UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

The cost of parasites – Metazoan parasite community of anadromous Arctic charr (*Salvelinus alpinus*) from Northern Norway

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Photo: Gabrielle Grenier

Acknowledgements

When I went into this project, I knew very little about parasites. After this project, I have not only gained knowledge, but also a massive fascination over these tiny creatures that are much more diverse and abundant than I had expected.

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I would like to thank all the people involved in the Laksvatn project, as well as all the members of the Freshwater Ecology group. You have all made these two years much more fun, both in and outside of working hours. Some people that have contributed to this thesis are Gabrielle Grenier, Sigurd Slåteng, Julia Mikhailova, Kristine Drage, Astrid Lægran, Karin Strand Johannessen, Runar Kjær and Hallvard Jensen. I would also like to thank friends and family for being there for me in this process and always believing in me. My five years in Tromsø have been amazing, and this is all thanks to all the great people I have met during my stay.

Hedda Auestad Nilsen

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Abstract

Anadromous salmonids migrating in the marine system to feed are at risk of accumulating trophically transmitted parasites that may have negative effects on the salmonid host. The aim of this study was to explore the metazoan parasite community of returning anadromous Arctic charr (*Salvelinus alpinus*) directly after entrance to freshwater. This is the first study conducted in Europe looking at the parasite community of anadromous Arctic charr. Anadromous Arctic charr were caught migrating upstream in the river outlet from Balsfjord into Laksvatnet. Anadromous Arctic charr (n=35) was analyzed for metazoan parasites in all organs. The parasite community of the returning anadromous Arctic charr consisted of 17 different taxa. There was no significant difference in number of freshwater parasite taxa (n=8) and marine parasite taxa (n=9) infecting the anadromous charr from Laksvatn. High abundances of parasites were found, with a mean abundance of 5754 individual parasites, with majority being of marine origin. There was a higher proportion of trophically transmitted marine parasites than actively transmitted marine parasites infecting the Arctic charr. This is most likely due to the excessive feeding pattern that the Arctic charr exhibits during their short stay in the marine system. It was discussed whether parasites could be one important reason for the high mortality rate for the Arctic charr at sea found in other studies. Parasites may be an important cost of an anadromous lifestyle; however, it appears as though the cost of parasites does not exceed the benefit of increased body mass and fecundity.

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1 Introduction

Parasites are organisms that live in or on other organisms (hosts), while deriving benefits from this relationship at the host's expense (Marcogliese & Price, 1997). They have been described as a double-edged sword (Marcogliese & Price, 1997), as they can be both detrimental and beneficial to the same ecosystem. Parasites can affect their hosts directly, by either damaging host tissue or influencing reproduction, or indirectly by functioning as ecological engineers (Jones et al., 1997; Mouritsen & Poulin, 2002) and regulating the abundance or quality of a resource needed by another organism. Within one host there can exist an entire community of parasites, which is called the infracommunity (Bush & Holmes, 1986a, 1986b). Infracommunities of parasites may be diverse, and organized the same way as free-living communities, competing over food and space (Marcogliese & Price, 1997). All infracommunities within one population of hosts make up the component community (Holmes & Price, 1986). Parasites may therefore affect their host at an individual level and at a population level. This leads them to also influence the structure of food webs (Amundsen et al., 2009; Lafferty et al., 2006).

Just like migrating animals, parasites take advantage of different environments to optimize their life cycles. The life cycles of parasites may be complex, often including a series of at least two different hosts (Marcogliese & Cone, 1997). Many parasites are trophically transmitted (Marcogliese & Cone, 1997); they depend on predator-prey interactions for transmission, and they can infect several trophic levels of the food web. Because of this trophic transmission, the diet of the host will strongly influence the infracommunity of parasites. For instance, Knudsen et al. (1996) found that resident charr with a preference for planktonic prey, often had higher abundances of parasites using plankton as an intermediate host. Due and Curtis (1995) also observed differences in parasite community, and attributed these differences on local environmental conditions, individual feeding behavior of the charr, and prey availability. Parasites that are actively transmitted have free-living life stages in the environment. One example of this is trematodes having free living miracidia and cercariae that penetrate the next host (Esch & Fernandez, 1994; Hobart et al., 2022). Parasites are affected by two different environments: the microenvironment, which is the environment within the host, and the macroenvironment in which the host lives (Rohde, 1984). In some cases, the macroenvironment may change drastically, such as with anadromous species that migrate between the freshwater and the marine environment (Klementsen et al., 2002).

Arctic charr (*Salvelinus alpinus,* Linneaus, 1758) has a circumpolar distribution, and is found in the arctic, subarctic, boreal and temperate regions of the Holarctic (Klementsen et al., 2002). Anadromous Arctic charr (henceforward charr) can be found in the two northernmost counties in Norway: Nordland and Troms and Finnmark (Svenning et al., 2012). In higher latitudes, the marine system is more productive than the freshwater system, which gives the fish greater feeding opportunities at sea, compared to the freshwater system (Gross et al., 1988; Näslund et al., 1993). Anadromous fish take advantage of these systems, and migrate to sea to feed, before returning to the freshwater systems to overwinter or to spawn (Figure 1). During their migration to sea, charr may experience fitness benefits such as an elevation of body mass (Jensen et al., 2019; Jensen et al., 2017; Opheim, 2022; Young et al., 2021) and an increased growth rate (Young et al., 2021); both of which may lead to a higher reproductive output (Jonsson & Jonsson, 1993).

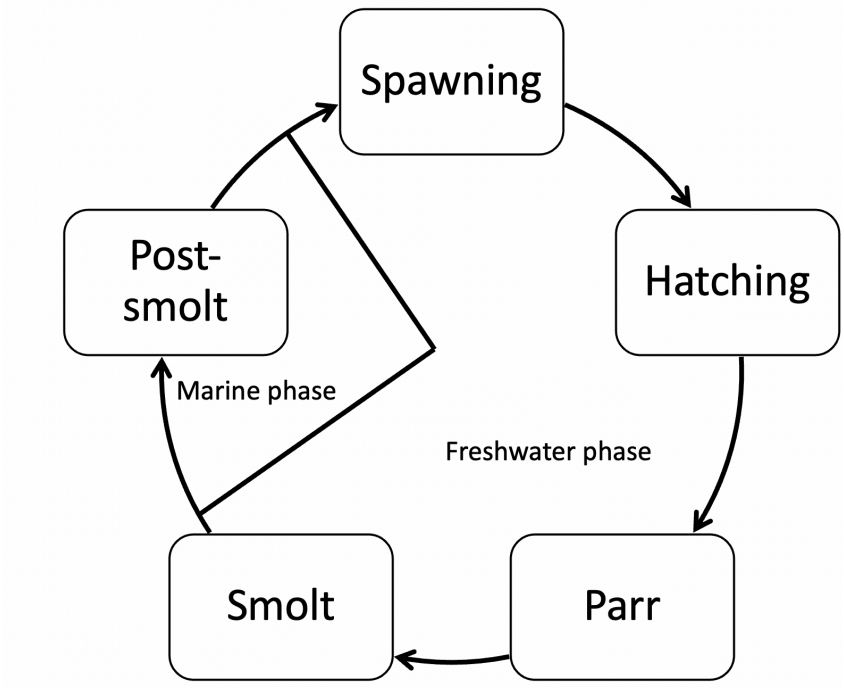

Figure 1: illustration of the life history of anadromous Arctic charr (S. salvelinus), based on (Klementsen et al., 2002; Rikardsen, 2000; Young et al., 2021). The different life stages are illustrated, from hatching to spawning, as well as which phases occur in the different environments. Some charr also overwinter instead of spawning.

The exploitation of marine resources has some costs, one of which is an increased risk of being infected by parasites. Anadromous salmonids may serve as accidental host for marine parasites during the marine migration (Due & Curtis, 1995). The charr feeds on the intermediate levels of the food web (Opheim, 2022), which is often where a large proportion of trophically transmitted parasites can be found (Amundsen et al., 2009; Lafferty, 2008). Although the anadromous charr often serves as a dead end to these parasites, as they are

unlikely to reproduce during the limited time the charr spends in the sea, they can still lead to damage of the host (Marcogliese, 1995).

Parasites can tolerate different levels of salinity over time (Kristoffersen, 1993), therefore the different parasite taxa infecting the anadromous charr will show different sensitivity towards an altered macroenvironment. Ectoparasites are the first parasites lost; not being able to withstand the osmotic difference (Frimeth, 1987b), while internal parasites have been shown to survive for some time during the marine migration. Studies conducted on parasite communities of anadromous salmonids (Bouillon & Dempson, 1989; Bristow et al., 1996; Bristow & Berland, 1991; Dalen, 2011; Dick & Belosevic, 1981; Due & Curtis, 1995; Frimeth, 1987b; Knudsen et al., 2005) have shown that the infracommunity consists of both freshwater parasites that have survived the marine journey, and marine parasites acquired at sea.

Charr falls within the Salmonidae family, which is a group of fishes having financial, cultural and ecological importance in Northern Europe (Chapman et al., 2012). Studies of the parasite community of anadromous salmonids have been conducted earlier, however no studies have investigated at the metazoan parasite community of anadromous charr in Norway. The aim of this study is to explore the metazoan parasite community of returning anadromous charr, migrating from the marine system into the freshwater system. The populations of anadromous salmonids from the study site, Laksvatnet, have been the subject of several studies. The anadromous charr from Laksvatnet doubles in body mass due to feeding during their marine migration (Opheim, 2022). When in the sea they migrate short distances and stay in the uppermost layers (0-3m) of the water masses (Nordli, 2021). The migration lasts for six weeks. There has also been conducted a study on sea lice intensities in this location, and it was described to medium intensity (Grenier et al., 2023).

Due to the charr's observed feeding behavior in the sea, combined with the expected reduction of freshwater parasites, I predict that the parasite community of returning anadromous charr will consist of both freshwater and marine taxa, with no significant difference in number of taxa between the two environments. For the same reason, I secondly predict a higher abundance of marine parasites than freshwater parasites. I finally predict that the returning anadromous charr will accumulate more trophically transmitted marine parasites than actively transmitted marine parasites, this is also due to a lack of aquaculture activity in this area.

2 Materials and methods

2.1 Location

The field work was conducted in Laksvatnet (69.39°N, 19.39°E), in Balsfjord Municipality, Troms og Finnmark county in Northern Norway. Laksvatnet (Figure 2, Figure 3) is a small lake, with an area of 0.8 km^2. The main water inlet is Storelva, which originates from a glacier, Gjømmedalsbreen. The main outlet, Buktelva, with a length of 300 m, runs into Laksvatnbukta, a shallow bay area, before it goes into Balsfjorden. The fjord has no aquaculture activity. The average depth of the lake is 6 meters, and the deepest point is 15 meters. The lake is an oligotrophic, subarctic lake. It holds a population of charr, brown trout (*Salmo trutta,* Linneaus, 1758) and three-spined stickleback (*Gasterosteus aculeatus,* Linneaus, 1758). The bottom is sandy, with some grass in the littoral zone and some benthic invertebrates. The vegetation around the lake is covered by birch (*Betula* sp.) and willows (*Salix* sp.). The bottom of the river is covered by rocks (Opheim, 2022).

Figure 2: map of Laksvatn and the surrounding landscape. Source: norgeskart.no

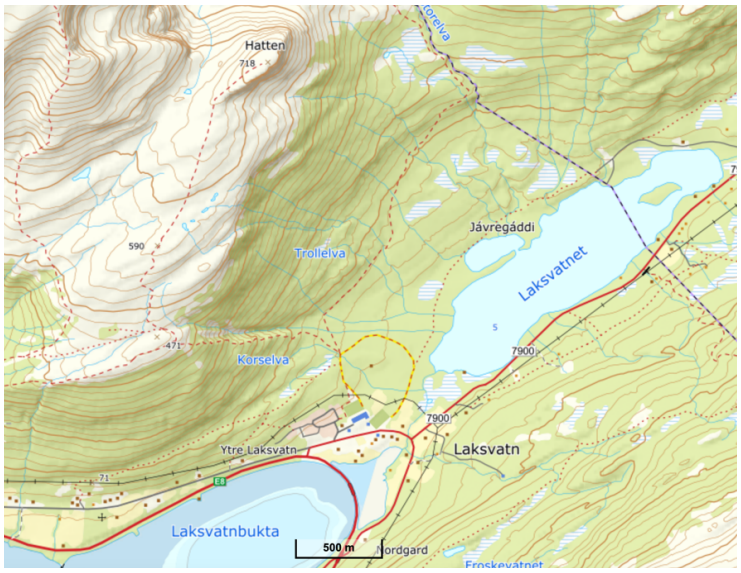

Figure 3: Close-up map of Laksvatn and the river running down to Laksvatnbukta and Balsfjord. Source: norgeskart.no

The population of charr in Laksvatnet is partly anadromous (Grenier et al., 2023; Opheim, 2022). In 2020 and 2021, 1125 and 1518 charr were registered migrating upstream, respectively. On average, the charr from Laksvatnet spent 47.7 days in the sea. The diet at sea consisted of mainly small marine fish, crustaceans, fish larvae, and insects.

2.2 Field work and data sampling

2.2.1 Fish trap

A fish trap was put up in the river in 2020 (Figure 4). The downstream trap was put up in May 2021, and fish have been registered migrating downstream from May 16th to June 23^{rd,} 2021. The trap consists of a wooden frame (147 x 104 x 90 cm), with metal mesh walls (net size 23 x 23 cm), and mesh fences going out to each side. The trap attached to the bottom with rebars. The trap can be opened from the top, allowing removal of fishes from the trap. The upstream trap is made the same way as the downstream trap, facing the opposite direction, so that the fish migrating upwards get caught in the trap. This study was part of a larger project, which tagged fish with Floyd-tags migrating upstream and downstream. The handling of the fish complied with national Norwegian animal welfare laws. Project was approved by the Troms and Finnmark County governor, and had a permit reference number of 2020/14374 (Grenier et al., 2023).

The charr described in this project were caught in a period between May 5th, 2021, and August 8th, 2021. Three of the charr in the sample were tagged migrating downstream. Weight (g) and length (total length, mm) were registered directly after capture (see Appendix 7.1 for size distribution).

In total, 97 charr were tagged migrating downstream, and 1302 were tagged migrating upstream. 35 charr were taken back to the lab at UiT for further analyses. They had a size varying from 250 to 400 mm (total length). It was estimated that these were first time migrants. They were killed with a hit to the head while sedated and kept frozen until further analyses.

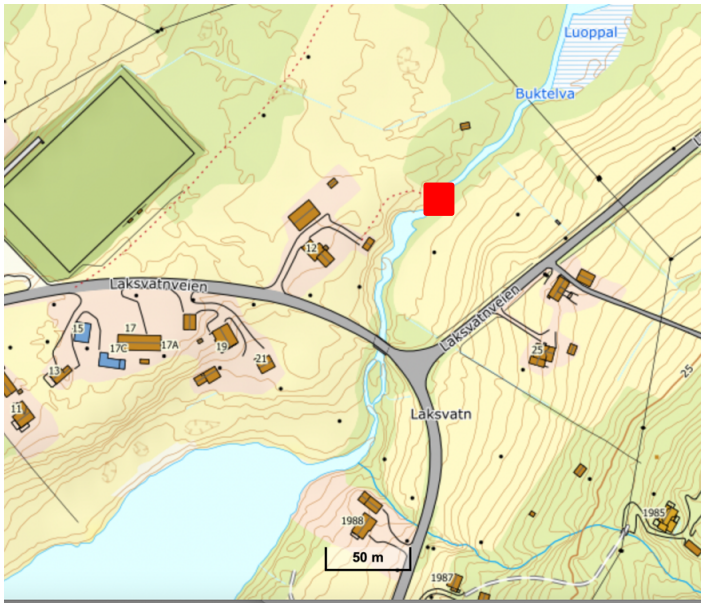

Figure 4: Close-up map of the river running down to Laksvatnbukta. Red square indicates where the trap was set up and the fish samples were collected. Source: norgeskart.no

2.3 Dissection and processing

35 fish were dissected and analyzed for parasites according to Cribb and Bray (2009) and Justine et al. (2012). Organ samples were kept in the freezer until analysis. All parasites were classified to the lowest taxonomic level possible, counted, and stored on ethanol. Moravec (2004) was used for morphological identification for all parasites.

The external part of the fish was analyzed for ectoparasites. Ectoparasites were classified to lowest taxonomic level, counted and stored on ethanol. Metacercariae cysts of *C. lingua* on the skin were counted. Mucus and flesh samples were taken for stable isotope analysis (See

appendix 7.8). Otoliths were taken out and stored on ethanol. The fish was opened by cutting the abdomen from the anterior to the posterior end.

Gills were removed from the fish, broken up into individual gill arches and added saline water. Each arch was analyzed separately in the loop. Trematodes found in the gills were counted as stomach parasites, as parasites might leak out of to gills from the stomach (Bouillon & Dempson, 1989).

Eyes were removed from the fish. The right eye was analyzed. The eye was cut open from the back. The lens and the vitreous humor (VH) were taken out and analyzed for parasites. The retina was scraped out and analyzed systematically three times. Parasites from the different parts of the eyes were combined. Due to analyzing only one eye, this value was multiplied by two.

The kidney was carefully removed from the fish. The external part was analyzed for myxozoa cysts, and the kidney was opened and analyzed for trematodes. The gonads were examined for parasites, as well as determining the sex of the fish. Heart, brain, gall bladder, liver, and spleen were analyzed for parasites by pressing the organs between two glasses.

The digestive track was removed from the fish. The stomachs were stored separately from the intestine. The external part of the stomach was examined for encysted plerocercoids of *Dibothriocephalus* spp. For the stomach, only a subsample of parasites was counted. This was due to a very high abundance of trematodes in the stomach. An incision was made vertically from the esophagus down to the stomach. The same part of the stomach was taken out for each fish. Trematodes were counted for this part. This number was multiplied by 4 to make an estimate of the stomach trematodes. The nematodes were all taken out and counted. A test was done to ensure the trematode estimate was a sound estimate (see Appendix 7.6 for more information about this test and estimate).

For the intestine, an incision was made vertically from the end of the pyloric caeca down the intestine. Content was carefully scraped out. Each caecum was analyzed individually. All trematodes and nematodes were counted. Cestodes were counted with the scolex intact.

2.4 Morphology analyses

Moravec (2004) was used for morphological identification for all species and taxa. Parasites were analyzed according to Cribb and Bray (2009) and Justine et al. (2012). Pictures of parasites can be found in Appendix 7.4.

2.4.1 Nematoda

Nematodes were studied using a microscope to identify to species level. Nematodes were put in a mixture of half 86% glycerol and half purified water 20 hours before examination. On the observation day, the nematodes were put onto concave microscope slides, covered by a glass slide, and observed in the microscope. Special attention was paid to the anterior and posterior end of the nematode.

2.4.2 Trematode staining

Trematodes in adult life stages were stained with aceto-carmine, left cold for 2-3 hours. They were put in regression, dehydrated in a series of ethanol, and then in a series with eugenol mixed with varying amount of ethanol. They were put in mounts of Canada balsam and left to dry for 2-3 weeks. Trematodes were examined in a microscope. Only the adult stages were stained. More detailed description of this procedure is found in Appendix 7.2 and pictures can be found in Appendix 7.4. Morphological traits used for taxonomic classification were placement and size of suckers and appendages.

2.4.3 Cestode & acanthocephalan staining

Cestodes in adult stages and acanthocephalans were stained in iron aceto-carmine, left cold for 15 minutes. They were put in regression, dehydrated in a series of ethanol, and then left in mixtures of eugenol and ethanol. They were put in mounts of Canada balsam and left to dry for at least 3 weeks. They were then studied in the microscope. Special attention was paid to the scolex and proboscis for the cestodes and acanthocephalans, respectively, according to Moravec (2004). Protocol for the staining process for cestodes and acanthocephalans can be found in Appendix 7.3.

2.5 Molecular identification

To confirm the morphological identification of the parasite taxa, molecular identification was conducted by one of my supervisors at the Natural History Museum of Geneva, Switzerland

(See appendix 7.7). The DNA of each specimens analyzed were extracted with 200 ml Chelex ® (5%) and 0.1 mM Proteinase K overnight. According to Blasco-Costa et al. (2016) the trematodes, cestodes and acanthocephalans were identified by amplifying a fragment of the large ribosomal subunit (28S rDNA). The 28S rDNA was amplified using primers (5′-CCA GCG CCA TCC ATT TTC A-3′) (LOCKYER et al., 2003); and LSU5F (5′-TAG GTC GAC CCG CTG AAY TTA AGC-3′) for the trematodes and acanthocephalans, and 1500R (5′-GCT ATC CTG AGG GAA ACT TCG-3′) primers for the cestodes (Blasco-Costa et al., 2009) .

For molecular identification of the nematodes, a part of the small ribosomal subunit (18S rDNA) was used (Černotíková et al., 2011) 18S rDNA was amplified using the primers PhilonemaF (5′-GCC TAT AAT GGT GAA ACC GCG AAC-3′) and PhilPCRr0 -primers (5′-CCG TT CAA GCC ACT GC ATT A-3′) and PhilPCRr0 -primers (5′-CCG TT CAA GCC ACT GC ATT A-3′) (Černotíková et al., 2011).

Electrophoresis was conducted for single band PCA product to verify amplicons generated. The amplicons were purified using exonuclease I and thermosensitive alkaline phosphatase enzyme (Werle et al., 1994). Samples were sent off to Macrogen Europe in Amsterdam for further sequencing. The results from the sequencing were assembled and inspected using Geneious prime ver. 8.1.9 (Kearse et al., 2012), as well as manually by eye. Nucleotide BLAST was used to check if the closest sequence was within the same genus as former identification.

2.6 Statistical parameters and indices

Infection parameters were calculated in Excel, and graphs were made using various packages of RStudio (script in Appendix 7.5). Prevalence of infection (Bush et al., 1997) is the percentage of individuals in the population infected by a parasite species or parasitic group. Graphs were made using the barplot function in the ggplot2 package (Wickham, 2016). Mean abundance (Bush et al., 1997) is the mean number of parasites per host in the total population of hosts. Mean intensity is the mean number of parasites per host in the infected population (Bush et al., 1997). This illustrated using the boxplot function in the ggplot2 package (Wickham, 2016). Taxon richness was calculated by finding the mean number of parasite taxa per individual. This was demonstrated using the histogram function in ggplot2 (Wickham, 2016). Fish having NA values were excluded from this calculation, to avoid underestimating. To test for statistical significance for the taxon richness, indices and transmission Mann-

Whitney U-test was used (Mann & Whitney, 1947). This test seemed appropriate for non-normally distributed data and small sample sizes. Calculations were made using the inbuild wilcox.test function in Rstudio.

Shannon-Weiner index and Simpson's index were used to compare diversity between the freshwater and marine parasite taxa. Two different indices were used to strengthen the results. Indices were calculated using the vegan package (Oksanen J et al., 2022). First, the indices were calculated for each infracommunity for marine parasites, freshwater parasites and then the total parasite community. Mean was calculated for each group.

The Simpson's index (Krebs, 1999) is a value between zero and one, and indicates the probability of picking two random individuals from a population that are of the same species. Common/dominant species will influence this index greatly. The calculation for Simpson's index used in this paper is listed in Formula 1.

$$Simpson's\ index\ (D) = 1 - \sum(p_i)^2 \qquad \text{Formula 1}$$

p_i refers to the proportion of individual species in the community.

The Shannon-Weiner function is used to calculate the uncertainty when trying to predict the next species collected from the population (Krebs, 1999). Larger uncertainty will lead to a larger value. This index is influenced by rare species. Formula is listed in Formula 2.

$$Shannon - Weiner\ index\ (H') = \sum(p_i)(log_2 p_i) \qquad \text{Formula 2}$$

Principal component analysis was conducted using the princomp function, and biplot was made using the inbuild biplot function in RStudio. Upset plots were made using the UpsetR package (Gehlenborg, 2019).

3 Results

3.1 Parasite identification and prevalence

A total of 17 taxa were identified. All charr were infected by at least 6 different parasite taxa. A total of eight freshwater taxa were observed. One crustacean gill parasite *Salmincola* sp. (Wilson 1915) was found and had a of prevalence less than 3%. The eye trematodes *Diplostomum* spp. (von Nordmann, 1832) had a 100% prevalence, while *Tylodelphys* sp. (Diesing, 1850) had a much lower prevalence, 11%. The kidney trematode *Phyllodistomum umblae* (Fabricius, 1780) and cysts of Myxozoa had prevalences of 97% and 81%, respectively. Plerocercoids larvae cysts of *Dibothriocephalus* sp. (Lühe, 1899) had a prevalence of 39%, while the adult cestodes *Proteocephalus* sp. (Weinland, 1858) had a prevalence of 83%, and *Eubothrium salvelini* (Schrank, 1790) had a prevalence of 34% (Figure 5).

Nine marine taxa were observed. Sea lice (*Caligus* sp. & *Lepeophtheirus* sp.) had a prevalence of 40%. Metacercariae of the trematode *Crytocotyle lingua* (Creplin, 1825) had a prevalence of 97%. The nematode *A. simplex* had a prevalence (Rudolphi, 1809) of 17%. High prevalences of gastrointestinal parasites were observed. The trematodes *Hemiurus levenseni* (Odhner 1905) had a prevalence of 100%, *Derogens varicus* (Müller, 1784) had a prevalence of 94%, while *Potoctyle atomon* (Rudolphi, 1802) had a prevalence of 97%. The nematode *Hysterothylacium aduncum* (Rudolphi, 1802) had a prevalence of 97%. The marine cestode *Abothrium gadi* (Van Beneden, 1871) had a prevalence of 11%, and the marine acanthocephalan *Echinorhynchus* sp. had a prevalence of 9% (Figure 6).

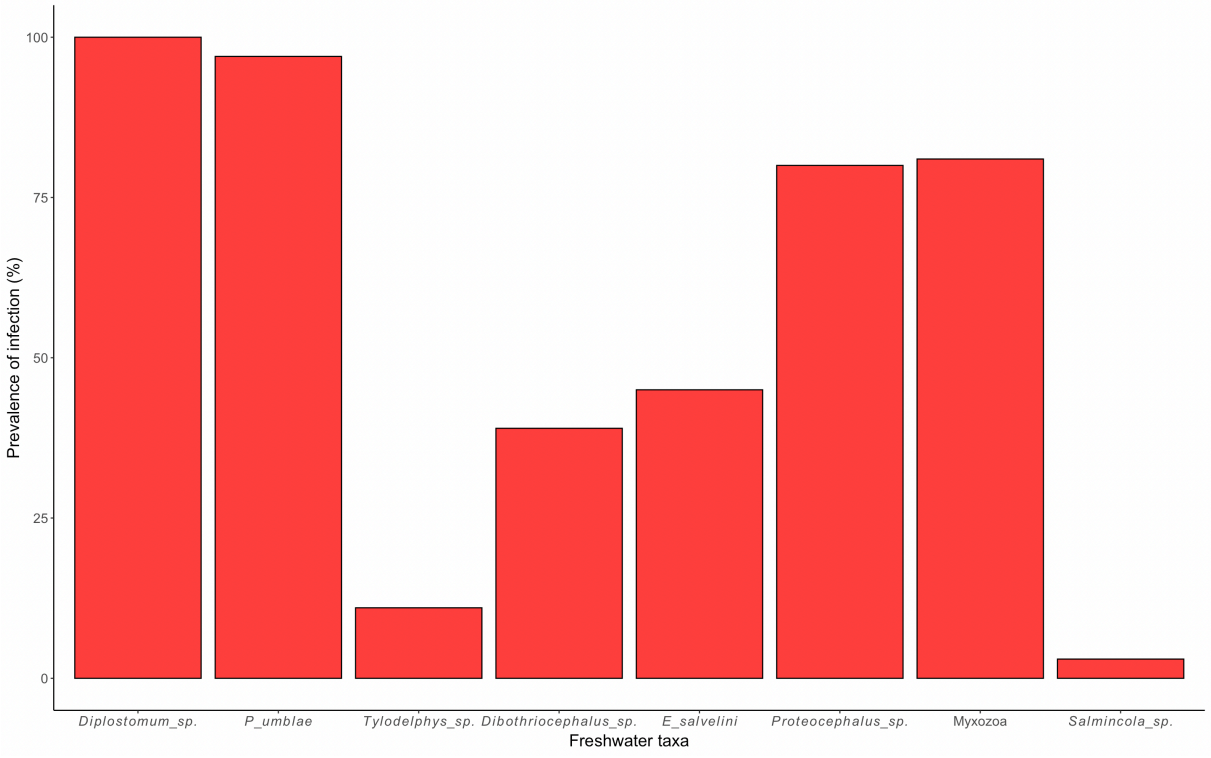

Figure 5: prevalence (%) of freshwater parasite taxa in anadromous Arctic charr from Laksvatn. Two taxa show almost 100% prevalence, while others vary. A total of eight freshwater taxa were observed.

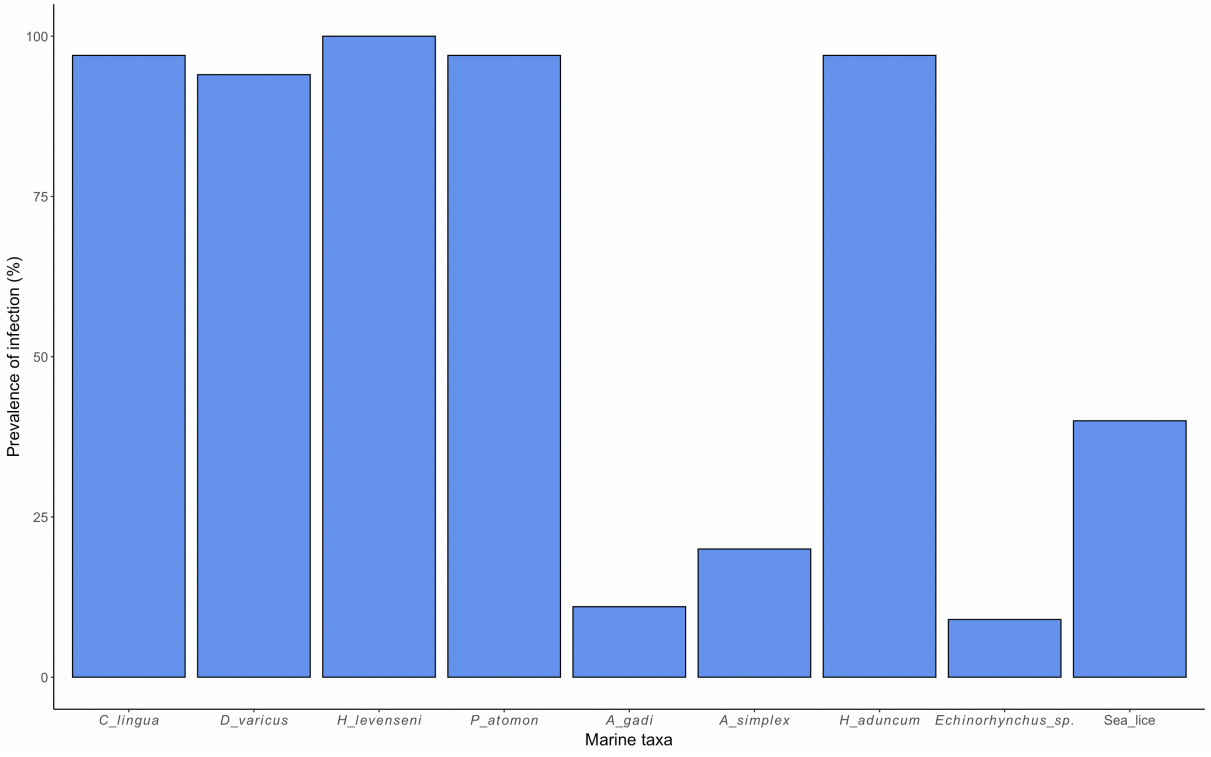

Figure 6: prevalence (%) of marine parasite taxa of anadromous Arctic charr from Laksvatn. Five taxa show almost 100% prevalence, while others are rarer. A total of nine marine taxa were observed.

3.2 Abundance

High abundances of parasites were found. In total, 181 557 individual parasites were counted/estimated. The abundance of marine parasites was significantly higher (Mann-Whitney U-test: $p<0.05$; n=33) than the abundance of freshwater parasites (n=27, Figure 7). 97% of the observed parasites were of marine origin, the remaining 3% were of freshwater origin. Median for the freshwater infracommunity was 136 parasites and for the marine infracommunity 4292 parasites. Parasites were infecting multiple organs within the charr, many found in the gastrointestinal tract of the fish (Table 1).

Large variations of mean abundance were observed between the hosts and the different taxa. On average, each fish had a total parasite abundance of 5754 individual parasites, 135 of these were freshwater parasites, and 5619 were marine parasites. Some taxa were categorized as at low mean abundance and had a mean abundance less than five individual parasites per fish. The marine parasite taxa sea lice and *A. simplex* had mean abundances of 1.00 and 0.29, respectively. For freshwater taxa, eye trematode *Tylodelphys* sp. had a mean abundance of 0.29, myxozoa had a mean abundance of 2.19, plerocercoid cysts of *Dibothriocephalus* spp. had a mean abundance of 2.50 and adult *E. salvelini* had a mean abundance of 2.00.

Some taxa had a medium mean abundance, which was higher than five and lower than 30. The trematodes *C. lingua* and *P. umblae* mean abundances of 11.64 and 12.00, respectively. The freshwater cestode *Proteocephalus* sp. had a mean abundance of 25.71 while the marine cestode *A. gadi* had a mean abundance of 7.83. *Echinorhynchus* sp. had a mean abundance of 9.23.

Some taxa had a high mean abundance over 30. *Diplostomum* spp. had a mean abundance 89.89. The marine nematode *H. aduncum* had a mean abundance of 44.94. For the gastrointestinal marine trematodes, some extremely high abundances were observed. The trematode species *H. levenseni*, *D. varicus* and *P. atomon* had mean abundances of 3738.51, 916.03 and 351.83, respectively.

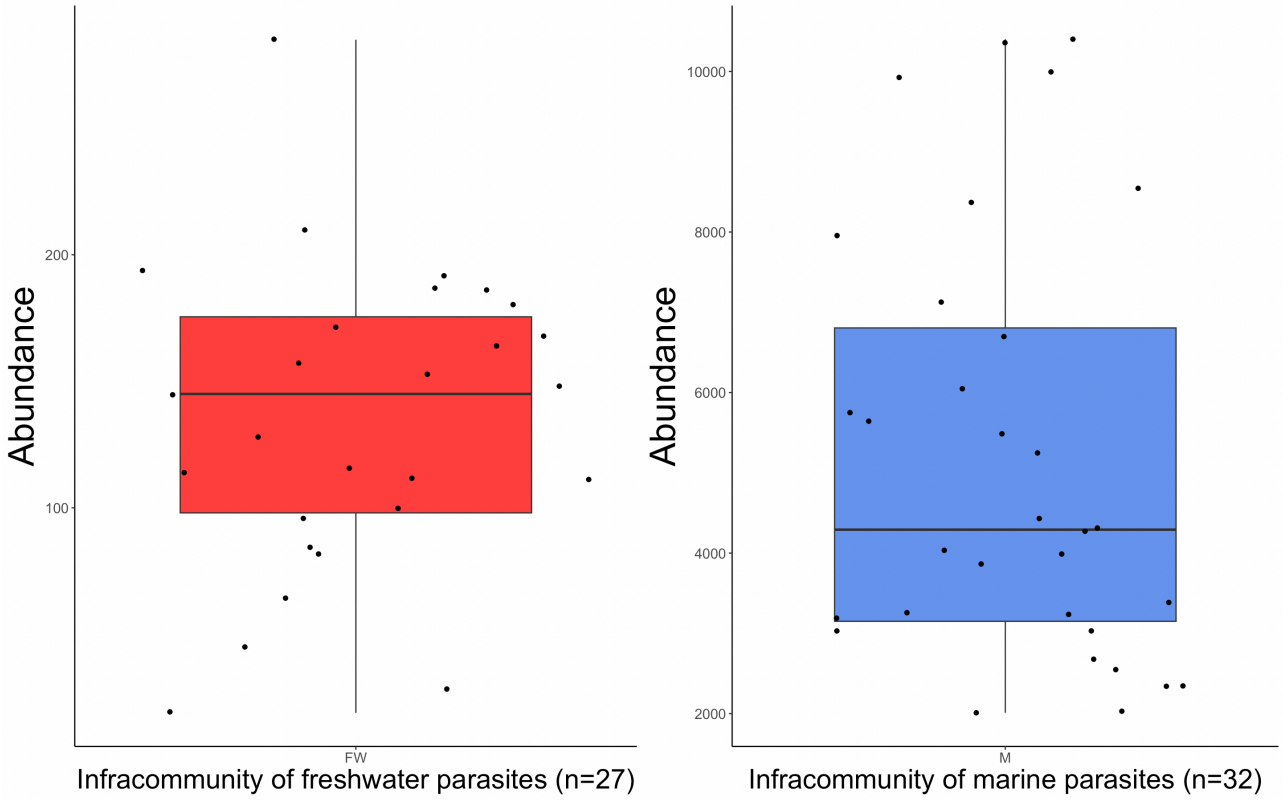

Figure 7: abundance of marine parasites (left) and freshwater parasites (right) in anadromous charr from Laksvatn. The scaling on the y-axes is different. Each dot represents one parasite infracommunity in the graphs. Horizontal black line is the median, which for freshwater parasites is 136 and for marine parasites 4292. The marine infracommunity is significantly (Mann Whitney U-test: $p<0.05$) higher in abundance than the freshwater infracommunity.

Taxa		E	H	T	P(%)	MA	MI	RI
Trematoda	*Cryptocotyle lingua*	M	Skin	AT	97	11.64	12.00	1-49
	Derogens varicus	M	Stomach, esophagus	TT	94	916.03	973.28	8- 2816
	Diplostomum spp.	FW	Eye	AT	100	89.89	89.89	6-276
	Hemiurus levenseni	M	Stomach, intestine	TT	100	3738.51	3738.51	564-9550
	Phyllodistomum umblae	FW	Kidney, ureter	U	97	12.00	12.39	1-52
	Potoctyle atomon	M	Intestine	TT	97	351.83	362.18	4-1694
	Tylodelphys sp.	FW	Eye	AT	11	0.29	2.00	2-4
Cestoda	*Abothrium gadi*	M	Intestine	TT	11	7.83	68.50	13-224
	Dibothriocephalus sp.	FW	Body cavity	TT	39	2.50	6.36	1-13
	Eubothrium salvelini	FW	Intestine	TT	34	2.00	4.12	1-37
	Proteocephalus sp.	FW	Intestine	TT	83	25.71	34.62	1-135
Nematoda	*Anisakis simplex*	M	Liver	TT	17	0.29	1.43	1-2
	Hysterothylacium aduncum	M	Stomach, intestine	TT	97	44.94	46.26	3-141
Acanthocephala	*Echinorhynchus* sp.	M	Intestine	TT	9	9.23	107.67	1-246
Crustacea	Sea lice	M	Skin	AT	40	1.00	2.33	1-7
	Salmincola sp.	FW	Gills	AT	3	0.03	1.00	1-1
Cnidaria	Myxozoa	FW	Kidney, ureter	AT	81	2.19	2.69	1-6

Table 1: overview of all taxa observed. Abbreviations: Environment (E), freshwater (FW), marine (M), habitat (H), transmission (T), actively transmitted (AT), trophically transmitted (TT), unknown (U), prevalence (P%), mean abundance (MA), mean intensity (MI) and range of intensity (RI)

3.3 Taxon richness and diversity

Each fish was on average infected by 4.5 (±1.01 SD) freshwater taxa and 5.6 (±0.87 SD) marine taxa (Figure 8), meaning that they generally had more marine parasite taxa than freshwater taxa. The difference between freshwater taxon richness and marine taxon richness was however non-significant (Mann Whitney U-test: $p>0.05$, Table 2). Total taxon richness of freshwater and marine parasites was 10.1(±1.38 SD).

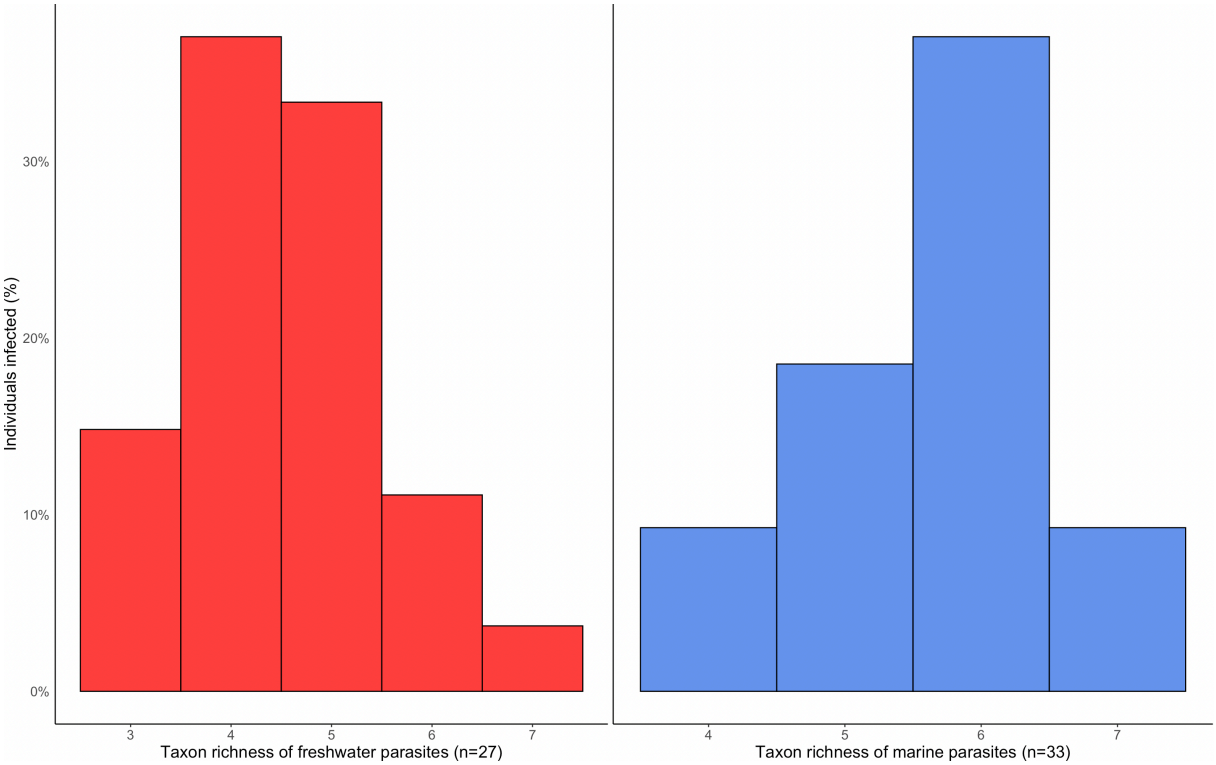

Figure 8: taxon richness of the marine parasites (left) and the freshwater parasites (right) for anadromous charr from Laksvatn. Non-significant difference between the two groups in taxon richness (p>0.05).

The Simpson's index was almost the same for the freshwater and marine infracommunity, with no significant difference (Mann-Whitney U-test: $p>0.05$). The Shannon-Weiner index was slightly higher for the freshwater infracommunity, however the difference was non-significant (Mann-Whitney U-test: $p>0.05$, Table 2).

Table 2: Mean abundance, taxon richness, Shannon-Weiner diversity index and Simpson's index of freshwater, marine and total parasite abundance in anadromous charr from Laksvatn. Mann-Whitney U-tests are used to test for difference, and a p-value less than 0.05 indicates significance. Abbreviations: standard error (SE), standard deviation (SD), freshwater (FW) and marine (M).

	Freshwater parasites (n=27)	***Marine parasites (n=33)***	***Total (FW&M)***	***P-value***
Mean abundance (±SE)	*135±12*	*5619 ± 467*	*5754 ± 508*	$P=2.2e^{-16}$
Taxon richness (±SD)	*4.5 ± 1.01*	*5.6 ± 0.87*	*10.1 ± 1.38*	*P=0.055*
Shannon-Weiner diversity index (±SD)	*0.75±0.27*	*0.69±0.21*	*0.81±0.35*	*P=0.72*
Simpson's index (±SD)	*0.39±0.16*	*0.38±0.33*	*0.41±0.20*	*P=0.95*

3.4 Transmission

Three freshwater taxa were trophically transmitted, and four freshwater taxa were actively transmitted. For the marine taxa, seven taxa were trophically transmitted while two taxa were actively transmitted. The life cycle of *P. umblae* is unknown, and therefore not included in these calculations. The charr had a significant higher abundance (Mann Whitney U-test: $p<0.05$) in marine trophically transmitted parasites and actively transmitted parasites (Table 3). On the contrary, the actively transmitted freshwater parasites were significantly higher (Mann-Whitney U-test: $p<0.05$) in abundance than the trophically transmitted freshwater parasites.

Table 3: overview of trophically transmitted and actively transmitted parasites and their significance, from anadromous charr from Laksvatn.

	Freshwater (n=27)	**Marine (n=32)**	**Total**
Trophically transmitted parasites abundance (±SE)	25±6.88	5160±466.15	5184±465.90
Actively transmitted parasite abundance (±SE)	98±11.67	13±1.94	111±9.60
Significance	$P=8.858e^{-7}$	$P=6.394e^{-12}$	$P=4.657e^{-10}$

3.5 Parasite community composition

The PCA biplot (Figure 9) shows that the infracommunities within the fish are spread out randomly. It appears as there are no trends for the infracommunities. *H. levenseni* and *Diplostomum* spp. appear to contribute to variance on both components.

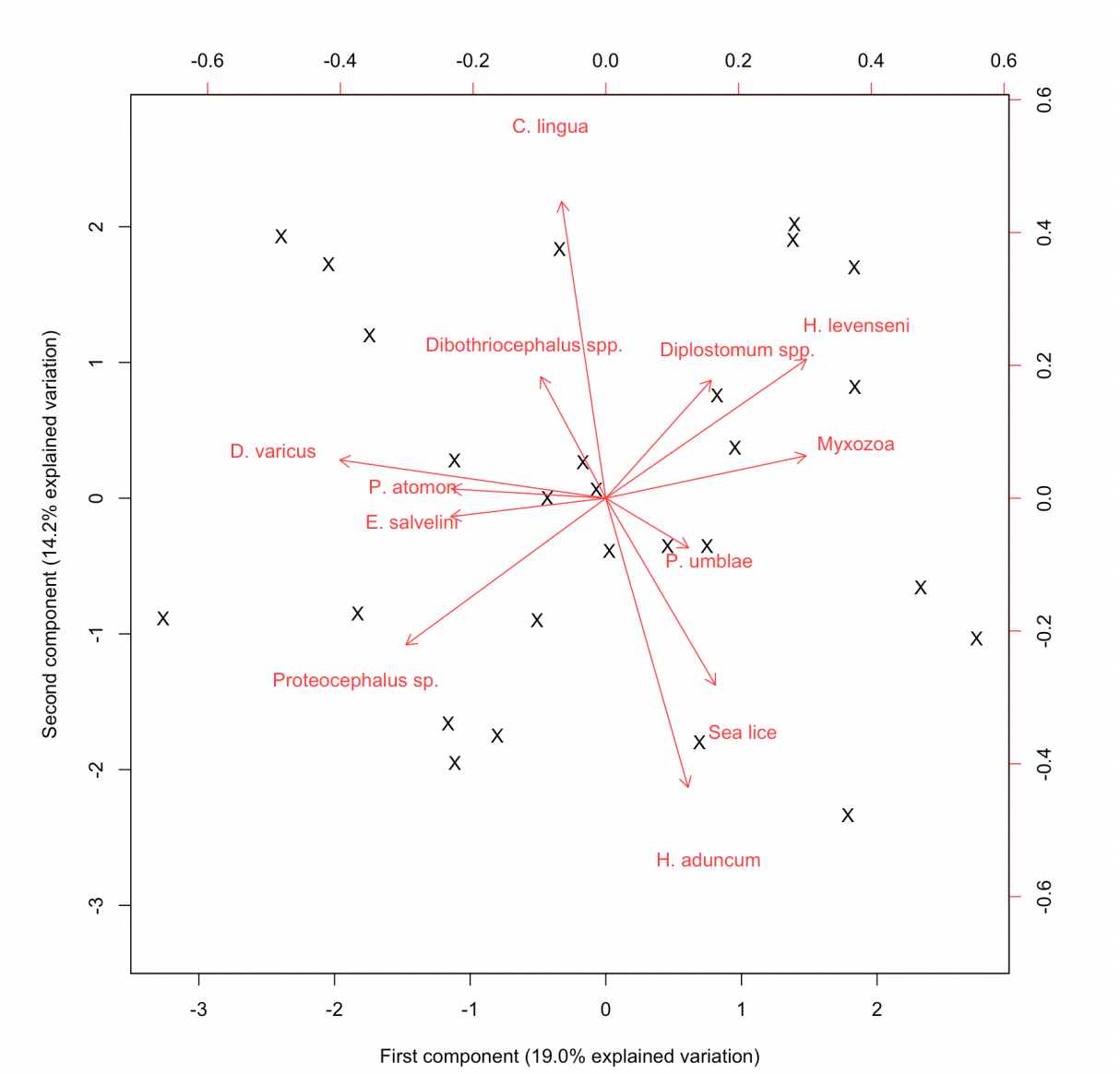

Figure 9: Standardized principal component analysis biplot of the parasite community of anadromous charr from Laksvatn. Each cross represents one infracommunity, and pointers show the variation of parasite taxa with a prevalence above 20%, and how they contribute to the variation within each infracommunity.

Figure 10 displays that for the freshwater infracommunity there are 11 combinations of taxa that reside within the anadromous charr during the migration. Figure 11 displays that for the marine parasites there is a more homogenous parasite infracommunity, with five or six species infecting almost all individuals in the anadromous population of charr.

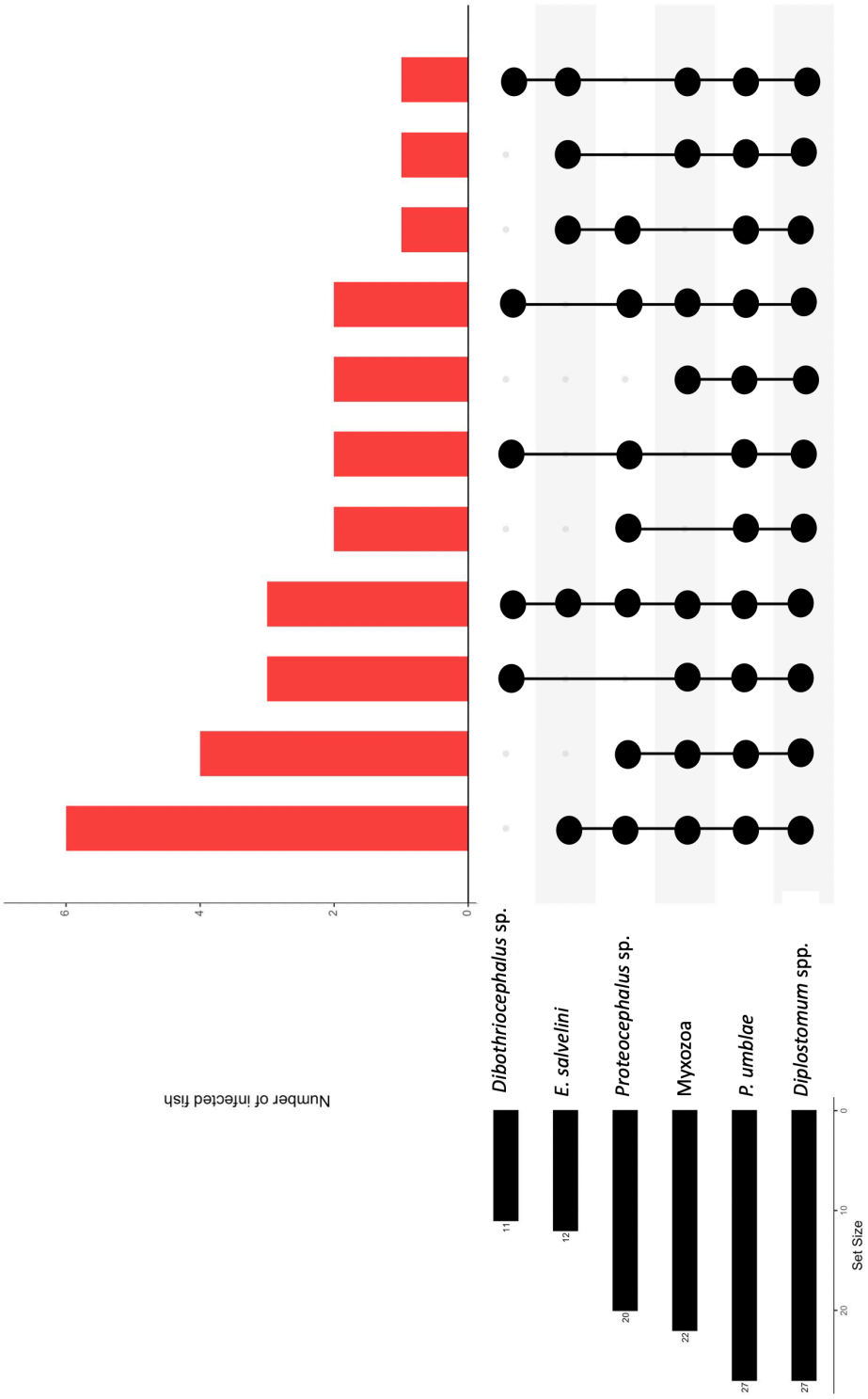

Figure 10: upset plot of the six most common freshwater parasite taxa infecting anadromous charr from Laksvatn. *The matrices (dots) show the combination of parasite taxa, and the vertical bars show how many hosts have this specific combination. The horizontal bars to the left show how many hosts the parasite taxa were observed in.*

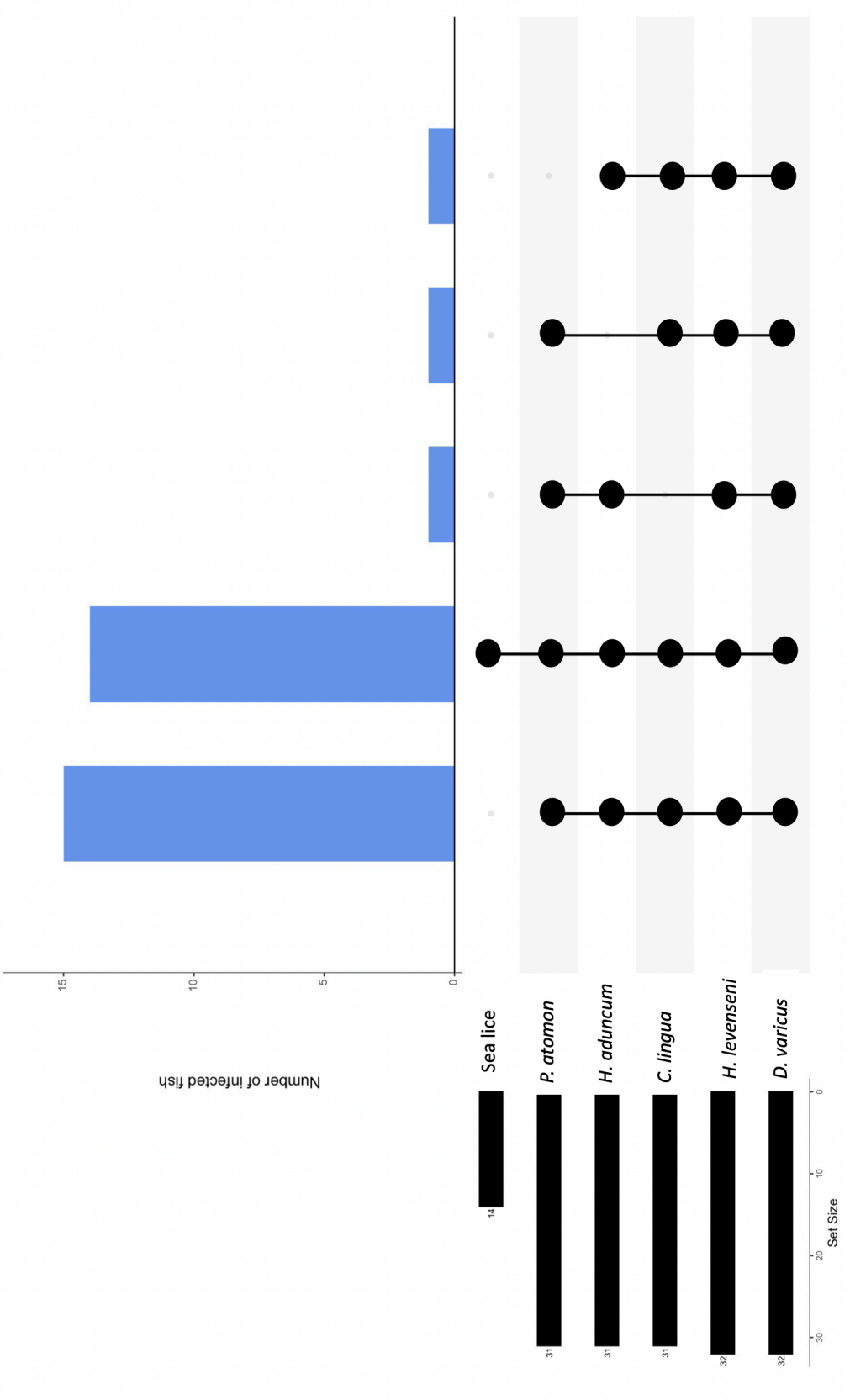

Figure 11: upset plot of the six most common marine parasite taxa in anadromous charr from Laksvatn. The matrices (dots) show the different combinations of parasite taxa, and the vertical bars show how many hosts have this specific combination. The horizontal bars to the left show how many hosts the parasite taxa were observed in.

4 Discussion

The parasite community of returning anadromous charr from Laksvatn, Troms og Finnmark, had a high taxon richness. There was no significant difference in taxon richness or diversity between the freshwater parasite infracommunity and the marine parasite infracommunity. This study revealed some very high abundances of parasites. Parasites of marine origin were significantly higher in abundance than the parasites of freshwater origin, and of the marine parasites, majority were trophically transmitted.

4.1 Parasite community

As hypothesized, the parasite community of the anadromous charr consisted of both marine and freshwater species, with no significant difference in taxon richness. Other studies of parasite community of anadromous salmonids have also found a community consisting of both freshwater and marine taxa. Knudsen et al. (2005) looked at the trophically transmitted parasites of Atlantic salmon (*Salmo salar,* Linneaus, 1758) in Norway, and they observed eight freshwater species and five marine species. A study of the parasite community of anadromous brown trout in Norway (Dalen, 2011) found seven marine taxa and four freshwater taxa. Frimeth (1987b) studied the parasite community of anadromous brook charr (*Salvelinus fontinalis,* Mitchill, 1814) and found a total of 36 different species: 18 of freshwater origin and 18 of marine origin. This shows that parasites can survive for some time in a host with an altered salinity in the external macroenvironment.

Some parasites found in anadromous charr from Laksvatn are commonly found in other fishes; both anadromous fishes (Bouillon & Dempson, 1989; Dalen, 2011; Knudsen et al., 2005) and strictly marine fishes (Hemmingsen & Mackenzie, 2001). The two most abundant trematodes in this study, *H. levenseni* and *D. varicus* are reported in other studies of anadromous salmonids, as well as being common in marine fishes (Hemmingsen & Mackenzie, 2001). The same goes for the most common nematode in the postsmolt charr, *H. aduncum*, a marine nematode that also has a wide variety of fish hosts (Balbuena et al., 2000; Køie, 1993). The larval marine trematode, *C. lingua,* also has a wide variety of hosts, and has been described as one of the most common marine trematodes of the North-East Atlantic (Hemmingsen & Mackenzie, 2001). The parasite was also very prevalent in this population of anadromous charr. Interestingly, it has been suggested that this trematode should be used as a biological indicator for marine migration, as the pigmented black spot can be seen after the

death of the parasite (Frimeth, 1987a). The marine cestode *A. gadi* has previously been described as parasite specific to cod and gadoid fishes (Hemmingsen & Mackenzie, 2001), however, it was observed in 11% of this population of anadromous charr. One taxon of Acanthocephala *Echinorhynchus* sp. was observed, which has also been found in the intestine of other migrating salmonids.

Findings in this study may suggest that many freshwater parasite taxa are able to survive in a macroenvironment with an altered salinity for some time. Eight different freshwater parasite taxa were observed in returning anadromous charr from Laksvatn, and the parasites were in high abundances. Studies of parasite community in anadromous salmonids (Bristow et al., 1996; Dalen, 2011; Knudsen et al., 2005) have also found that several taxa of freshwater parasites survive the marine journey. The freshwater cestodes *E. salvelini, Proteocephalus* sp. and *Dibothriocephalus* sp. have all been found to survive post-migration (Bouillon & Dempson, 1989; Due & Curtis, 1995), and interestingly, *E. salvelini* has shown to become gravid during the migration (Frimeth, 1987b). The large difference between the marine parasite abundance and the freshwater parasite abundance in the anadromous charr might suggest that there is some reduction in the freshwater infracommunity during the migration, as seen in other studies (Bouillon & Dempson, 1989; Dick & Belosevic, 1981). This reduction can come from intra- or interspecific competition (Goater et al., 2014), morphological changes in the intestine (MacLeod, 1978), or an altered salinity in the external environment (Bailey et al., 1989; Kristoffersen, 1993).

Bailey et al. (1989) tested the resilience for some freshwater parasites and found that they were able to tolerate a saline environment for varying lengths. Eye flukes, *Diplostomum* spp., started to decline after 10 weeks of exposure, which is longer than the length of the marine migration of the anadromous charr from Laksvatn (Opheim, 2022). This might explain why this parasite taxa not only have a 100% prevalence, but also has the highest mean abundance among the freshwater parasites. It is worth noting that this parasite was in a larval metacercarial stage, which could affect the reaction to the saline macroenvironment. The habitat of this trematode, the eyes, might be less affected by the change in macroenvironment than organs that are very exposed to saline water, such as the stomach or the gills. On the contrary, the kidney trematode *P. umblae* had a prevalence of 97%. This parasite has been shown to decline rapidly in saline environment, due to an altered environment in the kidney after entrance to sea water (Bailey et al., 1989). It is therefore surprising to find them being so prevalent in this population of anadromous charr, as to my knowledge they have also not been

detected in other studies of parasites in anadromous salmonids returning from the sea (Bouillon & Dempson, 1989; Pennel et al., 1971; Unger & Palm, 2016). One individual *Salmincola* sp. (gill lice) was observed. The likeliness of a gill crustacean parasites surviving the marine migration is low, as the ectoparasites are the first ones lost after sea water entrance (Frimeth, 1987b). Most likely the fish was infected while on its way up to the river, or in the trap. It is likely that this parasite is more abundant in the charr population during the stay in the freshwater system, compared to the stay in the marine system.

Parasites of belonging to the genus *Crepidostomum* were not observed in this population of anadromous charr. This was somewhat surprising as several other studies of parasite communities of anadromous salmonids have observed this parasite taxa (Bouillon & Dempson, 1989; Dick & Belosevic, 1981; Due & Curtis, 1995). However, for some studies the salmonid fish were caught at sea, meaning that they had not completed their migration (Bristow et al., 1996; Dalen, 2011; Knudsen et al., 2005). Alternatively, they had been back in freshwater for months (Frimeth, 1987b), giving the fish time to get infected by *Crepidostomum* in the freshwater environment. Another explanation could be competition over space and food (Goater et al., 2014), as the intestine was the organ with the highest diversity of parasites, with six different parasite taxa being found in this organ alone. High abundances of marine trematodes were also observed.

The freshwater parasites had a lower taxon richness than the marine parasites in the anadromous charr, however the difference was non-significant. Two indices were combined with the taxon richness to test for diversity with the evenness included. They also showed a non-significant difference between the freshwater and marine infracommunities. Although there are more marine parasites than freshwater parasites, the trends in abundance of parasites in the population appear to be similar. *H. levenseni* is the most abundant marine parasite, while *Diplostomum* spp. is the most abundant freshwater parasite in the anadromous charr. The trematodes *H. levenseni* make up 74% of the total marine infracommunity, while *Diplostomum* spp. make up 68% of the total freshwater infracommunity. It therefore seems like both taxa exhibit some sort of dominance in the population, although for the marine parasites it comes at a much higher abundance. Dalen (2011) studied the parasite community of anadromous brown trout on two locations, and found a Simpson's index at 0.7 and 0.75, indicating a lower diversity than the anadromous charr from Laksvatn. This could be explained by the low abundance of freshwater parasites in their study, with a mean taxon richness of 0.3 freshwater taxa. A study of anadromous brown trout in the Baltic sea (Unger

& Palm, 2016), found a Shannon-Weiner index of 1.04, which is higher than in the anadromous charr from Laksvatn. Their study had many rare species, which can increase this index. There are some indications (See Appendix 7.6) that the estimate for mean abundance for *D. varicus* is somewhat overestimated, thus it was not believed that this would impact the outcome too much, as the abundance is already very high.

The overall findings in this study correspond well with other findings in similar studies, with a few surprising finds (e.g., very high abundances of parasites) and some expected finds that were not observed (e.g., *Crepidostomum* sp.). The large difference in abundance of freshwater and marine parasites can be explained by a reduction and replacement of freshwater parasites with marine parasites throughout the marine migration period. Majority of the marine parasites were trophically transmitted, meaning that they stem from the active feeding pattern in the sea of important intermediate hosts for the present parasite taxa (e.g. fish, crustaceans, Opheim (2022)). None of the marine helminth parasite taxa are specific to salmonids, they appear to be generalists and have a wide host spectrum (Hemmingsen & Mackenzie, 2001; Hemmingsen & Mackenzie, 2013).

4.2 Arctic charr feeding patterns

The high abundances of parasites observed in this population of anadromous charr from Laksvatn consist mostly of trophically transmitted parasites that have infected the anadromous charr while feeding on marine resources. The smallest charrs from Laksvatn doubled their body mass during the marine migration, and the stomach contents showed that they fed on small marine fish, amphipods and airborne insects (Opheim, 2022). The same study showed that in the freshwater system the most important prey type for the charr was planktonic copepods, while in the marine system the anadromous charr from Laksvatn fed mostly on small marine fish or amphipods. It was therefore suggested that while in the marine system, the anadromous charr shifted their diet slightly, moving up in the food web and feeding on higher trophic levels than in the freshwater system. Studies of food webs where parasites were included (Amundsen et al., 2009; Lafferty, 2008) have shown that many species of parasites can be found on the intermediate trophic levels of the food web, so feeding on these trophic levels will most likely increase the risks of being infected by parasites. The excessive feeding pattern combined with a shift in diet to a higher trophic level could explain the high parasite abundances.

The two abundant parasites *H. levenseni* and *D. varicus* have a similar route of infection, with a gastropod as the first intermediate host, planktonic copepods as second intermediate host, small fish as possible paratenic host and large fish as final host (Krupenko et al., 2020; Køie, 1979). As planktonic copepods were not found in the stomachs of returning anadromous charr (Opheim, 2022), it seemed more likely that small marine fish was the main route of infection for the anadromous charr, as they make up 61% of the observed prey (Opheim, 2022). Also, the two gastrointestinal parasites often infect together, as almost all the observed charr were infected by both *H. levenseni* and *D. varicus*. which strengthens the theory that they used the same paratenic host (i.e., small marine fish).

Another marine trematode with a high abundance was *P. atomon.* This species uses *Littorina* sp. snails as first intermediate host, and *Gammarus* sp. as second intermediate host (Hunninen & Cable, 1943). *Gammarus* sp. makes up 13% of the observed stomach content from anadromous charr from Laksvatn. A study from lake Takvatn, another subarctic lake in the same geographic region (Shaw et al., 2020), mapped the parasites utilizing *Gammarus* sp. as a host and found that no less than seven species had this as their intermediate or final host. This reflects the importance of this specific host for parasites in the food web. It is therefore not unlikely that *Gammarus* sp. would also play a role in shaping the parasite community of anadromous charr from Laksvatn.

Trematodes are the clear dominating parasite taxa in this population of charr. Generally, trematodes are the most common parasitic group in intertidal animals (Mouritsen & Poulin, 2002). Post-smolt charr has shown a preference for depths from 0 to 3 meters, indicating that they stay and feed in this zone (Nordli, 2021). Another factor playing a role in the dominance of trematodes can be seasonal variation. Schade et al. (2016) studied the parasite communities of four marine fishes over all seasons for two years and found that trematodes had significantly higher prevalence and mean intensities during spring and summer. Other studies have shown that under elevated temperatures, cercarial shedding increased for some species (Koprivnikar & Poulin, 2009; Selbach & Poulin, 2020). The anadromous charr are in the marine system during the summer when water temperatures peak. The feeding behavior of the charr in shallow areas combined with a possible increase in trematode abundance in these systems, could explain some of these high abundances of trematodes in the returning anadromous charr from Laksvatn.

All in all, trophically transmitted parasites make up a significant larger part of the marine parasite community than actively transmitted parasites of the anadromous charr. This is due to a shifted feeding pattern the charr exhibits at sea, an increased feeding rate and possibly an increased abundance of trematodes in this system during the summer. The short stay in sea combined with no aquaculture activity nearby (Grenier et al., 2023) will also reduce the encounter rate with actively transmitted marine parasites, such as sea lice.

4.3 The effect of parasites

In this population of anadromous charr, very high abundances of parasites were observed. Parasites can have detrimental effects on their host (Dezfuli et al., 2016; Dezfuli et al., 1997; Goater et al., 2014), and this effect is dependent on many factors. Fish hosts have varying degrees of tolerance towards parasites, and this tolerance can depend on body size, condition factor, immune status and the intensity of infection from the given parasite (Goater et al., 2014; Holmes & Zohar, 1990). This means that some charr are more vulnerable than others and may be more susceptible to the pathogenic effects that some parasites have. Generally, the anadromous charr are vulnerable at sea (Thorstad et al., 2016). For first time migrants, mortality is estimated to 66,4%, which is 13 times higher than in the freshwater system (Jensen et al., 2019). Mortality can be caused by difficulties in osmoregulation (Handeland et al., 1998) or predation by birds or larger fishes (Thorstad et al., 2016). The population of returning anadromous charr from Laksvatn had very high abundances of parasites, but the abundance of parasites in the anadromous charr that did not return is unknown. This raises the question: could high abundances of marine parasites be another important reason for high mortality rates for anadromous charr during the marine migration?

Anadromous charr from Laksvatn doubled their body mass during their migration, due to feeding in the marine system (Opheim, 2022). Parasites also need resources to grow and reproduce, and this comes the expense of the host (Goater et al., 2014). Most parasites in this population of anadromous charr were found in the gastrointestinal tract, and this is the primary route of infection for many parasites (Dezfuli et al., 2016). Parasitic helminths are known to have the ability to reduce the fitness of their host, by causing structural modification to host tissue (Dezfuli et al., 2016). Other direct effect parasites may have on their hosts are withdrawal of nutrients, transfer of microorganisms and reduction of the host's immune system (Rohde, 1984). Ultimately, the effect of parasites cannot only be seen from the

viewpoint of the individual host, they must be seen from a host population and community perspective, which can again regulate whole ecosystems (Goater et al., 2014; Lafferty, 2008).

The parasite taxa found in this study have varying degrees of pathogenicity, which is often associated with the level of intimacy between the parasite and the host. The acanthocephalan taxa *Echinorhynchus* sp. had a relatively low prevalence in this population of anadromous charr (9%), however some parasites within this phylum are known to be highly pathogenic, as they attach their proboscis in the host tissue (Dezfuli et al., 2016). The anadromous charr in this study had very high abundances of trematodes, especially in the gastrointestinal tract. Here, the trematodes may feed on mucosa, epithelial tissue, blood and products of host digestion. They may attach themselves to the intestinal wall with suckers, but are not as integrated into the intestine as acanthocephalans, making them less pathogenic (Dezfuli et al., 2016; Dezfuli et al., 1997). The most abundant freshwater taxon in the anadromous charr was the eye fluke, metacercariae of *Diplostomum* spp., which are found in the retina of the eye. These parasites weaken the visual capacity of the charr, and cause an energy cost for the repair of the retina (Padrós et al., 2018). Regarding the cestodes, they were relatively high in prevalence but no so high in abundance. The degree of pathogenicity is largely dependent on the intensity of infection and how deeply the cestode has penetrated the host's tissue (Dezfuli et al., 2016). Studies of salmonids infected by *Eubothrium* spp. revealed that the parasite had effects on body mass and condition, and uninfected fish grew faster (Henriksen et al., 2019; Saksvik et al., 2001). Regarding the nematodes, in this population of anadromous charr they were high in prevalence and moderate in abundance. The nematode *H. aduncum* has shown to have high pathogenicity towards larval herring (Balbuena et al., 2000), however these are very small, so it might not be comparable to the anadromous charr. Overall, most parasites that infect anadromous charr are not highly pathogenic, however in such high densities as in this population, the parasites can have some pathogenic effect, but is unclear what effect and to which degree.

Sea lice (*Caligus* sp., *Lepeoptheirus* sp.) are a subject of much research due to the damage and financial costs it has put on Norwegian farmed salmon (Abolofia et al., 2017). Despite this, there is no aquaculture activity in the Balsfjord area that would increase the encounters with sea lice, and the sea lice burden for the Laksvatn population has been described as at medium intensity (Grenier et al., 2023). Even though the mean abundance of sea lice was lower than for some of the helminth parasites, this parasite may have had great effects on the individual anadromous charr. It has been shown that even at low intensities, infection of sea

lice can significantly change the behavior of the anadromous charr at sea (Strøm et al., 2022), and might lead to reduced marine residency and lower return rate for the anadromous charr (Bjørn et al., 2001). It is therefore likely that the sea lice have had some effect on the marine behavior of the anadromous charr from Laksvatn, despite a low mean abundance. The migration of the charr also only lasted for 6 weeks (Opheim, 2022), giving the sea lice short window to infect the charr. Most likely the true abundance of sea lice was somewhat higher than the findings in this study. The sea lice were counted after the fish had been frozen. The trap was checked at least once a day, so some individuals of charr could be in the trap for longer than others, which could potentially remove some of the sea lice. The benzocaine treatment could also remove some of the lice.

The mentioned effects of parasites can contribute negatively to reduction of fitness, growth and fecundity for the anadromous charr. Nonetheless, high abundances of trophically transmitted parasites are associated with high feeding rates, a benefit in which might exceed the pathogenic effects put on by the parasites (Henriksen et al., 2019; Johnson et al., 2010; Lafferty, 1992, 2008). Most of the parasites of the anadromous charr from Laksvatn were trophically transmitted. Some trophically transmitted parasites (e.g., acanthocephalans, Bakker et al. (2017)) are known to manipulate their hosts (often intermediate hosts) which makes them more susceptible for predation. By making the prey more susceptible, the parasites are reducing the cost of foraging for the final host, allowing for exploitation of prey that normally would be difficult to acquire. This could lead to a less energy demanding feeding pattern, with the cost of being infected by a parasite. Alternatively, the charr could attempt to only feed on non-infected prey. Since most animals are infected by at least one parasite (Windsor, 1995), this would reduce much of the prey available for the charr. Another alternative would be to try to get rid of the parasite by providing an immune response. However, the energetic cost of a sufficient immune response is high, and might reduce the energy invested in growth and body mass (Lysne et al., 2006).

During the marine migration, the charr from Laksvatn double their body mass (Opheim, 2022), but with this gain there is evidently the cost of high parasite accumulation. Although the most obvious impact of these high intensities is the pathogenic effects that they may have on the anadromous charr, the reality might be more complex. A study from Takvatn (Henriksen et al., 2019) found that there was a positive association between growth and intensities of some intestinal parasites. This raises an alternative question: can trophically transmitted parasites be a sign of a successful migration and feeding strategy? Elevated

abundances of trophically transmitted parasites can indicate high exploitation of marine prey, a benefit in which might exceed the cost of a pathogenic effect. Additionally, the anadromous charr from Laksvatn spend six weeks in the marine system (Opheim, 2022), and after entrance into freshwater, majority of the marine parasites are lost (Frimeth, 1987b). The pathogenic effect is therefore believed to be short-term for the returning anadromous charr. For that reason, it seems like the marine migration of the anadromous charr is a beneficial strategy to exploit the plethora of resources in the marine system, but it comes with the cost of trophically transmitted parasites and mortality for some. It cannot be concluded whether the high mortality rates of the anadromous charr can be caused by parasites, or other reasons such as predation or osmotic difficulties (Jensen et al., 2019). It can however be concluded that the returning anadromous charr from Laksvatn have been feeding while in the marine system, due to the high abundances of trophically transmitted parasites.

In the evolutionary arm's race, it appears as though the benefit of increase in body mass exceeds the cost of pathogenicity put on by the parasites. However, in the eyes of global climate change, the future is more unpredictable, and the consequences of these changes are unclear.

4.4 Future perspectives

The effects of global climate change are more pronounced in the Arctic, and are expected to develop even further in the upcoming decades (Serreze & Barry, 2011). According to the Intergovernmental Panel on Climate Change (IPCC), marine and freshwater systems in the Arctic are already prone to changes in ecosystem structure, a shift in species range and alteration in environmental ques (IPCC, 2022). Parasites depend on both the abiotic factors in the external environment and the environment within the host (Marcogliese, 2001). Alterations in these systems may therefore harm parasites directly by physically damaging the parasites, or indirectly by affecting the metabolism and growth of the host (Marcogliese, 2008). An increase in host range may also bring in parasites into new systems, which potentially can bring disease to the established host species. In elevated temperatures, the copepod parasite sea lice has shown an increased production of larvae, faster development of juvenile stages to infective stages and an increase in infectivity (Sandvik et al., 2021). This parasite is prevalent in the population of anadromous charr from Laksvatn, however increased temperatures could lead to a higher abundance of this parasite in the future.

Parasites of keystone species can play crucial roles in some ecosystems, and climate-induced changes in these parasite abundances can potentially cause cascade-effects throughout entire ecosystems (Marcogliese, 2008). This is highlighted in an intertidal system from Denmark (Jensen & Mouritsen, 1992; Mouritsen & Poulin, 2002; Mouritsen et al., 2005) where researchers discovered mass mortalities of the mollusk *Hydrobia ulvae* (Pennant, 1777) and the amphipod *Corophium volutator* (Pallas, 1776) , caused by parasitic trematodes. This had cascade-effects throughout the entire benthic system, reducing the secondary consumers by 76%, leading to much less food available for the benthic upper trophic levels. This sudden increase in trematodes was most likely caused by a warmer spring than usual, leading the cercariae to develop and emerge more frequently than usual (Koprivnikar & Poulin, 2009; Selbach & Poulin, 2020). The cascade effect these benthic invertebrates had on the upper trophic levels might reduce the food availability for generalist fish species such as anadromous charr. This is just one example of how climate can cause cascade-effects in a system through parasite-host interactions, potentially having effects on the higher trophic levels. With temperatures rising globally and a more unstable climate, more events like this are expected.

Anadromy as a life history strategy has developed due to a more productive marine system than the fish's native freshwater system (Gross et al., 1988; Näslund et al., 1993). Studies have shown that this life strategy is somewhat flexible, where an experimental rise in food availability in the native freshwater system has increased residency for the charr (Nordeng, 1983). This means that an elevated temperature in the native freshwater environment can lead to higher primary production in this area, decreasing the proportion of the salmonid population displaying anadromous behavior. Initially, this may be beneficial for some of the anadromous salmonids as it can reduce the cost of migration, however it may also expand the northern limits of subarctic and temperate species, as well as introducing new species to these environments (Reist et al., 2006). For the population of charr from Laksvatn, possible consequences may be a more productive freshwater system leading to increased residency, as well as the risk of introduction of new species. For the anadromous salmonids in Laksvatn, the invasive species pink salmon (*Oncorhynchus gorbuscha,* Walbaum, 1792*)* could be a potential threat to the population, as the invasive fish species has been observed along the coastline of Northern Norway (Sandlund et al., 2019). A study on the parasite community of the pink salmon found that it was not infected by any parasites that were not already known to infect anadromous salmonids (Fjær, 2019), however the invasive fish species could impact

Norwegian salmonids in other ways, such as displaying aggressive behavior in the rivers, or increase competition for spawning ground (Sandlund et al., 2019).

In the present study system, 1518 individual charr migrated upstream to Laksvatn in 2021 (Opheim, 2022), with a mean infracommunity of 5754 parasites. This means that an estimated eight million individual parasites are being brought into the lake every year, from the anadromous charr alone. This is a large input of biomass. Yet, little is known about the effect that these parasites have on the individual charr, the population of charr, or the ecosystem overall. In general, the role of parasites in food webs remains relatively unexplored, with a few studies incorporating parasites into the food web structures (Amundsen et al., 2009; Lafferty et al., 2006; Marcogliese & Cone, 1997). Studies predicting future scenarios on the effect of climate change on biodiversity and food webs, parasites are often not included. To fully comprehend the role that parasites play in ecosystems like this, more studies are needed about roles of parasites in food webs, effects of climate change on parasites, and how global climate change related alterations in parasite communities change host communities.

5 Conclusion

Large abundances of trophically transmitted marine parasites were discovered in a sample of anadromous Arctic charr (n=35) from Laksvatn, Northern Norway. There was no significant difference in diversity between the freshwater infracommunity and the marine infracommunity. Parasites of marine origin had a ten-fold higher abundance than parasites of freshwater origin, and of those marine parasites, and a majority was trophically transmitted. Anadromous Arctic charr has high mortality rates at sea and it was discussed whether parasites could be an important reason for these mortality rates. It appears the pathogenic cost of marine parasites is a cost that does not exceed the benefit of an increased body mass and fecundity for the anadromous Arctic charr. More research is needed on the role of parasites in food webs, how global climate change might impact parasites, and how climate change – induced impacts on parasite can affect host communities.

6 References

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Young, A. L., Tallman, R. F., & Ogle, D. H. (2021). Life history variation in Arctic charr (Salvelinus alpinus) and the effects of diet and migration on the growth, condition, and body morphology of two Arctic charr populations in Cumberland Sound, Nunavut, Canada. *NRC Research Press*, 436-453.

7 Appendix

7.1 Length-weight distribution

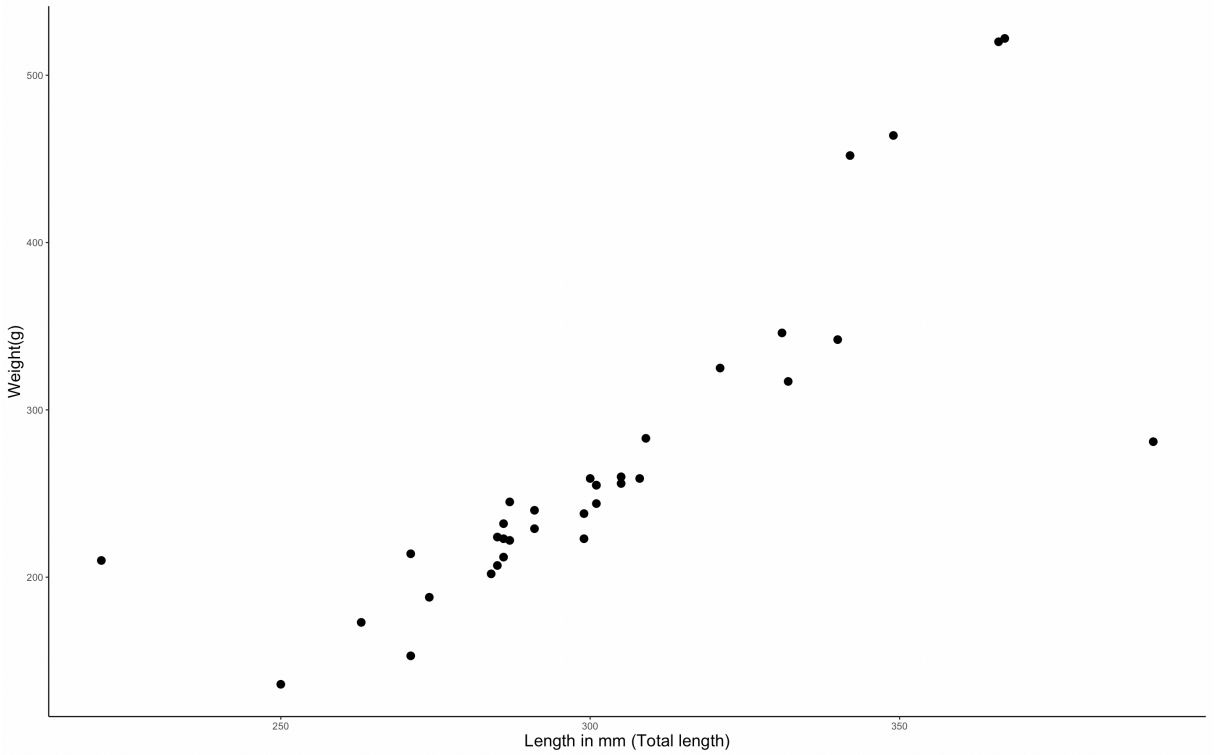

Figure 12: weight and length for the anadromous charr (S. alpinus) from Laksvatn. Total length (mm) on the y-axis and weight (g) on the x-axis. Most fish have a length between 25 and 30 mm, however some are larger.

7.2 Trematode staining protocol

Aceto-Carmine with CH_2COOH solution was used to stain the trematodes. The solution was made by my supervisor, Eloïse. Products used to create the solution was 500 mg of Carmine, 45 ml of glacial acetic acid, 55 ml of distilled water and iron dust. Protocols for staining trematodes, cestodes and acanthocephalans are based on (Cribb & Bray, 2009; Justine et al., 2012). Protocol for making the Aceto-Carmine goes as followed:

1. Erlenmeyer tube was cleaned with distilled water and 70% ethanol.
2. Carmine and a few drops of glacial acetic acid was added to a mortar. Carmine was grinded and mixed with the acid. Mortar was rinsed several times and content mixed with distilled water was poured into an Erlenmeyer tube.

3. A small amount of iron dust was added to a glass tube and mixed with 1 ml acetic acid. The content was carefully heated with a lighter until content was brown.
4. 5-10 drops of iron solution are added to the tube with the carmine-solution.

Protocol for staining and molting trematodes goes as followed:

1. Trematodes are moved to a bath of Aceto-carmine and left cold for 2-3 hours.
2. Trematodes are transmitted to a bath of 1% HCl-ethanol bath. Observer pays attention to when the trematode has lost some of the coloration from the Aceto-Carmin. This is to remove excess color. The trematodes will stay in this mixture for ca. 5 minutes.
3. Trematodes are transferred to a bath of clear, distilled water for 5-10 minutes.
4. Trematodes are transferred to a solution of 70% ethanol for 5-10 minutes.
5. Step 4 is repeated.
6. Trematodes are transferred to a solution of 80% ethanol for 5-10 minutes.
7. Trematodes are transferred to a solution of 90% ethanol for 5-10 minutes.
8. Trematodes are transferred to a solution of 96% ethanol for 5-10 minutes.
9. Step 8 is repeated.
10. Trematodes are transferred to a solution of 25% eugenol for 5-10 minutes.
11. Trematodes are transferred to a solution of 50% eugenol for 5-10 minutes.
12. Trematodes are transferred to a solution of 75% eugenol for 5-10 minutes.
13. Trematodes are transferred to a solution of 100% eugenol for 5-10 minutes.
14. A clean slide is added one drop of Canada-balsam. Trematode is put on top, adjusted in a way in which the internal traits can be seen. Coverslip is carefully put on top and pressed down.
15. Slide with trematode is kept warm for Canada-balsam to dry for at least 3 weeks.

7.3 Cestode and acanthocephalan staining protocol

Cestodes and acanthocephalans use the same staining protocol. A different carmine solution is used for these worms. Products used to make this solution were 5 g of Carmine, 10 cm^3 of 18% chlorohydric acid, 200 cm^3 of 95% ethanol, and small nail or piece of raw iron.

Protocol for making the Iron Aceto-Carmine goes as followed:

1. Carmine and HCl are added to a mortar, and mixed.
2. This is left for one hour.
3. 95% ethanol is added to the mixture.

4. This is boiled gently for two hours.
5. Iron nail is added to the solution.
6. Solution is filtrated.

The protocol for staining the cestodes and the acanthocephalans goes as followed:

1. For the cestodes, the hologenophone is removed carefully from the body before staining and kept on 96% ethanol.
2. Parasites are put in a bath of HCl Carmine and left cold for 15 minutes.
3. Parasites are then put in 1% HCl-ethanol bath to remove some of the excess color. This may be repeated if all excess color is not removed the first time.
4. Parasites are transferred to a solution of 70% ethanol for 15-20 minutes.
5. Step 4 is repeated.
6. Parasites are transferred to a solution of 80% ethanol for 15-20 minutes.
7. Parasites are transferred to a solution of 96% ethanol for 15-20 minutes.
8. Step 7 is repeated.
9. Parasites are transferred to a solution of 25% eugenol for 15-20 minutes.
10. Parasites are transferred to a solution of 50% eugenol for 15-20 minutes.
11. Parasites are transferred to a solution of 75% eugenol for 15-20 minutes.
12. Parasites are transferred to a solution of 100% eugenol for 15-20 minutes.
13. A clean slide is added one drop of Canada-balsam. Parasites is put on top, adjusted in a way in which the internal traits can be seen. Coverslip is carefully put on top and pressed down.
14. Slide with parasite is kept warm for Canada-balsam to dry for at least 6 weeks.

7.4 Parasite morphology

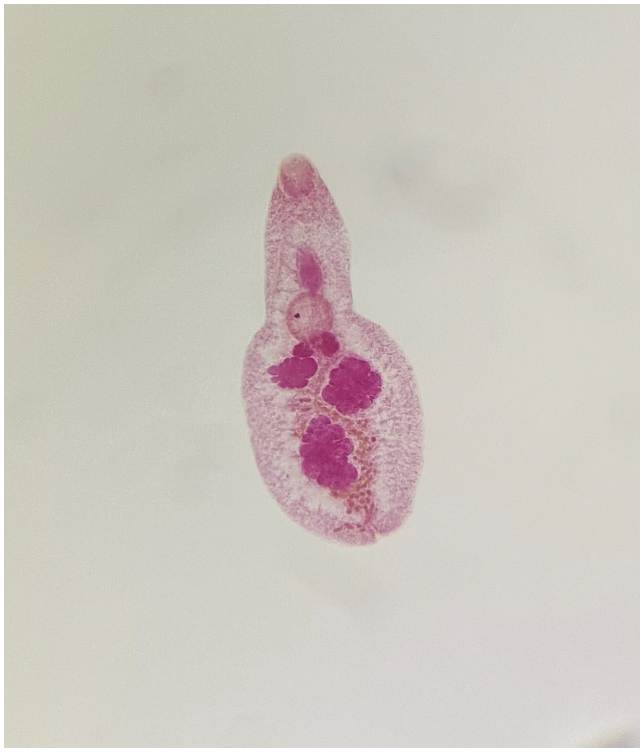

Figure 13: Stained Phyllodistomum umblae (trematode). 5.5x magnification.

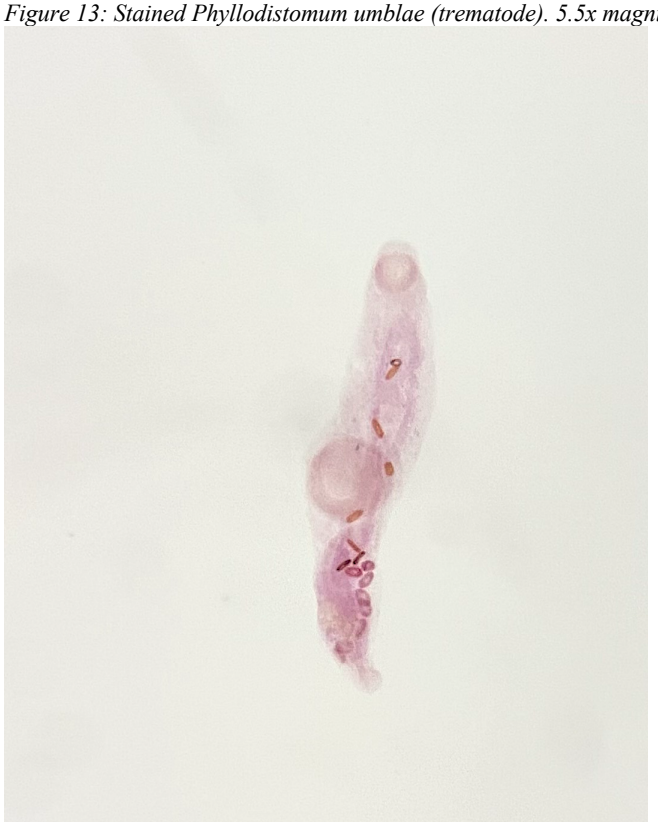

Figure 14: stained Derogens varicus (trematode), 5.5x magnification.

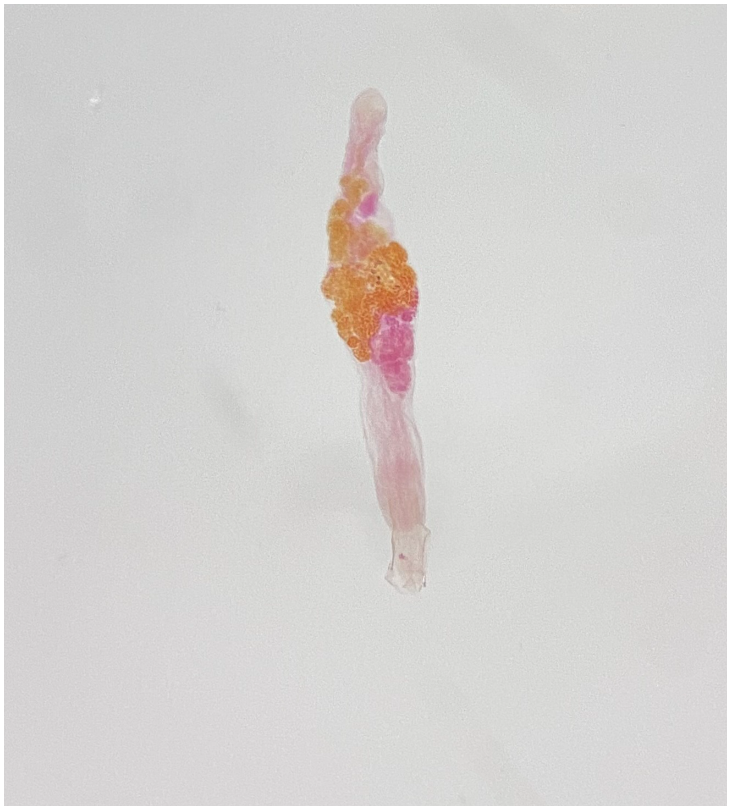

Figure 15: picture of stained Hemiurus levenseni (trematode), 5.5x magnification.

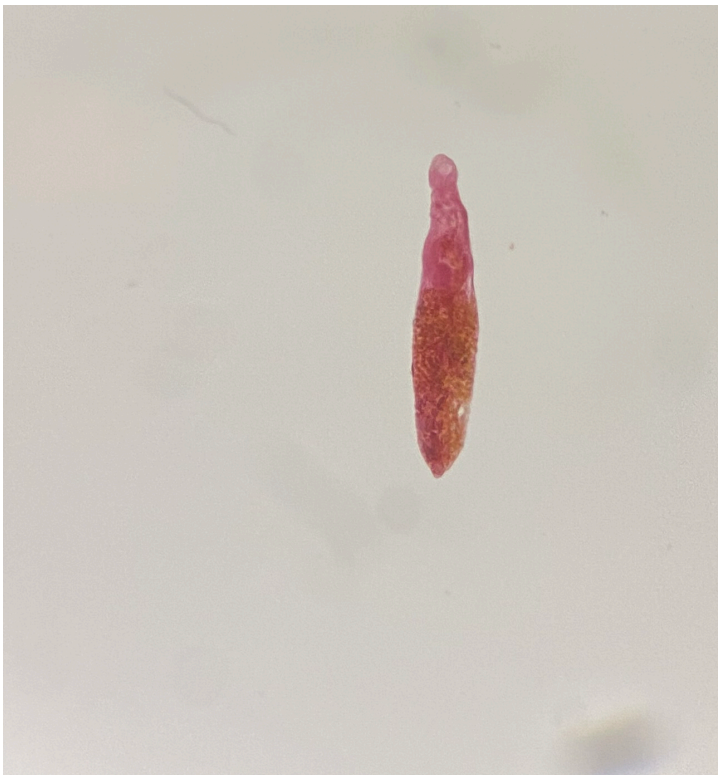

Figure 16: picture of stained Potoctyle atomon (trematode), 5.5x magnification.

Figure 17: picture of Diplostomum spp. (trematode), not stained. 5.5x magnification.

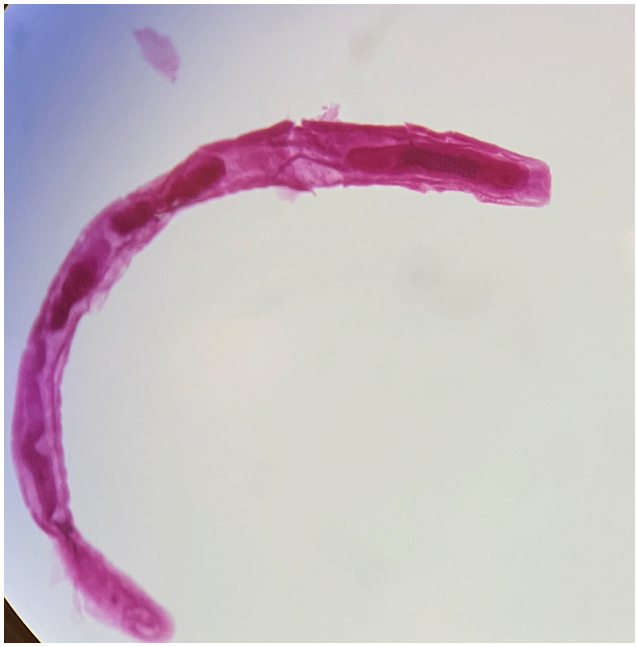

Figure 18: picture of stained Echinorhynchus sp. (acanthocephala). 4x magnification.

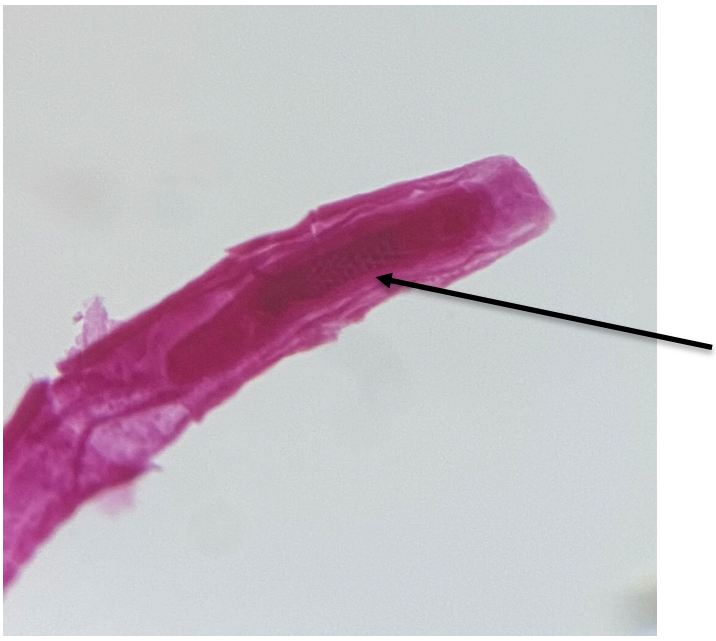

Figure 19: close-up picture of the anterior region of Echinorhynchus sp. (acanthocephala). Arrow pointing at the proboscis, which is intact. 5.5x magnification.

Figure 20: picture of the body of stained E. salvelini (cestode). 3x magnification.

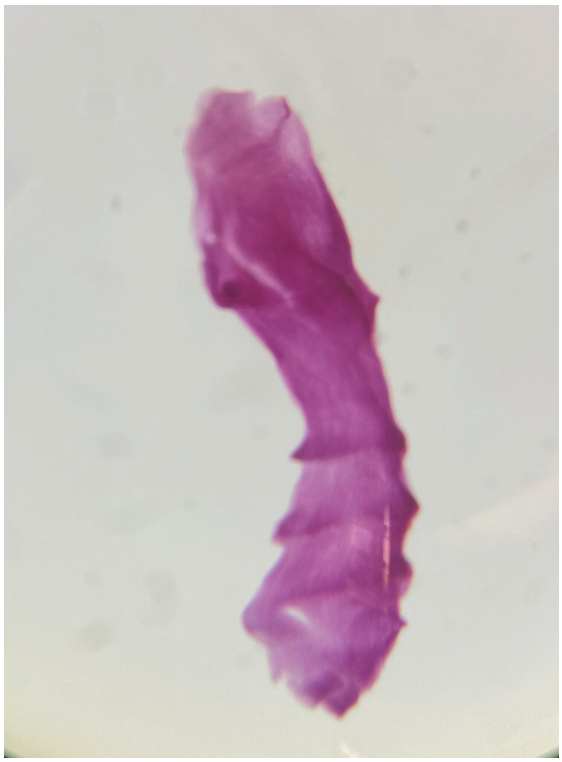

Figure 21: picture of stained E. salvelini (cestode) scolex. 4x magnification.

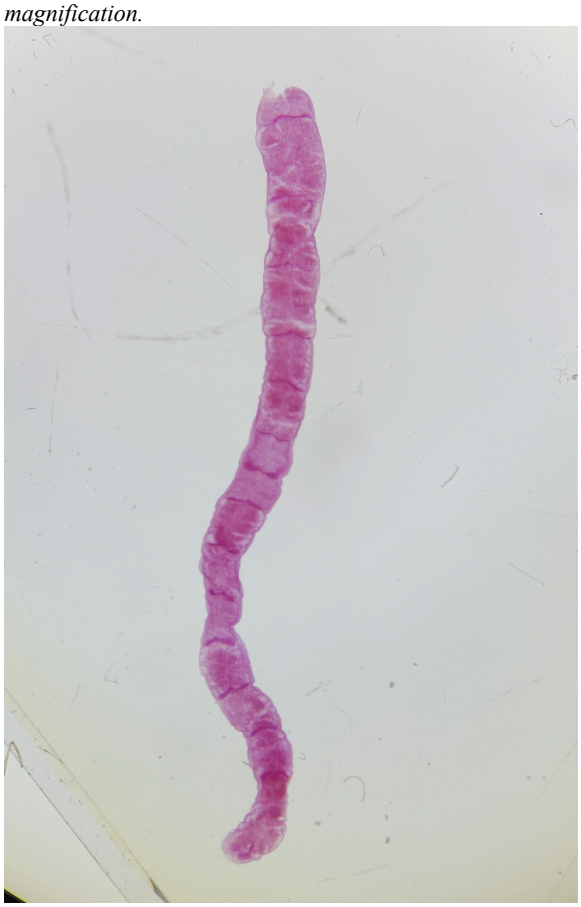

Figure 22: picture of the body of stained Proteocephalus sp. (cestode). 1x magnification.

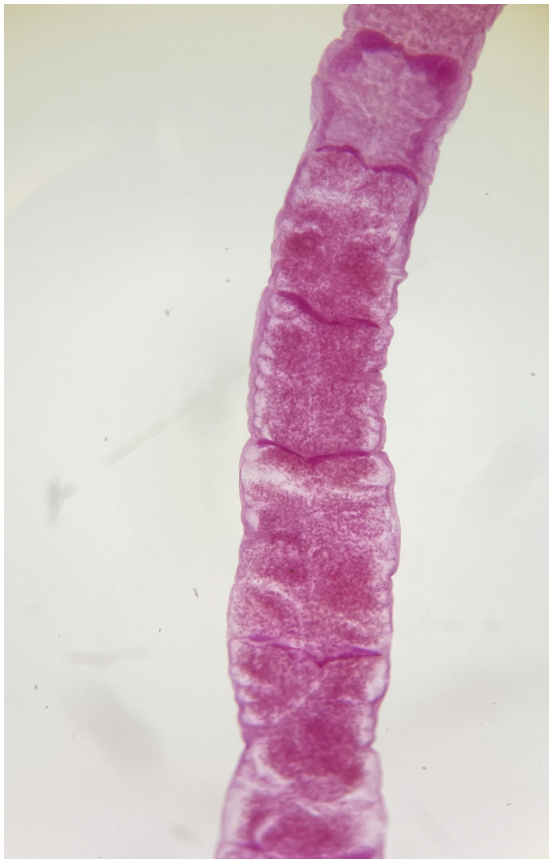

Figure 23: close-up picture of the body of stained Proteocephalus sp. (cestode). 2x magnification.

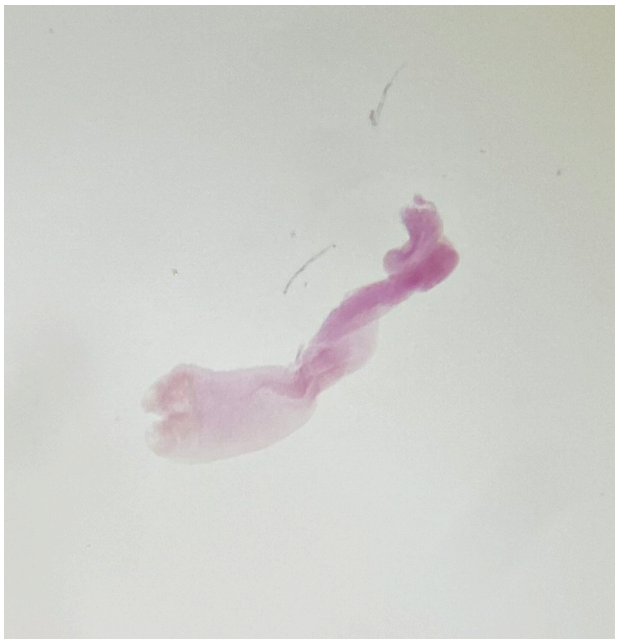

Figure 24: picture of scolex of stained Proteocephalus sp. (cestode). 4x magnification.

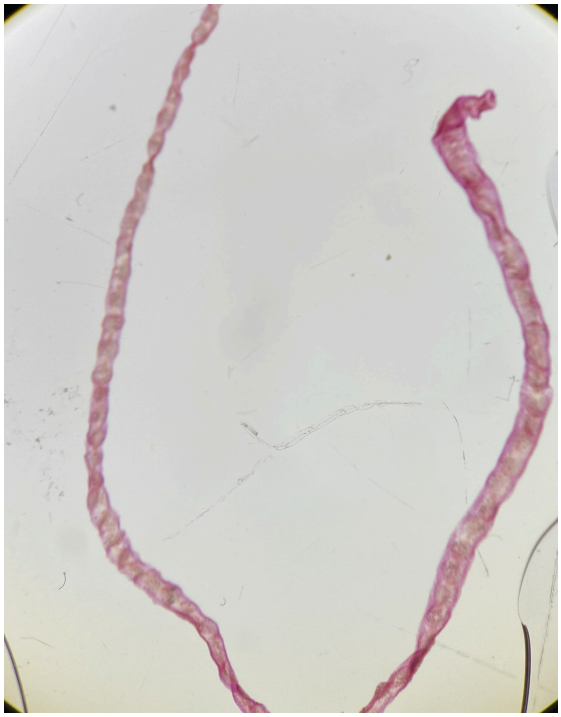

Figure 25: picture of stained A. gadi (cestode). 1x magnification.

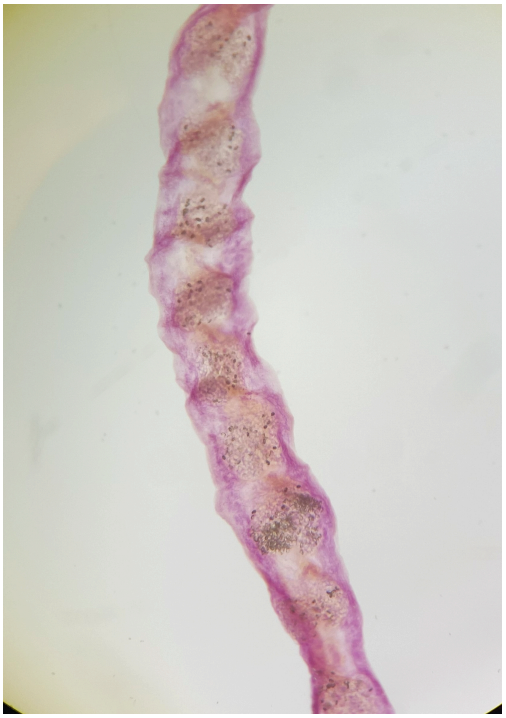

Figure 26: close-up picture of body of stained A. gadi (cestode). 3x magnification.

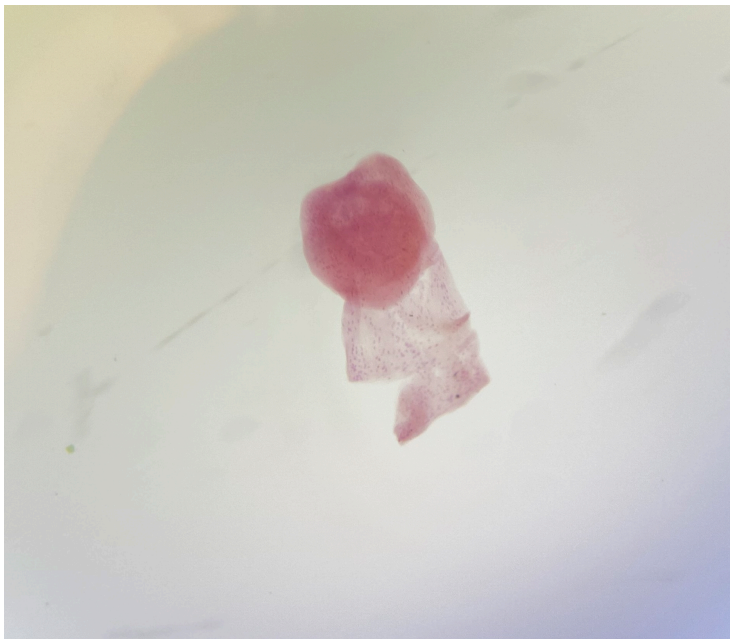

Figure 27: close-up picture of scolex of stained A. gadi (cestode).

Figure 28: picture of anterior end of H.aduncum (nematode). 20x magnification.

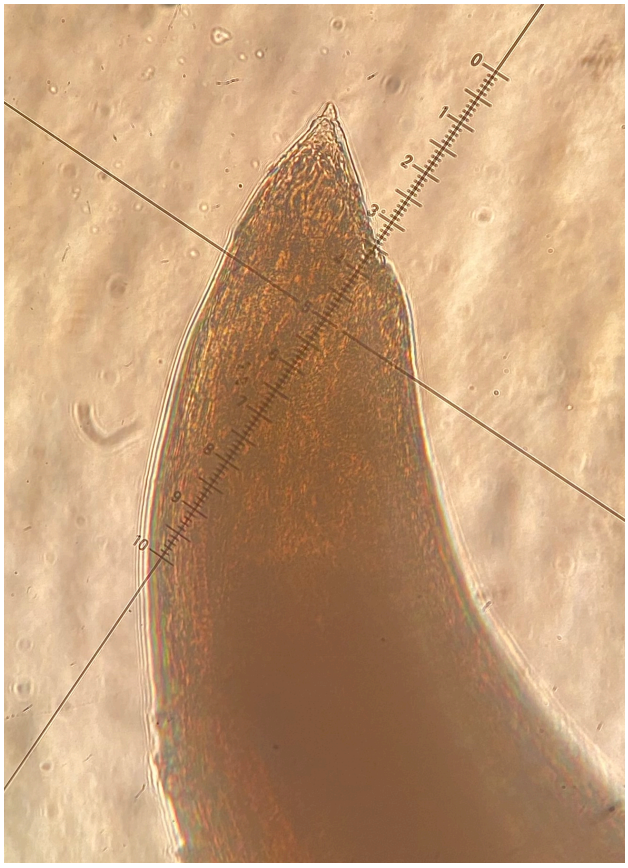

Figure 29: picture of the posterior end of H. aduncum (nematode). 20x magnification.

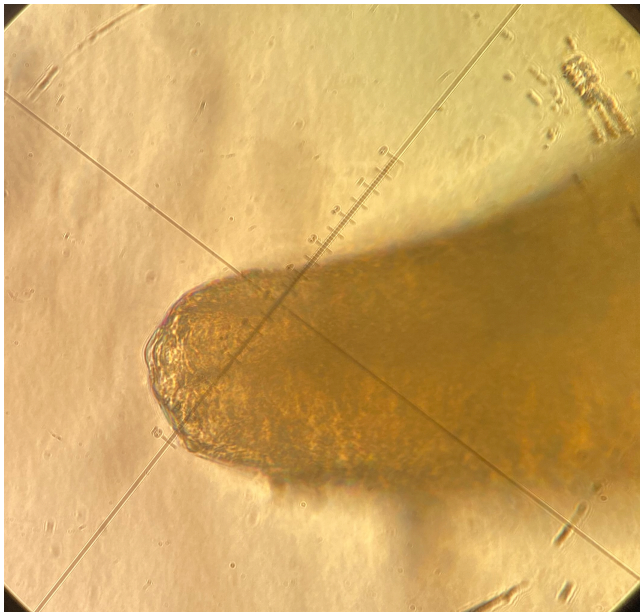

Figure 30: figure of anterior end of A. simplex (nematode). 40x magnification.

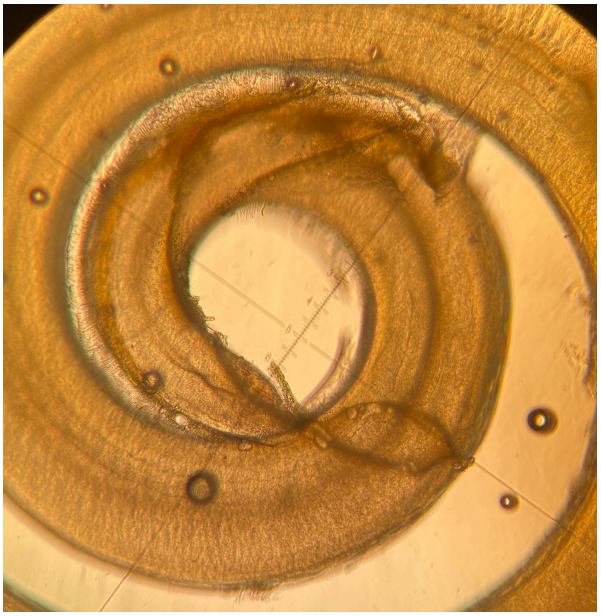

Figure 31: picture of posterior end of A. simplex (nematode). Parasite is coiled up, encysted in liver. 10x magnification.

Figure 32: picture of a living sea lice. Photo by Gabrielle Grenier

No pictures of *Salmincola* sp. and *Tylodelphys* sp. due to a low number of samples.

7.5 R-script

```
setwd("/Users/heddaauestadnilsen/Library/Mobile
Documents/com~apple~CloudDocs/Masterprosjekt/datasett")
install.packages('gridExtra')
```

```
library(plotrix)
library(ggplot2)
library(ggbiplot)
library(scales)
library(gridExtra)
library(grid)
library(cowplot)
library(dplyr)
library('patchwork')
library('ggpubr')
library('UpSetR')
library(tidyverse)

citation('ggplot2')
citation('vegan')
citation('ggbiplot')

d <- read.csv('datasett_feb10.csv', header=TRUE, sep=';', stringsAsFactors = TRUE)
d <- d[-c(36:66),]

#make the same graphs excluding individuals with NA values
fw_NA <- d[-c(1,4,5,6,7,8,9,10),]
m_NA <- d[-c(1,4,6),]


# Chapter 3.1 prevalence
prevalence <- read.csv('prevalence.csv', header = TRUE, sep = ";", dec=',',
stringsAsFactors = TRUE)
prev_split <- split(prevalence, prevalence$Environment)
fw_split <- prev_split$FW
m_split <- prev_split$M

fw_split$Taxa <- factor(fw_split$Taxa, levels=fw_split$Taxa)
m_split$Taxa <- factor(m_split$Taxa, levels=m_split$Taxa)

gg_fw <- ggplot(data=fw_split, aes(x=Taxa, y=Prevalence)) +
geom_bar(stat='identity', color='black', fill='brown1') + theme(panel.background =
element_rect(fill='transparent', color=NA),
axis.line = element_line(color='black'), axis.title.y=element_text(size=15),
axis.title.x = element_text(size=15), text=element_text(size=15)) +
scale_x_discrete(labels=expression(italic(Diplostomum_sp.), italic(P_umblae),
 italic(Tylodelphys_sp.), italic(Dibothriocephalus_sp.), italic(E_salvelini),
 italic(Proteocephalus_sp.), Myxozoa, italic(Salmincola_sp.))) + xlab('Freshwater
taxa') + ylab('Prevalence of infection (%)')
gg_fw
```

```
gg_m <- ggplot(data=m_split, aes(x=Taxa, y=Prevalence)) + geom_bar(stat='identity',
color='black', fill='cornflowerblue') + theme(panel.background =
element_rect(fill='transparent', color=NA),
axis.line = element_line(color='black'), axis.title.y=element_text(size=15),
 axis.title.x = element_text(size=15),
text=element_text(size=15)) + ylab('Prevalence of infection (%)') + xlab('Marine taxa')
+ scale_x_discrete(labels=expression(italic(C_lingua), italic(D_varicus),
italic(H_levenseni),italic(P_atomon), italic(A_gadi), italic(A_simplex),
italic(H_aduncum), italic(Echinorhynchus_sp.),
Sea_lice))
gg_m

#chapter 3.2 abundance
ab <- read.csv('abundance.csv', header=TRUE, sep=';', stringsAsFactors = TRUE)

split_abundance <- split(ab, ab$Env)
split_fw <- split_abundance$FW
split_m <- split_abundance$M
#removing abundances with NA values

new_split_fw <- split_fw[-c(1, 4:10),]
split_m <- split_m[-c(1,4,6),]
View(new_split_fw)
summary(split_m)

jitter_fw <- ggplot(new_split_fw, aes(x=Env, y=Ab)) + geom_boxplot(fill='brown1')
+ geom_jitter(width=0.5) +
 theme(panel.background = element_rect(fill='transparent', color=NA),
 axis.line=element_line(color='black'),axis.title.y = element_text(size=30),
 axis.title.x=element_text(size=23), text=element_text(size=15)) +
labs(x='Infracommunity of freshwater parasites (n=27)', y='Abundance')
jitter_fw

jitter_m <- ggplot(split_m, aes(x=Env, y=Ab)) + geom_boxplot(fill='cornflowerblue')
+ geom_jitter() + theme(panel.background = element_rect(fill='transparent',
color=NA), axis.line=element_line(color='black'),axis.title.y = element_text(size=30),
 axis.title.x=element_text(size=23), text=element_text(size=15)) +
labs(x='Infracommunity of marine parasites (n=32)', y='Abundance')
jitter_m

ggarrange(jitter_fw, jitter_m)
median(split_fw$Ab)
median(split_m$Ab)

#3.3 taxon richness and diversity
# histograms of taxon richness
```

```
hist_gg_m_tax <- ggplot(m_NA, aes(x=M_sp, y=after_stat(count/sum(count)))) +
  geom_histogram( binwidth=1, color='black', fill='cornflowerblue') +
  labs(y='Individuals infected (%)', x='Taxon diversity of marine parasites (n=33)') +
  scale_y_continuous(labels=percent_format()) +
  theme(panel.background = element_rect(fill='transparent', color=NA),
  axis.line=element_line(color='black'),axis.title.y = element_text(size=15),
  axis.title.x=element_text(size=15), text=element_text(size=15))
hist_gg_fw_tax <- ggplot(fw_NA, aes(x=FW_sp, y=after_stat(count/sum(count)))) +
  geom_histogram( binwidth=1, color='black', fill='brown1') +
  labs(y='Individuals infected (%)', x='Taxon diversity of freshwater parasites (n=27)')
+  scale_y_continuous(labels=percent_format()) +
  theme(panel.background = element_rect(fill='transparent', color=NA),
  axis.line=element_line(color='black'),axis.title.y = element_text(size=15),
axis.title.x=element_text(size=15), text=element_text(size=15))
hist_gg_m_tax
hist_gg_fw_tax

ggarrange(hist_gg_fw_tax + theme(axis.ticks.y=element_blank(),
plot.margin=margin(r=1)), hist_gg_m_tax + theme(axis.text.y=element_blank(),
axis.ticks.y=element_blank(), axis.title.y=element_blank(), plot.margin=margin(r=1,
l=1)),nrow=1)

#diversity indeces in own script
#testing for difference for taxon richness
m_tax_na <- mean(m_NA$M_sp)
m_tax_na #5.6
sd(m_NA$M_sp) #0.87

fw_tax_na <- mean(fw_NA$FW_sp)
fw_tax_na #4.5
sd(fw_NA$FW_sp) #1.01

tot_tax_na <- mean(fw_NA$Total_sp)
tot_tax_na #10.1
sd(fw_NA$Total_sp) #1.38

#finding the p-value for the mean abundance difference between fw taxa and m taxa,
# and for difference between taxon richness between fw taxa and m taxa
# looking at histograms, not normally distributed and small sample size.
# therefore using Mann-Whitney U-test to test for difference.


wilcox.test(fw_NA$FW_sp, m_NA$M_sp) #P=0.55, non-significant difference
wilcox.test(m_NA$M_abundance, fw_NA$FW_abundance) #p-value much smaller
than 0.05
```

```
# next: make pca biplot with parasites
pca_par <- d[,2:18]
pca_par
View(pca_par)
#taking only the parasite above 20% prevalence
pca_par1 <- pca_par[,c(1:5,7,8,11:14,16)]
pca_par1
pca_par2 <- princomp(na.omit(pca_par1), cor=TRUE)
biplot(pca_par2, col=c('black', 'brown1'), scale=0,
      xlabs=rep('X', 27), xlab= 'First component (19.0% explained variation)',
      ylab='Second component (14.2% explained variation)')

#3.4 transmission
tt_fw <- fw_NA[,19]
tt_m <- m_NA[,20]
at_fw <- fw_NA[,21]
at_m <- m_NA[,22]
#finding the mean of each subset
mean(na.omit(tt_fw))
mean(tt_m)
mean(at_fw)
mean(at_m)
#finding the total for marine and freshwater tt and at
mean(na.omit(tt_fw)) + mean(tt_m)

mean(at_fw) + mean(at_m)

hist(tt_fw)
hist(at_fw)
hist(tt_m)
hist(at_m)

# none normally distributed
#making the values into vector to test for difference

tt_m_v <- as.vector(tt_m)
tt_fw_v <- as.vector(tt_fw)
at_m_v <- as.vector(at_m)
at_fw_v <- as.vector(at_fw)

wilcox.test(tt_m_v, at_m_v)
wilcox.test(tt_fw_v, at_fw_v)

total_tt <- tt_fw + tt_m
total_at <- at_fw + at_m
total_at_tt <- as.vector(total_tt + total_at)
```

```
wilcox.test(total_at_tt)

#also finding standard error for each
std.error(tt_fw)
std.error(at_fw)
std.error(tt_m)
std.error(at_m)
std.error(total_tt)
std.error(total_at)

#parasite community composition
#upset plot
upset_plot <- read.csv('upset.plot1.csv', header=TRUE, sep=';', stringsAsFactors =
TRUE)
View(upset_plot)
citation("UpSetR")

fw <-upset_plot[-c(28:36),]
fw <- fw[,1:6]
View(fw)

m <- upset_plot[-c(33:36),]
m <- m[,7:12]
View(m)

text_scale_options1 <- c(1,1,1,1,0.75,1)
text_scale_options2 <- c(1.3, 1.3, 1, 1, 2, 0.75)
text_scale_options3 <- c(1.5, 1.25, 1.25, 1, 2, 1.5)

mb_ratio1 <- c(0.55,0.45)
upset(fw, mainbar.y.label = "Number of infected fish",
      order.by = "freq",
      point.size = 2,
      line.size = 1,
      nsets=6,
      text.scale= text_scale_options3,
      mb.ratio=mb_ratio1,
      set_size.show = TRUE,
      main.bar.color = 'brown1',
      sets.bar.color='grey1',
      matrix.col='grey1',
      show.numbers = TRUE)

upset(m, mainbar.y.label = "Number of infected fish",
      order.by = "freq",
      point.size = 2,
```

```
      line.size = 1,
      nsets=6,
      text.scale= text_scale_options3,
      mb.ratio=mb_ratio1,
      set_size.show = TRUE,
      main.bar.color = 'cornflowerblue',
      sets.bar.color='grey1',
      matrix.col='grey1',
      show.numbers = TRUE)

#appendix: weight-length distribution
we_le <- ggplot(data=d, aes(x=Length..TL., y=Weight)) + geom_point(size=3) +
  theme(panel.background = element_rect(fill='transparent', color=NA), axis.line =
element_line(color='black'), axis.title.y=element_text(size=15),
        axis.title.x = element_text(size=15)) + xlab('Length in mm (Total length)') +
  ylab('Weight(g)')
we_le
```

7.6 Parasite estimate from stomach

The three last stomachs analyzed were tested to see if the ¼ sample was a sound estimate, and if trematodes were equally distributed in the stomach. Stomach was divided into four equal parts and given a number from one to four, where one is the uppermost part of the stomach (Figure 34). Trematodes were divided into species and counted for each of the parts (Table 4 & Table 5). The different parts were kept on ice awaiting analysis. The second part of the stomach was used for the estimate. All nematodes in the stomach were counted.

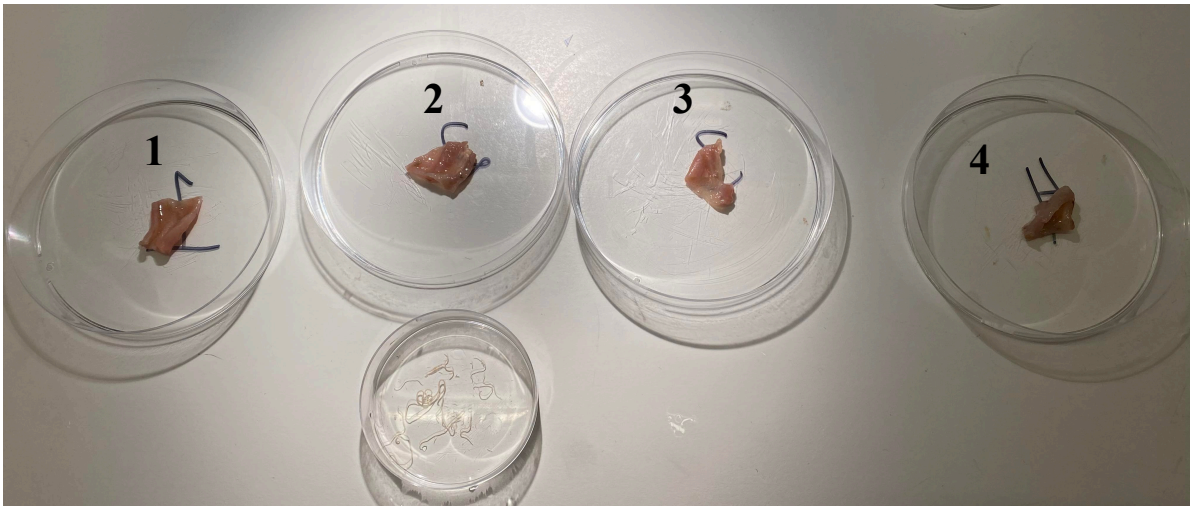

Figure 33: picture of the four stomach parts used in test for parasite estimate from stomach. Parts are numbered from one to four, starting from the upper part of the stomach/esophagus. The second part of the stomach was used for estimate.

*Table 4: Test conducted on the abundance of H. levenseni in the stomach to check if estimate is correct. *part used for estimate.*

FISH ID/ STOMACH PART	LS-21-131	LS-21-132	LS-21-133	TOTAL	PERCENTAGE OF TOTAL (%)
1	643	77	381	1101	13.8
2*	584	431	1113	2128	26.6
3	960	386	1251	2597	32.5
4	815	343	1007	2165	27.1
TOTAL	3002	1237	3752	7991	

*Table 5: Test conducted on the abundance of D. varicus in the stomach to check if estimate is correct. *part used for estimate.*

FISH ID/ STOMACH PART	LS-21-131	LS-21-132	LS-21-133	TOTAL	PERCENTAGE OF TOTAL (%)
1	295	204	21	520	40.8
2*	61	470	144	675	52.9
3	5	49	8	62	4.9
4	4	10	4	18	1.4
TOTAL	365	733	177	1275	

For *H. levenseni* it appeared that 25% was a good estimate to calculate the abundance. It also appeared that the true abundance was relatively close to the estimated mean abundance. For *D. varicus* it appeared as the parasites were not equally distributed in the stomach. Multiplying by four could therefore lead to an overestimate. However, only three stomachs were involved in this test, so a larger sample size would be necessary to create a better estimate. Reader is advised to keep in mind that for *D. varicus* there might be an overestimate. This is however not believed to influence the overall results too much, as abundances are already very high.

7.7 Molecular and morphological analyses

Table 6: parasite taxa and the type of identification (i.e., morphological and/or molecular). For the molecular analyses, the gene (ribosomal subunit) used for amplification is also included for the ones that were successfully identified under molecular analyses.

Species/taxa	Morphological analysis	Molecular analyses:	Note
C. lingua	No	No	Black spots on skin used as indicator. PCR did not work.
Diplostomum spp.	Yes	Yes (28S)	Identified to genus on molecular analyses. Not stained.
D. varicus	Yes	Yes (28S)	Identified to genus level on molecular analyses.
H. levenseni	Yes	Yes (28S)	Identified to genus level on molecular analyses.
P. atomon	Yes	No	PCR did not work.
P. umblae	Yes	Yes (28S)	Identified to species level on molecular analyses.
Tylodelphys sp.	Yes	No	Cercarial stages not stained.
A. gadi	Yes	Yes (28S)	Identified to genus level on molecular analyses.
Dibothriocephalus sp.	No	No	Cysts used as indicator.
E. salvelini	Yes	Yes (28S)	Identified to species level on molecular analyses.
Proteocephalus sp.	Yes	Yes (28S)	Identified to genus level on molecular analyses.
Echinorhynchus sp.	Yes	Yes (28S)	Identified to genus level on molecular analyses.
A. simplex	Yes	Yes (18S)	Identified to species level on molecular analyses.
H. aduncum	Yes	Yes (18S)	Identified to genus level on molecular analyses.
Sea lice	No	No	Counted only
Salmincola sp.	No	No	Counted only
Myxozoa	No	No	Cysts counted as 1.

7.8 Stable isotope analysis

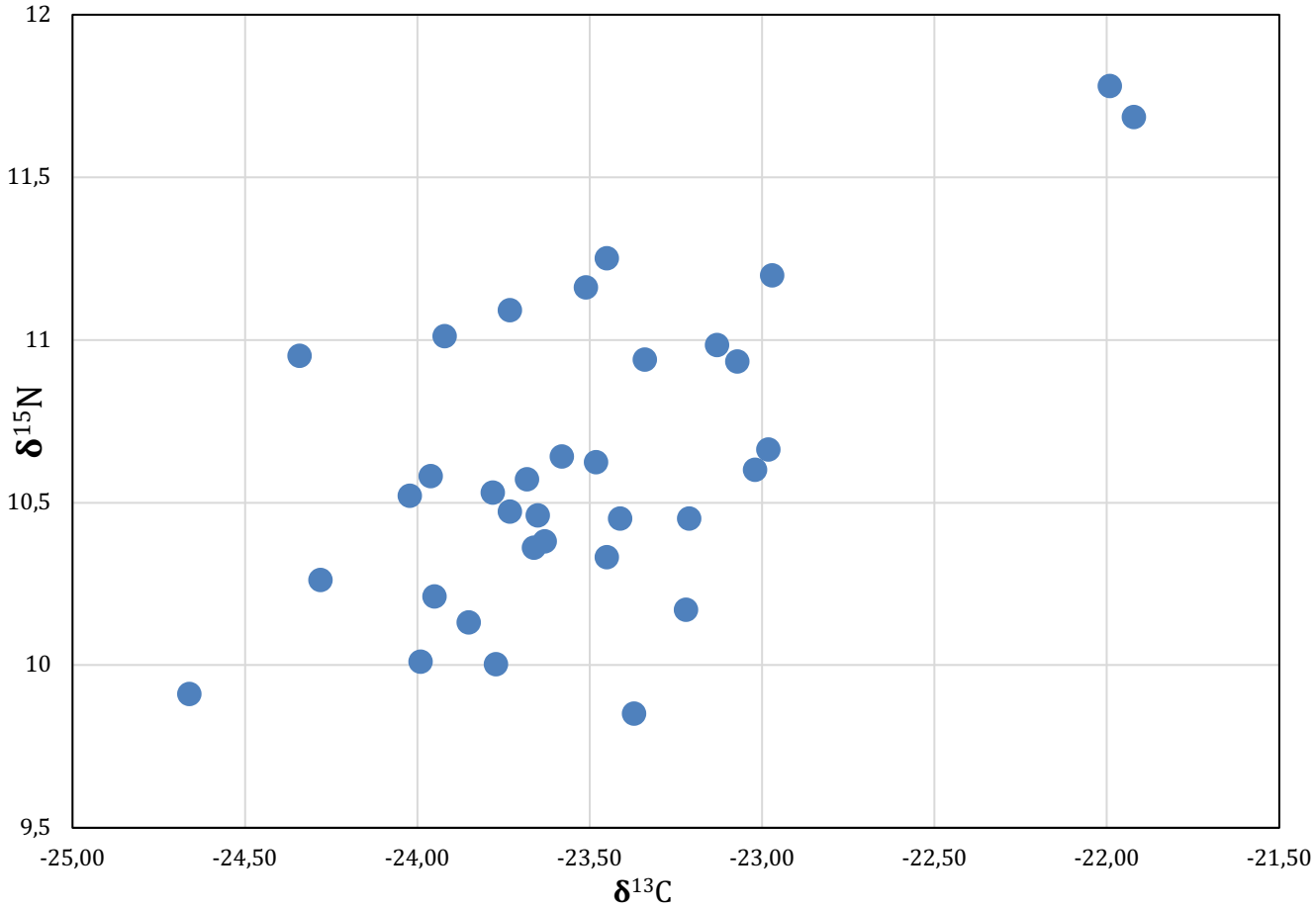

Figure 34: Plot of stable isotope analysis for a muscle sample. X-axis shows δ^{13}Carbon isotope while y-axis shows δ^{15}Nitrogen isotope. Samples were taken from muscle below dorsal fin from anadromous charr from Laksvatn.