parasite species pool between the lakes suggest that stochastic events, as well as way of transmission, determine the occurrence of site specific parasite species in a lake.

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Appendix

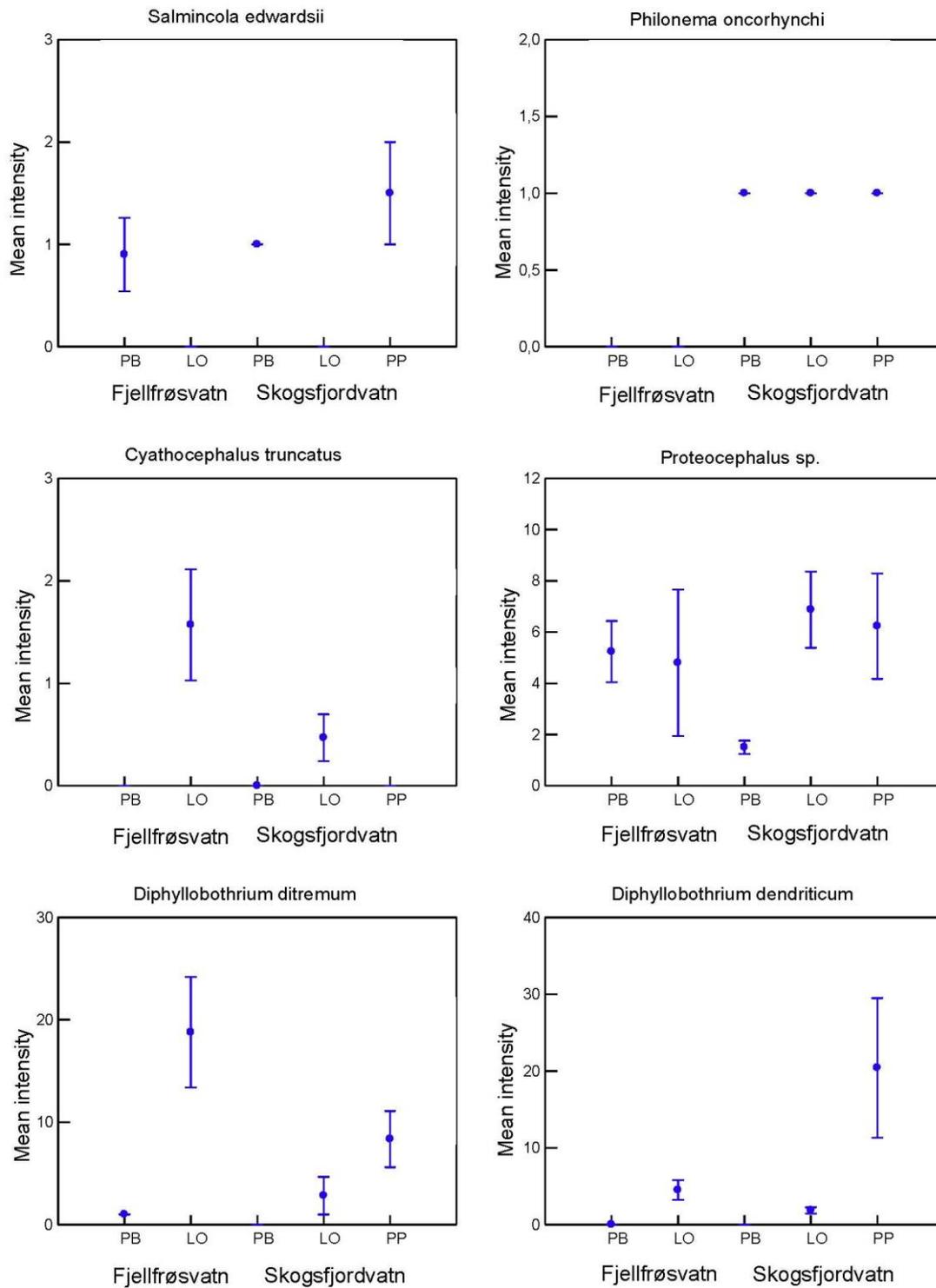


Figure A1. Mean intensity (\pm S.E) of all parasite species* in the PB-and LO-morph in Fjellfrøsvatn and PB-LO and PP-morph in Skogsfjordvatn * *P. umblae* not included

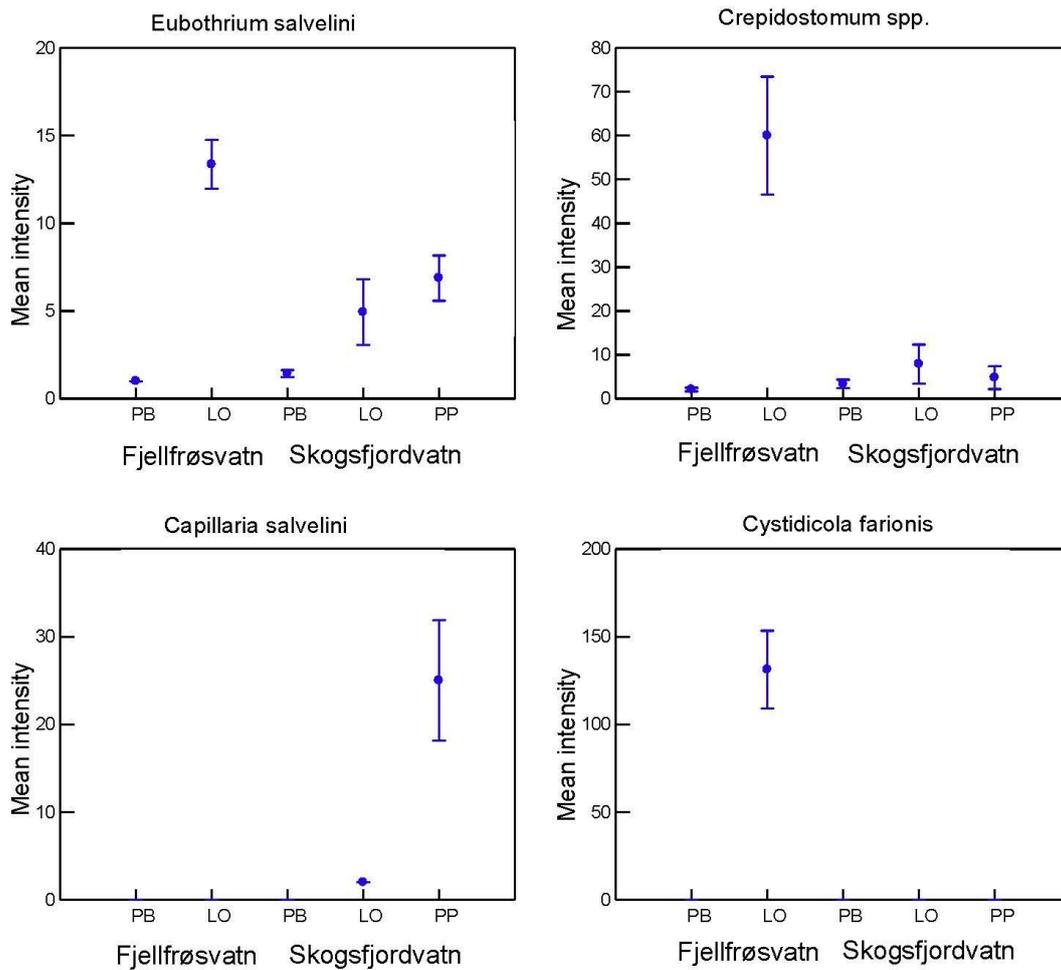


Figure A1. continued. NOTE the scale differences

Table A1. Total number of individuals of each parasite species within each morph in Fjellfrøsvatn and Skogsfjordvatn, as well as the total number of parasites in each morph and lake

Lake	Fjellfrøsvatn		Skogsfjordvatn		
	PB	LO	PB	LO	PP
<i>S. edwardsii</i>	0	82	3	0	3
<i>Crepidostomum</i> spp.	25	4138	44	142	67
<i>Proteocephalus</i> spp.	110	48	18	165	106
<i>E. salvelini</i>	1	1122	10	69	165
<i>D. ditremum</i>	1	1202	0	17	142
<i>D. dendriticum</i>	0	198	0	13	347
<i>C. truncatus</i>	0	143	0	15	0
<i>C. farionis</i>	0	9188	0	0	0
<i>P. oncorhynchi</i>	0	3	1	1	1
<i>C. salvelini</i>	0	0	0	4	600
<i>P. umblae</i>		*		*	
Tot. nr of parasite individuals	137	16124	76	426	1431
Tot. nr. of parasites in the lake		16261		1933	

Table A2. Mean intensity and abundance (\pm S.E) of the different parasite species found in the LO-and PB-morph in Fjellfrøsvatn and the LO-PB and PP-morph in Skogsfjordvatn

Parasite species	Fjellfrøsvatn				Skogsfjordvatn					
	LO		PB		LO		PB		PP	
	<i>I</i>	<i>A</i>	<i>I</i>	<i>A</i>	<i>I</i>	<i>A</i>	<i>I</i>	<i>A</i>	<i>I</i>	<i>A</i>
<i>Crepidostomum spp.</i>	60.0 (13.5)	45.5 (10.5)	2.1 (0.4)	0.8 (0.2)	7.9 (4.5)	4.5 (2.6)	3.4 (6.5)	1.5 (0.5)	4.8 (2.6)	2.5 (1.4)
<i>Cyathocephalus truncatus</i>	9.5 (2.5)	1.6 (0.5)	0.0 (0.0)	0.0 (0.0)	2.5 (0.8)	0.5 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>Eubothrium salvelini</i>	13.4 (1.4)	12.3 (1.3)	1.0 (0)	0.03 (0.03)	4.9 (1.9)	2.2 (0.9)	1.4 (0.8)	0.3 (0.1)	6.9 (1.3)	6.1 (1.2)
<i>Diphyllobothrium dendriticum</i>	4.5 (1.3)	2.2 (0.7)	0.0 (0.0)	0.0 (0.0)	1.9 (0.4)	0.4 (0.2)	0.0 (0.0)	0.0 (0.0)	20.4 (10)	12.9 (6.0)
<i>Diphyllobothrium ditremum</i>	18.8 (5.4)	13.2 (3.9)	1.0 (0.0)	0.03 (0.03)	2.8 (1.8)	0.5 (0.4)	0.0 (0.0)	0.0 (0.0)	8.4 (2.7)	5.3 (1.8)
<i>Proteocephalus sp.</i>	4.8 (2.9)	0.5 (0.4)	5.2 (1.2)	3.6 (0.9)	6.9 (1.5)	5.2 (1.2)	1.5 (0.3)	0.6 (0.2)	6.2 (2.0)	3.9 (1.4)
<i>Capillaria salvelini</i>	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.0 (0.1)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	25.0 (7.0)	22.2 (6.0)
<i>Cystidicola farionis</i>	131.3 (22.2)	100.1 (18.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>Philonema oncorhynchi</i>	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)	0.1(0.0)	1.0 (0.0)	0.1 (0.0)	1.0 (0.0)	0.1 (0.0)
<i>Salmincola edwardsii</i>	4.8 (19)	0.9 (0.4)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	1.0 (0)	0.1 (0.5)	1.5 (0.5)	0.11 (0.1)

Table A3. Differences in parasite infection between the sympatric morphs within Fjellfrøsvatn and Skogsfjordvatn, based on a Man-Whitney U test and Kruskal-Wallis test (Skogsfjordvatn), with P-values. Significant values are shown in bold text. These tests were performed in MYSTAT (2012).

Parasite species	Fjellfrøsvatn	Skogsfjordvatn	PB vs.PB	LO vs. LO
<i>Crepidostomum spp.</i>	0.00	0.48	0.56	0.00
<i>Cyathocephalus truncatus</i>	0.02	0.01	1.00	0.97
<i>Eubothrium salvelini</i>	0.00	0.00	0.02	0.00
<i>Diphyllobothrium dendriticum</i>	0.00	0.00	1.00	0.01
<i>Diphyllobothrium ditremum</i>	0.00	0.00	0.33	0.00
<i>Proteocephalus sp.</i>	0.00	0.00	0.00	0.00
<i>Capillaria Salvelini</i>	1.00	0.00	1.00	0.02
<i>Cystidicola farionis</i>	0.00	1.00	1.00	0.00
<i>Philonema oncorhynchi</i>	0.56	0.99	0.30	0.45
<i>Salmincola edwardsii</i>	0.01	0.20	0.07	0.01