



Department of Arctic and Marine Biology

**Parasite communities in pink salmon (*Oncorhynchus gorbuscha*) along their invasion gradient in Norway – a cause for concern?**

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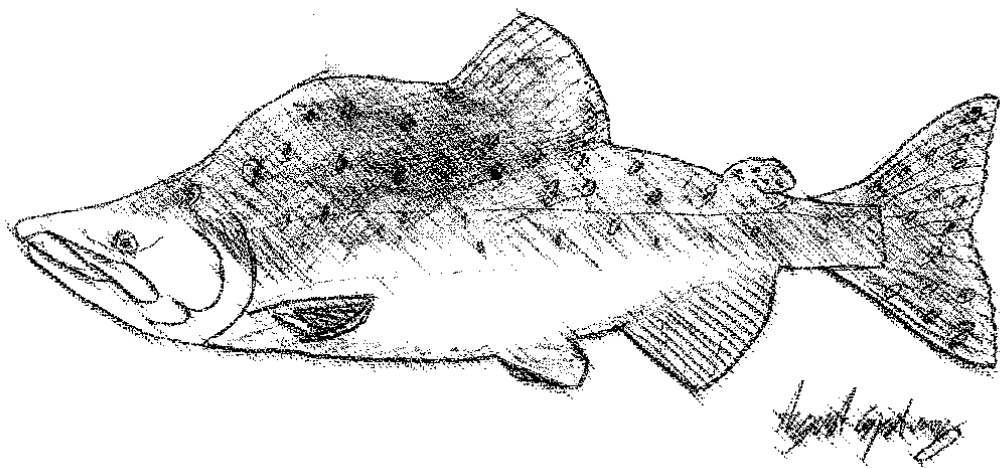
2024, The Arctic University of Norway

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**Front cover:** An adult pink salmon being prepared for the dissection in the lab. (Photo credit: Josefine Eilerts).

**Sketch drawing (next page):** Self-drawn pencil sketch of an adult male pink salmon with the infamous hump on the back.

**Keywords:** marine parasites, non-indigenous species, parasite acquisition, enemy release, Norwegian coastline, biological invasions



# Acknowledgement

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- ..........Tromsø, August 2024 -

## Abstract

Globally, non-indigenous species (NIS) are increasing in both number and distribution. Sometimes NIS are intentionally introduced to provide food or financial gain. If NIS are moved to a new environment without their competitors, predators and parasites they may gain an advantage over native species. This is explained by the enemy release hypothesis, which also includes parasites, as NIS might lose their parasites as they move further into the new environment.

In the 1950s, anadromous Pacific pink salmon (*Oncorhynchus gorbuscha*, Walbaum, 1792) were introduced to the White Sea, western Russia, and have since established and expanded along the whole Norwegian coastline. Since pink salmon were introduced as eggs, it is not likely the fish brought their own parasites. Thus, pink salmon may get an advantage from parasite release. However, pink salmon might still acquire parasites in the new environments over time. To investigate this, I have compared pink salmon caught in Varangerfjord and Agdenes in a north-south gradient in Norway, respectively. I hypothesised that 1) the northernmost location would have a higher parasite diversity, taxa richness and abundance, 2) location would have a higher effect on parasite communities than fish size, and 3) the parasite community I found would differ from previous studies.

To do this, sea-caught adult pink salmon from the Varangerfjord and Agdenes were dissected, and parasites in the stomach and the intestines were counted and identified. In total, 13 different parasite taxa were revealed. One of these taxa has never been observed in pink salmon earlier. The findings did not reveal any differences in diversity (Margalef's index), taxa richness nor abundance between Varangerfjord and Agdenes, however, there was a higher dominance (Berger-Parker index) in Varangerfjord. Location exhibited a higher effect on dominance, whereas size had a higher effect on the diversity. Therefore, no clear pattern of enemy release was proven. Although it is difficult to pinpoint any clear reasons, the lack of significant effects by location and fish size indicates that other factors play a crucial role in parasite acquisition. When comparing the parasite community of this study's pink salmon with the parasite communities in pink salmon of other studies, it was revealed that there was no full overlap of parasite taxa. Thus, the community composition differs, emphasizing the need for further research due to the complexity of host-parasite interactions.

# Table of Contents

1	Introduction .....	1
2	Methods .....	5
2.1	Sampling.....	5
2.2	Dissection .....	6
2.3	Organ analysis and parasite counting.....	6
2.4	Parasite identification .....	7
2.5	Indices and statistical analysis.....	7
3	Results .....	11
3.1	Parasite taxon richness, diversity, and dominance .....	11
3.2	Prevalence .....	12
3.3	Abundance.....	13
3.4	Comparison to other studies .....	15
4	Discussion .....	16
5	References .....	21
6	Appendix .....	30
6.1	Taxa pictures .....	30
6.2	Models for selected taxa.....	36

# 1 Introduction

Non-indigenous species (NIS) are recognized by the Convention on Biological Diversity as organisms not belonging to a specific environment, which may negatively affect human health, cause environmental or economic harm, and contribute to biodiversity loss (CBD, 2021). Globally, NIS are increasing in both number and distribution (Elton, 2000; Roy et al., 2024). Sometimes NIS are translocated to new environments through human-mediated activity, or by migration and range expansion of the NIS themselves (Ricciardi et al., 2000, 2013). For many marine NIS, the most common mode of transportation into new environments is as stowaways in ballast water or attached to the hull of ships (Clarke Murray et al., 2011; Costello et al., 2022). Sometimes NIS are also intentionally introduced to provide food or financial gain. For example, in Norway, farmed rainbow trout (*Oncorhynchus mykiss*), a species native to northern Pacific Ocean tributaries (McCusker et al., 2000; Sandlund et al., 2019), were introduced and have since escaped from cages and established in Norwegian freshwater ecosystem (Jensen et al., 2010).

When a NIS arrives in a new environment without their native competitors or predators, they have the chance to establish (Colautti et al., 2004; Ricciardi et al., 2013; Roy et al., 2011). This can be explained by the enemy release hypothesis (Middleton, 2019). This hypothesis suggests that the further away a NIS moves on a geographical range from the starting point of a biological invasion (the invasion core) to the edge of the affected areas (the invasion front), the NIS could experience a lack of their native competitors or predators, thus increase their chances in the new environment (Keane & Crawley, 2002; Middleton, 2019; Torchin et al., 2002).

However, this theory is not only limited to free-living plants or animals, as parasites can be involved in biological invasion processes, or accordingly, may be considered as NIS themselves (Goedknecht et al., 2016; MacLeod et al., 2010; Ricciardi et al., 2000). A concern linked to NIS is often parasite co-introductions and spillover events (Chalkowski et al., 2018; Sokolov et al., 2024), whereby the NIS brings along its native parasite species that may be transmitted to the native hosts in the new environment (Goedknecht et al., 2016). Whether a NIS brings along its parasites or not are described by MacLeod et al. (2016) using boat-related terms, where ‘miss the boat’ refers to whether parasites are present in the host or not, as parasites need to be present in the host to be translocated. ‘Sink with the boat’ describes how the host needs to establish in order for the parasite to establish. If the host cannot overcome the barriers of



translocation or establishment and dies, the parasite will die with the host. Meanwhile ‘lost overboard’ describes that if the host establishes, the parasite might still not establish due to lack of suitable additional hosts to complete their life cycles (MacLeod et al., 2010; Sokolov et al., 2024).

In mainland Norway, there are a total of 65 fish species on the ‘Fremmedartslista’ (alien species list), of which 24 are considered to pose a very high risk. One of these high-risk species is the anadromous Pacific pink salmon (*Oncorhynchus gorbuscha*, Walbaum, 1792) (Figure 1) (Artsdatabanken, 2021), a fish species that has its native range in the northern Pacific Ocean (Sandlund et al., 2019). In the 1950s, pink salmon eggs were translocated from their native range to the White Sea, Russia (April et al., 2023; Lennox et al., 2023; Mo et al., 2018), to exploit pink salmon as a food resource (Hindar et al., 2020). Multiple attempts to establish pink salmon stocks were made (Sokolov et al., 2024), and since the 1960s observations of pink salmon in Norwegian coastal areas and rivers increased (Hindar et al., 2020; Mo et al., 2018) from 25 tonnes in 1960 (Hindar et al., 2020) to 183 tonnes in 2023 (Baklien, 2023). The northernmost area of Norway, Finnmark, are the closest to the invasion core and, hence have the highest observations of pink salmon. Nevertheless, pink salmon has been observed along the entire Norwegian coast (Berntsen et al., 2022).



Figure 1: Pink salmon caught in Kongsfjordelva, summer of 2023. Foto: Line Framnes Voldmo.

In Norway, pink salmon is considered unwanted for several reasons. Pink salmon may compete with native salmonid species, and thus pose a threat to species like the Atlantic salmon (*Salmo salar*) or brown trout (*Salmo trutta*). This can be due to overlaps in diet, spawning times, and spawning grounds (Hansen & Quinn, 1998). After spawning, Pacific salmonids die (Gende et al., 2004; Schindler et al., 2003), and release additional nutrients and bacteria into river systems (Hindar et al., 2020). In their native range, other organisms like bears (genus *Ursus*) or different types of vegetation are adapted to this phenomenon and benefit from the nutrient input (Gende et al., 2004; Helfield & Naiman, 2001, 2006; Schindler et al., 2003), whereas in Norwegian

rivers this is a new process with unknown impacts and nutrient pollution might happen (Hindar et al., 2020; Lennox et al., 2023; Sandlund et al., 2019).

A third risk factor from pink salmon is their potential impact on the dynamics of different parasites and pathogens (Hindar et al., 2020; Mo et al., 2021). The “Norwegian” pink salmon was introduced as eggs (Mo et al., 2021), and could not have brought their native parasites (Lennox et al., 2023). Therefore, possible co-introduction and spillover of parasites are unlikely. However, NIS can acquire native parasite species in their new environments (Goedknecht et al., 2016; Kelly et al., 2009). Parasite acquisition in NIS freshwater fish has been found to be positively correlated (however not always significant) with size, higher trophic level, a high richness in fish species in the new environment, time since introduction to the new environment, as well as a phylogenetic relatedness to native species in the new environment (Paterson et al., 2012). Several of the same factors, like time since introduction (Blakeslee et al., 2013), trophic level (foraging) and fish size are also true for marine fish species regarding parasite acquisition (Luque et al., 2004; Rohde, 1984). Marine parasite species are often more generalists when it comes to host compatibility (Rohde, 1984). This, combined with pink salmon's relatively large size, several native salmonid species in Norway, like brown trout, Atlantic salmon or Arctic charr (*Salvelinus alpinus*) (Guay et al., 2024; Pethon, 2019), makes pink salmon likely to be a compatible host for native marine parasites here in the invasive range. If this should happen, and pink salmon acquire native parasites, two different scenarios are possible that can affect native host-parasite dynamics: a dilution effect or a spillback effect. When a spillback effect occurs, the NIS amplifies the transmission dynamics by an increased host diversity, resulting in an increased infection level of parasites for native fish in the same environment. Sometimes, the NIS might not function as a compatible host for the native parasites. If so, the parasite transmission might stop in the NIS and ‘dilute’ the infection level for the native fish species (Goedknecht et al., 2016; Kelly et al., 2009; Poulin et al., 2011). These complex host-parasite interactions and outcomes highlight the importance of considering hosts and their parasites as a unit in biological invasion processes.

In their native range, pink salmon are infected by 36 different macroparasite taxa (McDonald & Margolis, 1995). In contrast to this, studies from the introduced range have shown a reduced diversity: two recent studies from the White Sea found 20 different macroparasite taxa in local pink salmon populations (Barskaya et al., 2005; Sokolov et al., 2024), whereas Norwegian studies have reported on a total of 17 macroparasite taxa in invasive pink salmon in Norwegian coastal areas, including nematodes, cestodes, trematodes, and three species of parasitic

crustaceans (Fjær, 2019; Rullestad, 2021; Serra-Llinares et al., 2023). These findings suggest that pink salmon appear to be compatible hosts for a wide range of native parasite taxa in their invasive range. However, one thing that has not been accounted for in these studies is the change in the parasite communities in pink salmon as it spreads further away from the invasion core in the White Sea to the more southern locations. Since NIS usually experience a parasite release as they move from the invasion core to the invasion front (Romeo et al., 2023), this might result in a reduced prevalence, infection intensity, or a reduced taxonomic richness in parasite communities further along the invasion gradient (Colautti et al., 2004; Ricciardi et al., 2013; Roy et al., 2011).

Therefore, this study aims at investigating the patterns of parasite acquisition in pink salmon along the Norwegian coastline to test for a potential enemy release along the gradient from the invasion core to more southern locations. To achieve this, this study compared the distribution of parasites in the digestive tract of pink salmon between two locations in northern and southern Norway. In detail, the following hypotheses were tested:

- H<sub>1</sub>: There will be a lower parasite prevalence and abundance, as well as lower parasite taxa diversity and evenness in the southernmost location.
- H<sub>2</sub>: Location will have a greater effect on the parasite community than fish size
- H<sub>3</sub>: The parasite community in the digestive tract of pink salmon of this study will differ from the parasite community of other studies in the Norwegian sea due to the investigation of new locations and a longer time span since introduction.

## 2 Methods

### 2.1 Sampling

Sampling was conducted in two locations, Varangerfjord and Agdenes (Figure 2). The Varangerfjord is located in the most northeastern area of Norway, Finnmark, and extends into the Barents Sea, not far from the Russian border and the invasion core of pink salmon. Whilst Agdenes, Trøndelag, is at the very edge of the mouth of the Trondheimsfjorden.

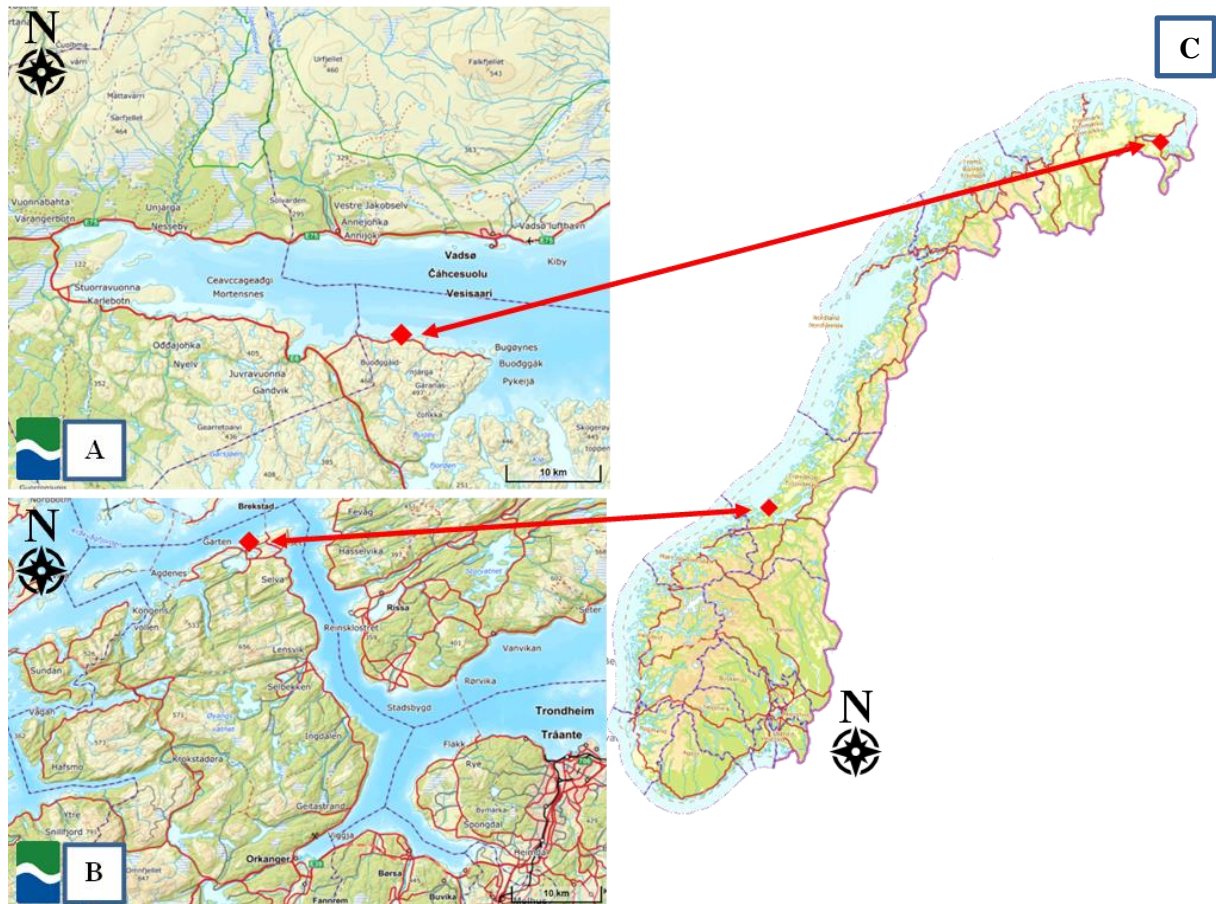


Figure 2: Map over Varangerfjord (A) and the inlet of Trondheimsfjorden (B). The red dots in map A and B symbolises where the kilenot was put to catch the pink salmon. Map over Norway (C) shows both locations; Varanger is the northernmost, while Agdenes is the most southern of them. All maps are collected from Norgeskart.no (kartverket).

At both study locations, adult pink salmon returning to coastal Norway were captured in a ‘kilenot’ (Berntsen et al., 2020; R. Skern, personal communication 18<sup>th</sup> August 2023). Kilenot is composed of a guide net, leading the fish into a catch part consisting of slot-shaped chambers. The catch chambers have side walls and a bottom and are attached at a 90° angle on the guide net (Regulations on tools etc. in salmon fishing, 2003, §4). In Varanger, 38 fish were caught on 27<sup>th</sup> June 2023 by the Norwegian Institute of Marine Research. Pink salmon from Agdenes were caught by the Norwegian Institute for Nature Research in three different years: 2017 (n = 1), 2021 (n = 12), and 2023 (n = 9). The sampling for pink salmon in outer

Trondheimsfjord in 2017 was conducted between 1<sup>st</sup> July and 10<sup>th</sup> August; in 2021 between 3<sup>rd</sup> July and 24<sup>th</sup> July, and in 2023 between 28<sup>th</sup> June and 22<sup>nd</sup> August. Whole fish were frozen immediately and stored at - 20°C before dissection and parasite screening.

## **2.2 Dissection**

Although more individuals were caught, only 30 pink salmon were dissected from Varanger, as this is a large enough sample size to minimize sample size bias (Shvydka et al., 2018). All 22 fish caught from Agdenes were dissected.

The fork length (millimetres) and weight (grams) of all fish were taken prior to dissection. The belly of the fish was cut open from between the two pectoral fins, all the way down to the anus. Care was taken to not cut the intestines in order not to lose potential parasites located there. With the belly open, different organs were individually removed and put in separate zip-lock bags. Once the organs were removed, the body cavity was examined for parasites. A small quantity of saline water (0.9 % salinity) was added to each zip-lock bag to prevent freezer burn. Each bag was labelled on the outside with fish ID, date of catchment, and content of the bag. A small paper label with a matching ID was also put inside. The bag was then frozen at - 20°C.

## **2.3 Organ analysis and parasite counting**

For this study, the digestive tract (stomach and intestines) was screened for macroparasites. The organ was defrosted, taken out of its bag, and moved into a large glass petri dish. The bag was washed with saline water and examined under a stereomicroscope to check for parasites that could have remained in the bag. The organ was then cut open and the contents within the organ were transferred to another dish, washed down, and also screened for parasites. Stomachs were also examined to estimate the percentage of fullness, and any food items were placed in ethanol in lidded glass vials and stored for future analysis. In some cases, the organ content was cleaned through a plankton cloth to remove fine particles. The cloth was checked afterwards with a stereomicroscope to see if some parasites were stuck to the pores and if the smallest parasites would wash through the pores.

The organ walls were scraped clean with a scalpel and washed in saline water before being moved to a separate dish (one additional step in this process on the intestines was to squeeze all the pyloric caeca). The walls were screened for parasites attached. The remaining organ content, mostly mucus, was divided into smaller dishes and analysed under the stereomicroscope. Nematodes were picked out with A-shaped tweezers, while cestodes were

removed with a glass pipette. All parasites from each fish were collected in separate watch-glasses with saline water, counted, and stored in 1.5 mL Eppendorf tubes with 96 % ethanol, sorted by parasite taxa. The count of the taxa *Anisakis simplex* also includes individuals found in the body cavity of the observed fish.

In cases of high infection intensities of individual parasite taxa, e.g. cestodes, subsamples were taken after all other parasite groups had been removed. This was done after the method of Rabeni (1996). The remaining tissue was cut into smaller pieces, diluted to an appropriate volume tailored to the size and amount of content in the organ and thoroughly mixed. From this solution, 10 aliquots (ranging from 0.5 % - 2 %) of the total solution were taken with a two-stop pipette in an 8-shaped movement across the whole water column. Parasites were counted and identified (see section 2.4) in each subsample, averaged, and scaled up to represent 100 %.

## **2.4 Parasite identification**

Parasites were morphologically identified based on the keys of Moravec's (2004). In some cases additional literature was necessary (Atopkin et al., 2020; Bouguerche et al., 2023; Gibson et al., 2002; K oie, 1995; Krupenko et al., 2022; Moravec, 1994, 2004). In cases where specimens could not be identified based on the literature, experts in the field were contacted (T. Scholz, personal communication, 22<sup>nd</sup> February 2024).

Parasites were removed from their tube and transferred to a petri dish with some saline water (nematodes were put into a 50/50 mix of glycerol and saline water to make them reabsorb hydration). First, the parasites were divided into smaller groups based on structural differences, then put on a microscope slide with a few drops of saline water and a cover glass on top for screening under the microscope. Nematodes were placed on a flat microscope slide, while trematodes and cestodes were put on a wellled microscope slide to prevent damage. The different parasites were identified to the lowest possible taxonomic level, re-counted, and stored in a 1.5 mL Eppendorf tube with 96 % ethanol and a label describing fish ID, organ and taxa.

## **2.5 Indices and statistical analysis**

Mean abundance (total number of individual parasites divided by the number of examined hosts) and prevalence (number of infected hosts divided by the number of examined hosts) per parasite taxa was calculated for each individual fish (infracommunity) and for each location (component community) after definitions following Bush et al. (1997). All statistical analyses were carried out using R (version 4.3.3, R Core Team, 2024).

Margalef's diversity index ( $D_{Mg}$ : Equation 1) was also calculated for each individual pink salmon and was used to compare the diversity of parasite taxa between the two locations.  $S$  is the number of (parasite) taxa, and  $N$  is the total abundance (of parasites) (Margalef, 1957).

$$D_{Mg} = \frac{S-1}{\ln N} \quad \text{Equation 1: Margalef's diversity index}$$

Higher values indicate higher taxa diversity. Margalef's diversity index was selected over the more common Shannon's index due to Shannon's index sensitivity to sample size. Margalef's index compensates for this by dividing the number of taxa with the natural logarithm of the total abundance (Gamito, 2010; Magurran, 2004). Margalef's index is often paired with other indices like the Berger-Parker evenness index (Berger & Parker, 1970) (Equation 2) because they complement each other in the understanding of biodiversity by evaluating both taxa richness and dominance. The Berger-Parker index does this by evaluating the proportion of the taxa with the highest abundance (Gamito, 2010; Magurran, 2004).

$$d = \frac{N_{max}}{N} \quad \text{Equation 2: Berger-Parker dominance index}$$

$N_{max}$  is the abundance of the most common (parasite) taxa, and  $N$  is the total abundance of parasites in that fish taxa (Berger & Parker, 1970; Magurran, 2004). This was calculated per individual fish, i.e. for every infracommunity. The index is on a proportional scale and varies between 0 and 1, where a value close to 1 indicates a single dominant species, while lower values closer to 0 indicate few or no dominant species, thus a high evenness (Magurran, 2004).

To investigate the similarities between the parasite communities in the current study with parasite communities of other studies (Fjær, 2019; Rullestad, 2021; Sokolov et al., 2024), Jaccard's similarity index ( $C_J$ : Equation 3) was used (Magurran, 2004). As with Berger-Parker, Jaccard's is also an index from 0-1, where a closer output to 1 is indicating a high similarity in the parasite communities of the two studies being compared.

$$C_J = \frac{a}{a-B+C} \quad \text{Equation 3: Jaccard's similarity index}$$

$B$  is the number of taxa only found study 1,  $C$  is the number of taxa only found in study 2, whilst  $a$  is the total number of taxa common in both studies (Magurran, 2004). The index was calculated using the "bayesbio" package in R (McKenzie, 2016). One advantage of this package is that one can write taxa names into the script, making it possible to compare actual taxa instead of numbers. The studies of Fjær (2019) and Rullestad (2021) were selected for comparison with

the current study because the studies were conducted in other places in Norway (Figure 3), while Sokolov et al. (2024) were chosen due to the study's location in the White Sea (Figure 3). In order to use Jaccard's index was nomenclature and synonyms of species unified to allow a comparison between the studies. *Diphyllobothrium* spp. was used over *Dibothriocephalus*, due to uncertainty over the correct taxa (Waeschenbach et al., 2017), and the other studies found *Diphyllobothrium* sp. most likely to be *D. schistochilos*, a species that has ringed seals (*Pusa hispida*) as the final hosts (Rullestad, 2021; Sokolov et al., 2024; Waeschenbach et al., 2017). The two taxa of *Scolex pleuronectis* found in Fjær (2019) and Rullestad (2021) were treated as one species considering it has only been differentiated morphologically. The order *Bothriocephalidea* was used instead of *Eubothrium crassum* to minimize the uncertainty between the different studies. Taxa usually not found in the digestive system, e.g. *Apatemon gracilis* (Blair, 1976) were excluded. *Scolex bothriosimplex*, as used by Fjær (2019) and Rullestad (2021), was changed to *Tetrabothrius* sp., as in Sokolov et al. (2024), as sequencing displayed a high relatedness (95 %) between the two taxa.

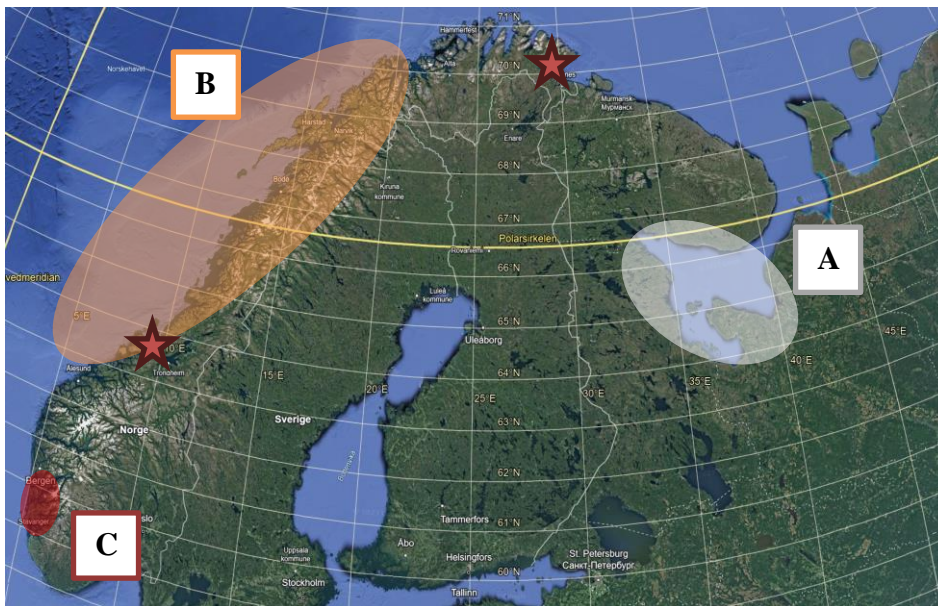


Figure 3: Field A (white) highlights the White Sea, where the study of Sokolov et al. (2024) was conducted. Field B (orange) highlights the area where Rullestad (2021) collected her pink salmon, while field C (red) highlights the area where Fjær (2019) collected her pink salmon. The two stars pinpoint the location of Varanger (northernmost) and Agdenes (southernmost) in relation to the other studies. Map is collected from Google Earth (Map data ©2013 Google).

Separate generalized linear models (GLMs) were used to investigate the relationship between each response variable (i.e., abundance, diversity, dominance, and taxa richness), location and fish size. Fish size was represented by length and weight, instead of other scales like Fulton's body conditions (Fulton, 1904). This was because Fulton's body conditions rely on assumptions of isometric growth (Flatén et al., 2016), whereas pink salmon are considered to have an allometric growth curve (Young, 2005). Shapiro-Wilks test (Shapiro & Wilk, 1965) together



with visually inspecting the histogram was used to determine the distribution of the response variable. However, if the data was not normally distributed, the Poisson family was the better approach. For each response variable that did not conform to a normal distribution, the variance was compared to the variable's mean. If the variance was substantially larger than the variable's mean, the Quasi-Poisson family was used to compensate for the overdispersion. The exception was when a Beta Regression from the "betareg" package (Cribari-Neto & Zeileis, 2010) was used for Berger-Parker's index because the index has strict values between 0-1 (Ferrari & Cribari-Neto, 2004). All models had the same initial formula:

$$glm(\text{response variable} \sim (\text{location} + \text{weight} + \text{length})^2, \text{family} = *, \text{data} = \text{df})$$

\*Selection of family was based on the distribution of the response variable.

Two models were made for abundance, one including extreme outliers and one excluding those extreme outliers. Outliers were identified with the use of  $3 \times \text{IQR}$  (Inter quartile range) (Schwertman et al., 2004; Tukey, 1977).

In order to select the best model for each of the response variables, the "dredge" function from the "MuMIn" package (Barton, 2023) was used. It suggests the best model based on the AICc score. By combining the "summary" function with the "get.model" function (also from MuMIn package), the output of the best model was presented (Table 3). The same method was used to compare the abundance of the most common parasite taxa (prevalence above 35 %) at each location. Except for two taxa: *Scolex pleuronectis* and *Lecithaster gibbosus*, due to the number of zeros in the count, a zero inflated model was a better approach. This was done with the "zeroinfl" function from the "pscl" package (Zeileis et al., 2008).

### 3 Results

#### 3.1 Parasite taxon richness, diversity, and dominance

In total, 13 parasites taxa of nematodes, trematodes, and cestodes were identified in the digestive tract of pink salmon between the two locations Varanger and Agdenes (Table 1). Pink salmon in both locations contained 12 taxa of intestinal parasites each (Table 1). Each individual fish harboured three or more parasite taxa, with a maximum of eight and nine parasite taxa occurring in the stomachs and intestines of pink salmon captured at Varanger and Agdenes, respectively (Figure 4). However, there was no significant difference in the number of observed parasite taxa per individual (taxon richness) between the two locations (Figure 5), nor for Margalef's index of diversity (Table 2). Conversely, for Berger-Parker's dominance index there was a higher effect in Varanger than in Agdenes (Table 2), despite the five extreme outliers of *S. pleuronectis* in Agdenes. The interaction between weight and length is significant for diversity and dominance, as well as the interaction between location and weight on dominance (Table 3).

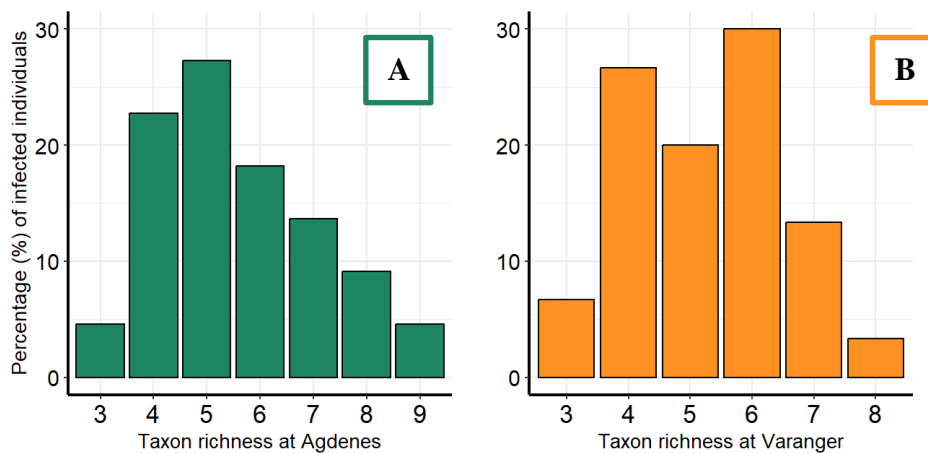


Figure 4: Bar charts showing intestinal parasite taxon richness in pink salmon at Agdenes (A) and Varanger (B).

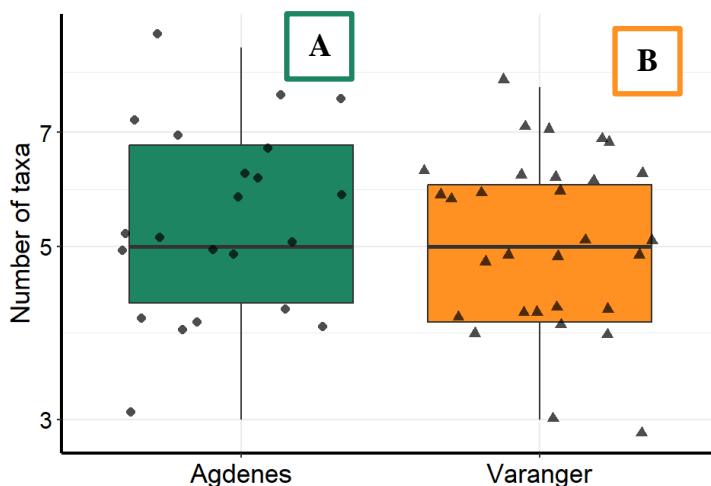


Figure 5: Boxplots showing the taxa richness in pink salmon at Agdenes (A) and Varanger (B). There is no significant difference in the number of parasite taxa observed per individual (taxon richness) between Varanger and Agdenes.

Table 1: Overview of parasite taxa found in the digestive system of pink salmon in Varanger and Agdenes. Abbreviations: Intestine (I), Stomach (S), Prevalence (Prev), Mean Abundance (MA), Standard Error (SE).

Parasite taxa		Varanger (n = 30)		Agdenes (n = 22)		Intermediate host
	Site	Prev (%)	MA (± SE)	Prev (%)	MA (± SE)	Source before infection (Reference)
<b>Trematoda</b>						
<i>Brachyphalus crenatus</i>	S	-	-	22.7	3.3 (± 1.8)	Genus <i>Acarita</i> , <i>S. elegans</i> and <i>Pleurobrachia pileus</i> (Køie, 1992; Moravec, 2004)
<i>Derogenes varicus</i>	I & S	100	250.9 (± 28.6)	81.8	123.05 (± 61.3)	Hermit crab <i>Pagurus pubescens</i> (Moravec, 2004)
<i>Hemiurus communis</i>	S	6.7	0.07 (± 0.05)	59.1	338.2 (± 235.3)	Copepod of genus <i>Acarita</i> (Køie, 1995; Moravec, 2004)
<i>Hemiurus levinseni</i>	S	73.3	2.3 (± 0.5)	27.3	4.8 (± 4.1)	<i>Sagitta elegans</i> (Moravec, 2004)
<i>Hemiurus luehei</i>	I & S	10	0.3 (± 0.2)	22.7	0.95 (± 0.4)	Copepod of genus <i>Acarita</i> (Køie, 1990)
<i>Lecithaster gibbosus</i>	I	60	2.9 (± 0.7)	36.4	7.1 (± 3.2)	Copepod of genus <i>Acarita</i> (Køie, 1989)
<b>Cestoda</b>						
Order Bothriocephalidea**	I	3.3	0.03 (± 0.03)	13.6	3.95 (± 3.3)	Copepod**** (Moravec, 2004)
Family Hymenolepididae **	I	3.3	0.2 (± 0.2)	-	-	Not known****
<i>Diphyllbothrium</i> sp. A*	S	23.3	0.3 (± 0.1)	4.5	0.05 (± 0.05)	Copepod**** (Waeschenbach et al., 2017)
<i>Diphyllbothrium</i> sp. B*	I	16.7	0.4 (± 0.2)	31.8	2.7 (± 1.1)	Copepod**** (Waeschenbach et al., 2017)
<i>Scolex pleuronectis</i>	I	36.7	2.4 (± 0.8)	81.8	1276.4 (± 597.3)	Not known (Moravec, 2004)
<b>Nematoda</b>						
<i>Anisakis simplex</i> ***	I & S & BC	93.3	5.1 (± 0.8)	81.8	5.3 (± 1.2)	Crustaceans & other invertebrates (Moravec, 1994)
<i>Hysterothylacium auduncum</i>	I/S	100	53.7 (± 8.5)	95.5	56.7 (± 16.6)	Copepod (González, 1998; Moravec, 1994)
Species richness:		12		12		

\*Due to differences in morphology and site of infection, *Diphyllbothrium* was divided into two different taxa. \*\*Family Hymenolepididae and Order Bothriocephalidea were identified to the closest possible taxonomic rank. This was done due to difficulties in accurate identification. \*\*\*Due to procedure during dissection, *A. simplex* from the digestive tract and body cavity were grouped together. \*\*\*\*The uncertainty of correct species of *Diphyllbothrium*, Family Hymenolepididae and Bothriocephalidea makes it difficult to determine the correct host.

## 3.2 Prevalence

The trematode species *Derogenes varicus* and nematode *Hysterothylacium auduncum* were both observed in all 30 individuals of pink salmon examined from Varanger. In Agdenes, the prevalence of *D. varicus* was 81.8 % and 95.5 % for *H. auduncum*, although these species were not observed in all pink salmon examined, they were still highly abundant. The other nematode species, *A. simplex* was also observed in most fish at both locations with a prevalence of 93.3 %

at Varanger and 81.8 % at Agdenes. The nematode *H. communis* was more common in fish caught in Agdenes and had a prevalence of 59.1 %, while the species was only observed in 6.7 % of fish from Varanger. The trematode *Brachyphalus crenatus* was only observed in pink salmon from Agdenes and had a prevalence of 22.7 %, whereas cestode of the family Hymenolepididae was only observed in Varanger, though with a low prevalence (3.3 %). The cestode, *Diphyllobothrium* sp. A, had a prevalence of 23.3 % in Varanger, compared to only 4.5 % in Agdenes. The cestode, *Scolex pleuronectis*, was highly abundant in fish from Agdenes, and much more prevalent (81.8 %) than in Varanger (16.7 %).

### 3.3 Abundance

There was no significant difference in the abundance of parasites in pink salmon between the two locations (Figure 6), both with and without outliers (Table 3). Varanger had a higher mean abundance for certain parasite taxa, such as *Derogenes varicus* with a mean abundance of 250.9 parasites per examined fish, compared to Agdenes where the fish had a mean abundance of 123.05. All *Hemiurus* spp. and cestodes had a very low mean abundance in both locations, except for *H. communis* and *Scolex pleuronectis* in Agdenes, which had a mean abundance of 338 and 1276.3, respectively. Besides *D. varicus*, it is *Hysterothylacium auduncum* that had the highest abundance in Varanger, whereas all other taxa had a mean abundance below 5 individuals per fish.

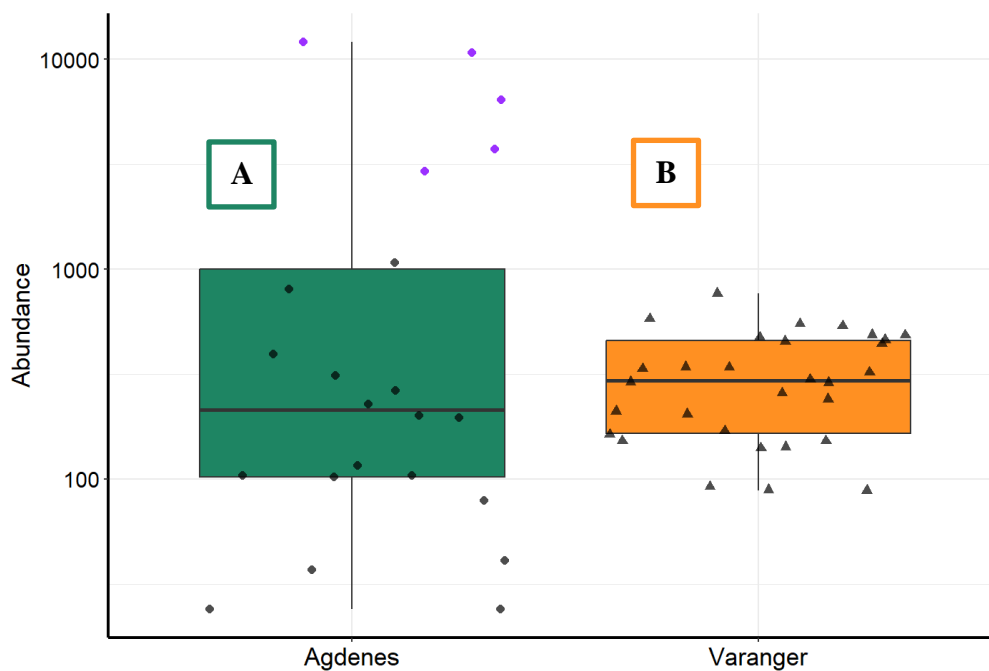


Figure 6: Abundance of parasites in Agdenes (A) and Varanger (B). Varanger has the higher mean of the two. Y-scale is log<sub>10</sub> transformed. The five purple dots over Agdenes (A) highlights the outliers.

Table 2: Mean taxa richness, mean abundance, and Margalef's index, and Berger-parker index of Varanger and Agdenes, with standard error ( $\pm$  SE). The p-values for taxa richness and abundance as the selected model did not include a coefficient for location, thus location was not significant (NS).

Category/ measurement:	Varanger (n = 30)	Agdenes (n = 22)	p-value
Taxa richness	5.3 ( $\pm$ 0.24)	5.6 ( $\pm$ 0.34)	Location: NS
Mean abundance	318.53 ( $\pm$ 31.55)	1822.41 ( $\pm$ 744.73)	Location: NS
Margalef's diversity index	0.76 ( $\pm$ 0.04)	0.85 ( $\pm$ 0.07)	p = 0.077
Berger-Parker index	0.76 ( $\pm$ 0.02)	0.57 ( $\pm$ 0.04)	p = 1.04 <sup>-4</sup>

Table 3: Output of the glm-models, testing either diversity (represented by Margalef's diversity index), dominance (represented by Berger-Parker's dominance index), abundance (both including and excluding outliers), or the taxa richness against location, fish length and fish weight . Significant differences ( $p < 0.05$ ) are highlighted in bold.

Coefficients	Estimate	Std. error	z value	p-value
<b>Margelef's index</b>				
a) glm(formula = margalefs ~ Length + Location + Weight + Length:Weight + 1, family = gaussian) AIC: 8.24				
Intercept	-3.87	1.48	-2.61	<b>0.012</b>
Length	0.01	0.003	3.11	<b>0.003</b>
LocationVaranger	-0.16	0.09	-1.81	0.077
Weight	0.003	1.1e-03	2.89	<b>0.006</b>
Length:Weight	-6.9e-06	2.1e-06	-3.26	<b>0.002</b>
Null deviance: 3.8037 on 51 degrees of freedom, Residual deviance: 2.8320 on 47 degrees of freedom				
<b>Berger-Parker's index</b>				
b) betareg(formula = bergerparker ~ Length + Location + Weight + Location:Weight) AIC: -52.3				
Intercept	14.19	4.05	3.50	<b>4.6e-04</b>
Length	-0.03	0.01	-3.88	<b>1.1e-04</b>
LocationVaranger	2.95	0.76	3.87	<b>1.1e-04</b>
Weight	-0.01	0.003	-1.49	0.134
Length:Weight	1.3e-05	5.9e-06	2.27	<b>0.024</b>
LocationVaranger:Weight	-1.5e-03	4.9e-04	-2.92	<b>0.004</b>
Type of estimator: ML (maximum likelihood), Log-likelihood: 36.02 on 7 Df				
<b>Total abundance – outliers included</b>				
c) glm(formula = No_parasites ~ 1, family = quasipoisson) AIC: NA				
(Intercept)	6.86	0.34	19.9	<b>&lt;2e-16</b>
Null deviance: 129752 on 51 degrees of freedom, Residual deviance: 129752 on 51 degrees of freedom				
<b>Total abundance – outliers excluded</b>				
d) glm(formula = No_parasites ~ 1, family = quasipoisson) AIC: NA				
Intercept	5.67	0.11	51.08	<b>&lt;2e-16</b>
Null deviance: 7132.2 on 46 degrees of freedom, Residual deviance: 7132.2 on 46 degrees of freedom				
<b>Taxa richness</b>				
e) glm(formula = Sp_richness ~ 1, family = poisson) AIC: 205.32				
Intercept	1.69	0.06	28.3	<b>&lt;2e-16</b>
Null deviance: 19.797 on 51 degrees of freedom, Residual deviance: 19.797 on 51 degrees of freedom				

### 3.4 Comparison to other studies

Varanger and Sokolov et al. (2024) had the lowest overlap in parasite community of all investigated studies, with a similarity of 0.44 on Jaccard's index, while Agdenes had a similarity with Sokolov et al. (2024) of 0.53 (Table 4). The parasite taxa composition of Agdenes was more similar than what Varanger was to the studies of Fjær (2019) and Rullestad (2021).

*Table 4: Results from Jaccard's similarity index in geographical order from the shortest to the furthest distance to the invasion core. Varanger and Agdenes are of the current study.*

<i>Comparison</i>	Sokolov et al. 2024	Varanger	Rullestad, 2021	Agdenes
Varanger	0.44			
Rullestad, 2021	0.70	0.62		
Agdenes	0.53	0.83	0.75	
Fjær, 2019	0.53	0.70	0.75	0.83

The biggest difference between the present study to the other studies, is the occurrence of the cestode family Hymenolepididae in Varanger. Out of the 13 taxa that were found in total in the present study, 11 taxa were found at both locations. Rullestad (2021) reported on 10 taxa of macroparasites that are commonly found in the digestive system, whereas Fjær (2019) reported one more. Comparing Fjær's findings to Agdenes, there are 10 shared taxa, whereas Varanger had one less. Sokolov et al. (2024) reported on 12 taxa, eight of these taxa was found in Agdenes, and just seven in Varanger.

## 4 Discussion

In this study, I investigated whether parasite communities in pink salmon change along their invasion gradient in Norway. Counter to expectations, neither parasite taxa richness, diversity, or abundance were significantly different between the northern and southern locations. Therefore, no apparent enemy release was observed along the invasion front of pink salmon on the Norwegian coast. Moreover, only dominance exhibited a stronger effect of location, than the effect of fish size. For diversity, location was not significant, thus size was more influential. Neither location nor fish size had a significant impact on taxa richness or abundance, despite the large differences in the count. However, my study revealed one new parasite record in Norwegian pink salmon and showed a different parasite community to previous reports from invasive pink salmon in the invasive range in Norway (Fjær, 2019; Rullestad, 2021; Sokolov et al., 2024).

Firstly, I hypothesised that according to the enemy release hypothesis, there would be a decrease in the parasite load from Varanger to Agdenes, due to Agdenes being the location the furthest away from the pink salmon invasion origin in the White Sea (Hindar et al., 2020; Lennox et al., 2023), this however, was not observed. A possible explanation for the absence of parasite release might be due to a similar availability of prey items between Agdenes and Varanger. This is supported by a reportedly similar diet between pink salmon and Atlantic salmon (*Salmo salar*) found in the Norwegian Sea and Barents Sea (Diaz Pauli et al., 2023), and an overlapping diet for Atlantic salmon between Trondheimsfjord and a side fjord to Varangerfjord (Rikardsen et al., 2004). As parasites often transmit via trophic transmission (Lafferty et al., 2008), diet could explain some of the patterns in the parasite acquisition. Varanger had a higher value of Berger-Parker dominance index, actually indicating less dominance of certain parasite taxa in Agdenes. Something that appears to be rather robust, since parasite communities in Agdenes were more even, despite the few extreme outliers.

A comparative research study about biological invasions in marine environments and different mechanisms involved parasite release, Blakeslee et al., (2013) found evidence for parasite release from the native to the new environment, as well as from the invasion core to the invasion front. However, the evidence for geographical influence was stronger when seen together with other factors, such as available hosts and vectors (Blakeslee et al., 2013). This pattern was also observed in the present study as there was only a significance of dominance on location, thus location needs to be seen together with other factors as well.

Secondly, I hypothesised that there would be a stronger effect of location, than fish size on the parasite community. Conversely, for diversity, there was a no significant effect of location. However, the interaction between length and weight was negative, meaning for the largest fish, the effect on diversity is no longer determined by weight. Thus, it is likely that other factors affect the diversity. A ‘mirrored’ effect was observed for dominance: the positive interaction between length and weight makes the effect of weight more comprehensive as the length increases, meaning the parasite infracommunity in the longest and heaviest fish exhibits a higher evenness. This reflects the correlation of parasite acquisition with size (Luque et al., 2004; Paterson et al., 2012), as larger fish have a reduced likelihood of having one or few dominant parasite taxa, and rather harbour more and less dominant taxa. The contrastive effects of weight and length in different settings, might be reflected by the allometric growth curve of pink salmon (Young, 2005) in combination with food availability (Rohde, 1984). Allometric growth is when one part of the body grows at a different rate compared to the rest of the body (Huxley & Teissier, 1936), thus a smaller fish could be heavier than another fish that is longer. Pink salmon’s fixed two-year life cycle (Heard, 1991; Hindar et al., 2020; Irvine et al., 2014; Lennox et al., 2023), might also play a role as it could limit the chance of substantial differences in size. However, other investigations indicates that the length of pink salmon fluctuates enough between individuals to be significantly different (Dickerson et al., 2002), hence making it difficult to determine the effect of size in this very setting.

There were no observed effect of fish size and location on abundance and taxa richness. This indicates that parasite acquisition and community structure are not simply driven by only geographical distribution and host size alone, but other abiotic and biotic factors, might be highly relevant as well (Luque & Poulin, 2008). Previous studies have highlighted that parasite transmission and community patterns are determined by a wide range of factors ranging from effects of changes in environmental conditions (Studer et al., 2010), such as salinity (Luque & Poulin, 2008; Rohde, 1984) and temperature (Rohde, 1984; Selbach & Poulin, 2020; Studer et al., 2010), as well as feeding habits (Luque et al., 2004) and host traits (Blasco-Costa & Poulin, 2013). Summarizing that several factors need to be addressed in order to investigate parasite acquisition fully, thus explaining the lacking effect of location and size in the present study.

In my third, and last hypothesis, I expected to find a different parasite community in the digestive tract of pink salmon, than what earlier studies had observed due to a longer timespan since the introduction of pink salmon to Norwegian coastal areas. McDonald and Margolis (1995) found 36 macroparasite taxa in pink salmon in their native range. That is a much more



species-rich parasite community than what I observed, and to what has been previously observed in the invasive range of European pink salmon populations (Barskaya et al., 2005; Fjær, 2019; Hindar et al., 2020; Norwegian Environment Agency, 2023; Rullestad, 2021; Sokolov et al., 2024). This highlights a shift in parasite community composition from the native to the invasive range. This was expected, considering pink salmon were introduced as eggs to the White Sea (April et al., 2023; Lennox et al., 2023; Mo et al., 2018), hence making it unlikely that they brought their native parasites. However, this could only be a preliminary state, as NIS tend to host more parasite taxa with an increasing time since the introduction (Guégan & Kennedy, 1993; Mitchell et al., 2010; Paterson et al., 2012). It is therefore likely that pink salmon might accumulate more parasites in the future. For example, parasites in the native range of pink salmon can ultimately find their way into the invasive pink salmon populations, e.g., via mobile bird hosts that can transport parasites. Pink salmon are also expanding their invasive range, and are now found all along the Norwegian coastline (Berntsen et al., 2022). With a continuous expansion of its range, pink salmon might also encounter and harbour more parasite taxa.

When comparing my findings with studies conducted within Norway (Fjær, 2019; Rullestad, 2021) and the start point of the invasion in the White Sea (Sokolov et al., 2024), differences in the parasite community composition were found. Agdenes exhibited a higher similarity in the parasite community than Varanger, compared to the parasite communities in the studies of Fjær (2019), Rullestad (2021) and Sokolov et al. (2024). These results are only based on the taxa that were found, thus are not evidence to prove an infection gradient. The lowest similarity of my findings was found with the parasite community of Sokolov et al. (2024). This is due to unique taxa in both studies. Sokolov et al. (2024) identified the trematode *Lecithaster salmonis*, the cestode *Clistobothrium* sp., and the nematode *Phoconema bulbosum*. These three taxa were not found in my study, nor in other studies conducted in Norway (Fjær, 2019; Rullestad, 2021). Within my study, there was a difference between the two study locations, explained by two reasons: first, the trematode taxa *Brachyphalus crenatus* was only found at Agdenes. Additionally, larvae of a hymenolepidid cestode (Family Hymenolepididae) was only found in a single fish from Varanger. To date, cestodes of this order have not been observed in pink salmon in its native range or its invasive range (Ahyong et al., 2024; Fjær, 2019; McDonald & Margolis, 1995; Rullestad, 2021; Sokolov et al., 2024). The finding of cestode larvae of this particular order might just have been an accidental infection, as this order is usually found in waterfowl (T. Scholz, personal

communication, 22<sup>nd</sup> February 2024) or rodents (Richards & Montgomery, 2012). However, it might also indicate that pink salmon can serve as an accidental host or accumulate new parasites in their invasive range. Due to the low prevalence and abundance (five individuals in one fish), it is impossible to confirm any host-parasite relationship for this taxon at this point.

Pink salmon from this study and previous studies (Barskaya et al., 2005; Fjær, 2019; Rullestad, 2021; Sokolov et al., 2024) have been shown to harbour an overlapping parasite fauna with Atlantic cod (*Gadus morhua*) (Perdiguero-Alonso et al., 2008) and native anadromous fish species like Atlantic salmon or brown trout (Moravec, 2004). Highlighting that pink salmon can potentially harbour species-rich and abundant parasites communities along the Norwegian coast. These parasites appear to be mainly generalists that are shared by native marine and anadromous fish and could spill-back into native host populations and increase disease dynamics in these fish.

On the other hand, if pink salmon actually are a compatible host for several parasites, the fish might actually contribute to a dilution effect by decreasing the infection level in other native hosts (Goedknecht et al., 2016; Kelly et al., 2009; Poulin et al., 2011). Considering that pink salmon die after spawning (Heard, 1991), the parasites on their pink salmon “island” will most likely meet a dead-end when the fish die off. With their host gone, survival of the harbouring parasites is not possible. Even before host death, the parasites will be exposed to a hostile environment when the fish migrate into freshwater, as several organs and the digestive tract of pink salmon disintegrate to focus energy on spawning (Gende et al., 2004; Heard, 1991; Schindler et al., 2003). However, with large quantities of pink salmon ending up dead in the river (Hindar et al., 2020), it is likely that terrestrial animals in Norway might use carcasses of pink salmon as a food source. This could facilitate the transmission of some parasites from marine environments to terrestrial environments. Currently, observational studies have recorded red fox (*Vulpes vulpes*) and white-tailed eagles (*Haliaeetus albicilla*), as well as other birds and scavengers, to forage on pink salmon carcasses in the river (Bonde, 2023; Dunlop et al., 2021).

Moreover, future research should also focus on some taxonomically problematic parasite taxa that are hard to distinguish based on morphological criteria. In order to correctly identify some of the parasite taxa, further analysis with DNA sequencing for substantial identifications is suggested. For example, the commonly found trematode species *Derogenes varicus* is morphologically quite similar to other species from the same genus (Bouguerche et al., 2023).

Another trematode species, *Lecihaster gibbosus*, is also difficult to distinguish from the closely related *L. confusus* or *L. salmonis* (Krupenko et al., 2022). Sequencing conducted by Sokolov et al. (2024) identified the trematode as *L. salmonis*, a trematode native to the Pacific (Krupenko et al., 2022; Sokolov et al., 2024). If so, that means the native parasites of pink salmon have already found their way into invasive pink salmon populations, and the matter should be further investigated. *Scolex pleuronectis* is a collective term for cestode plerocercoids that are morphological identical with a scolex with five suckers (Gharbawi & Maghrabi, 2011; Rullestad, 2021; K. Mackenzie, personal communication, 04<sup>th</sup> June 2024). It is likely that *S. pleuronectis* is synonymous with the genus *Clistobothrium* (Fjær, 2019; Rullestad, 2021; Sokolov et al., 2024), thus this will require further molecular identification.

This study gives new insights into parasite communities in pink salmon, and the trends do not reveal any evidence for enemy release in terms of parasites along the invasion route from Varanger to Agdenes. This emphasises the complexity of parasite acquisition and that a range of factors play a role. The lack of significant effects by location and fish size on diversity, abundance, and taxa richness might indicate that parasite acquisition in pink salmon is stabilizing. My findings revealed diverse and abundant parasite communities in pink salmon in Norway, including one new record of a parasite taxon in this host. There are findings of pink salmon all along the Norwegian coastline, thus future research with expanded geographical attention and including more factors, a clearer picture of parasite-host interactions can be accomplished. Nevertheless, the topic of pink salmon and parasites is far from fully understood and will require careful monitoring in the future. Pink salmon has most likely come to stay, and the fish seem to be a competent host for several parasite taxa in Norway. This thesis, therefore, provides valuable baseline data for future studies of host-parasite interactions in pink salmon, and for the risk assessment and management of this invasive species.

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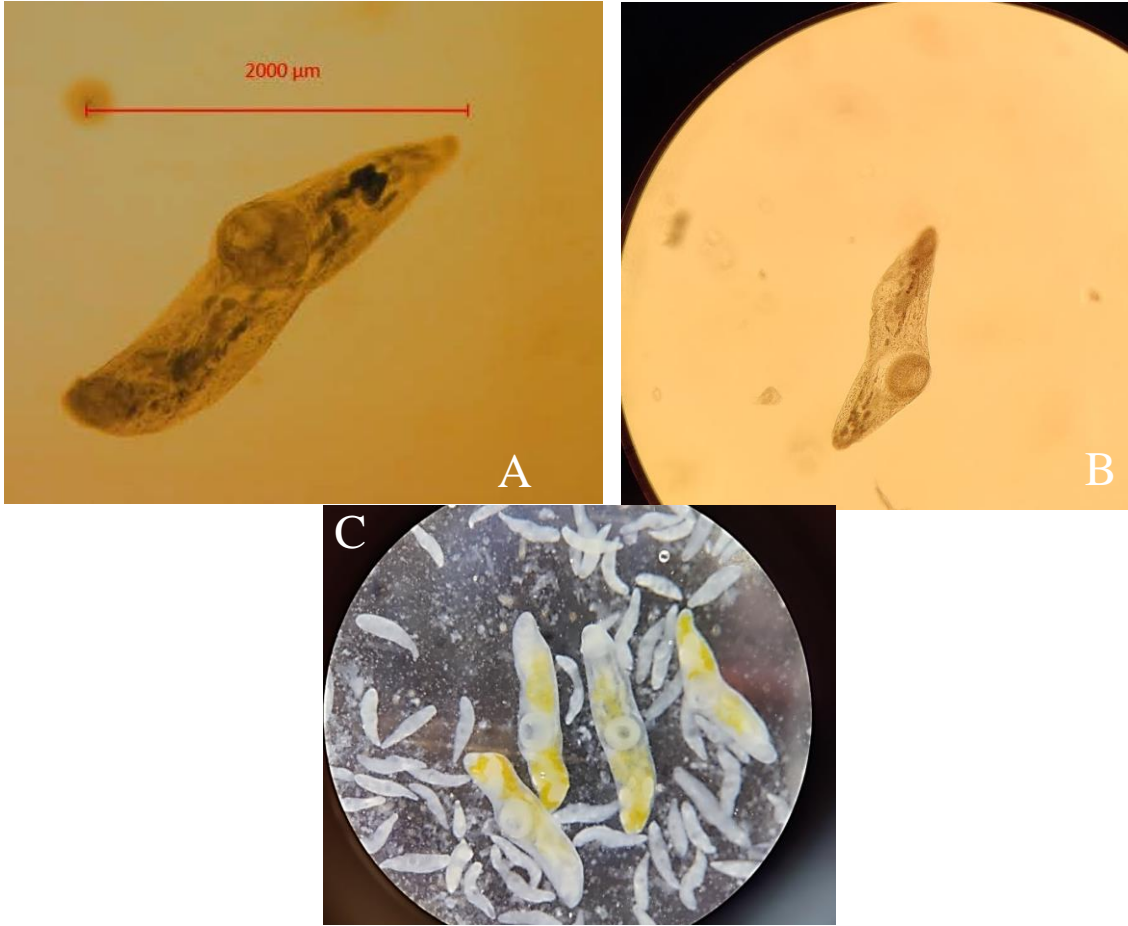
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# 6 Appendix

## 6.1 Taxa pictures

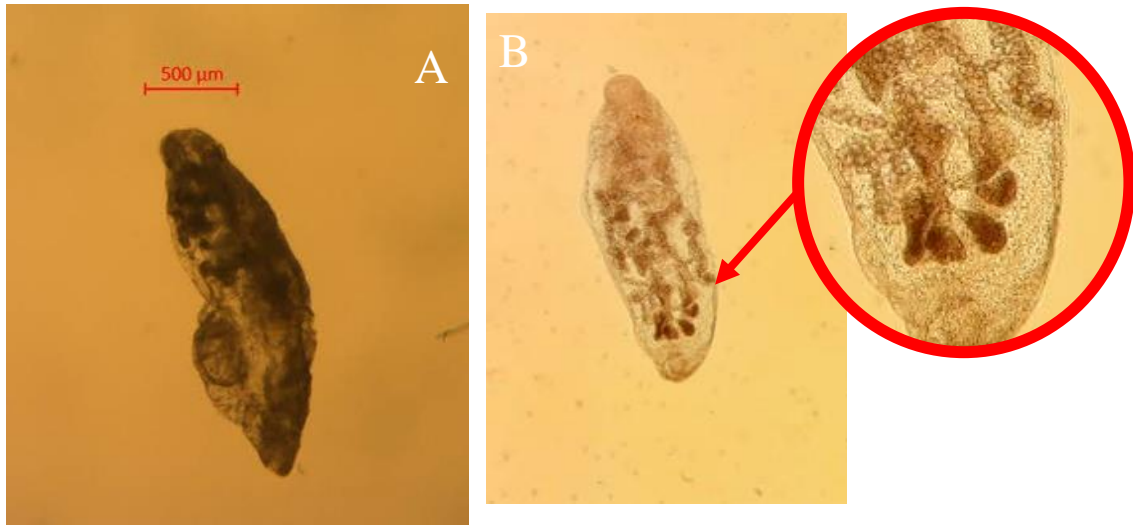
*Derogenes varicus*

Notation: The size of the individuals in A and B is approximately the same. In picture C, the largest individuals also approximately the same as those in A and B.



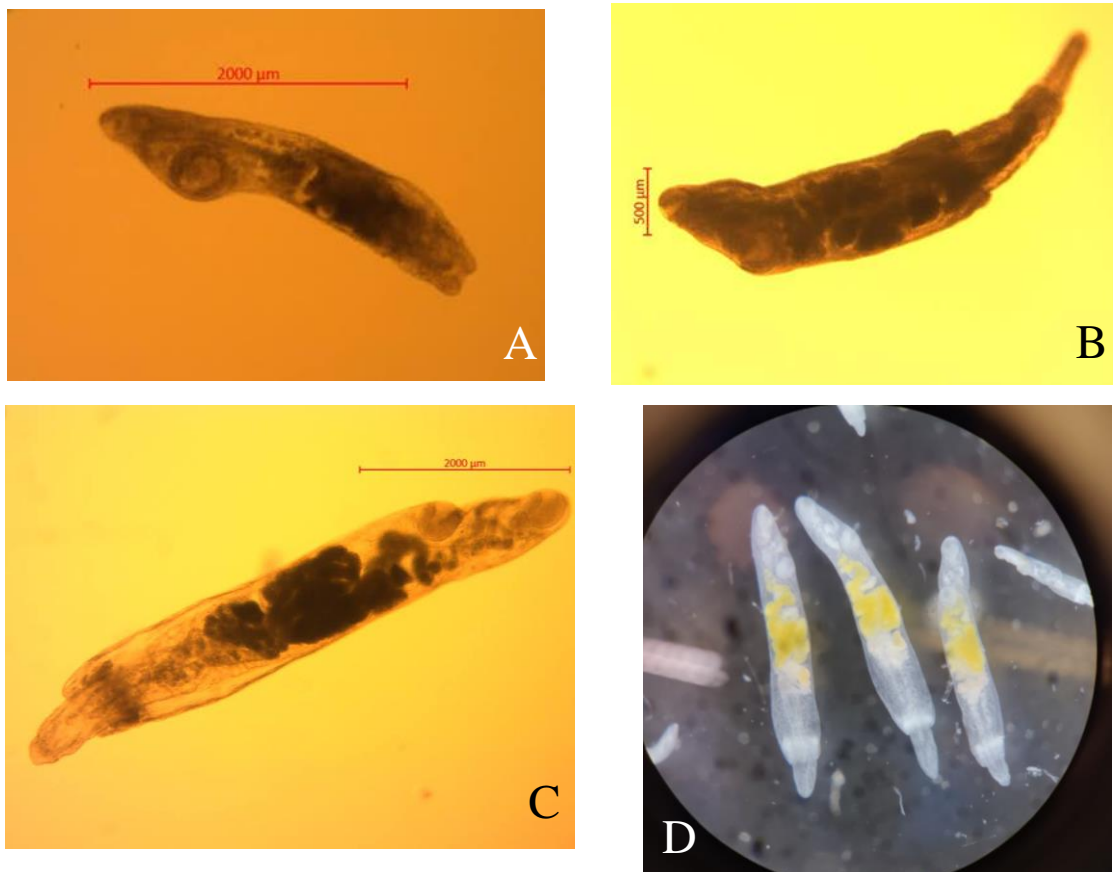
*Lecithaster gibbous*

Notation: Scalebar of picture B is not included because picture was taken with phone. The size of the individuals in A and B is roughly the same. In picture B the seven-lobed vitellarium, as described by Moravec (2004) and Krupenko et al. (2022), are visible.



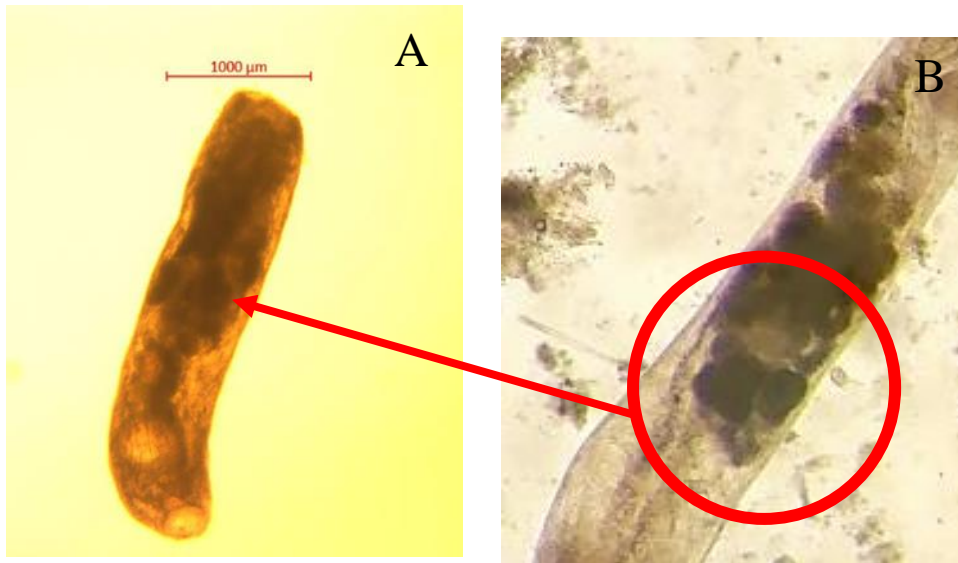
*Trematoda Hemiurus* spp.

Notation: *H. luehei* in picture A, *H. communis* in picture B, and *H. levinseni* in picture C and D. The individual in picture C is one of the individuals in picture D.



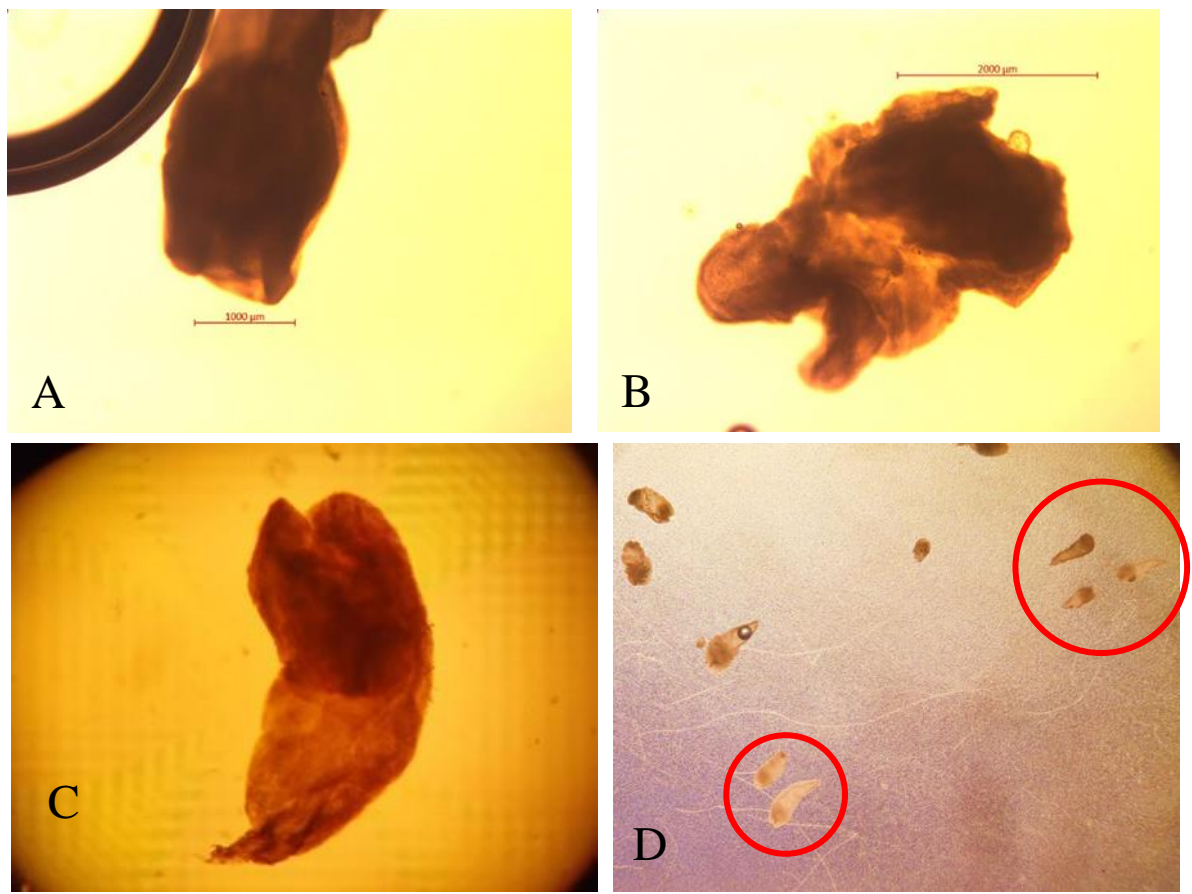
*Brachyphalus crenatus*

Notation: in picture A, is more to get the size of *B. crenatus*. In picture B the three and four lumped vitellarium, a reconcilable feature on the species (Moravec, 2004), are visible.



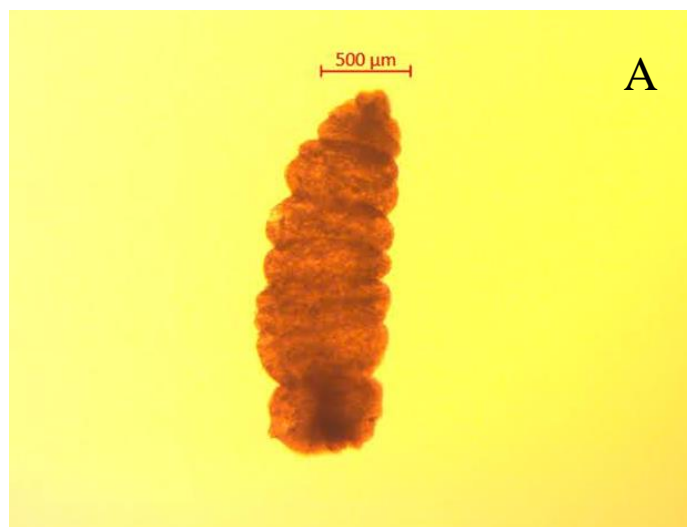
*Diphyllobothrium* sp.

Notation: Picture A captures *Diphyllobothrium* sp. A, while picture B is of *Diphyllobothrium* sp. B. In picture C and D, one can more easily see the shape of *Diphyllobothrium* sp. A. Picture A gives the scale of the size, therefore are there no scalebars in picture C or D.



Order *Bothriocephalidea*

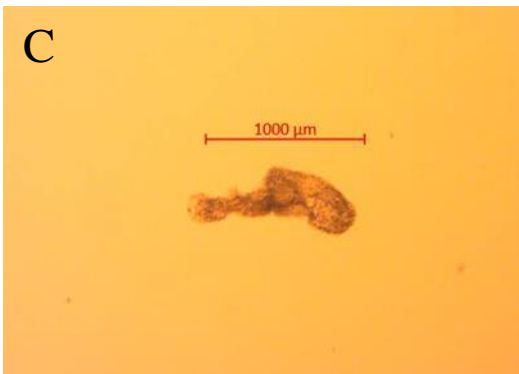
Notation: Picture of individual of *Bothriocephalidea*





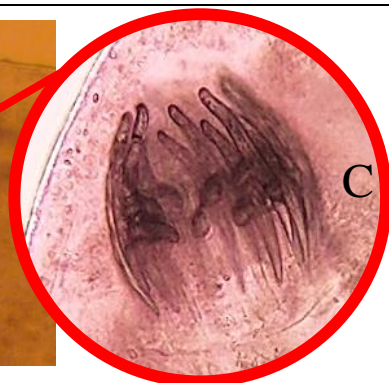
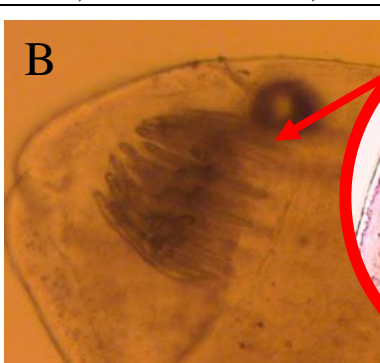
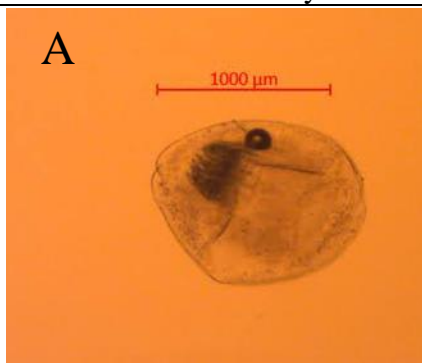
***Scolex pleuronectis* (and lv)**

Notation: Picture A and B are of *Scolex pleuronectis*. The taxa vary a lot in size, and a lot of them are quite small. In picture C and D is what I believe to be a larva-stage of *Scolex pleuronectis*.



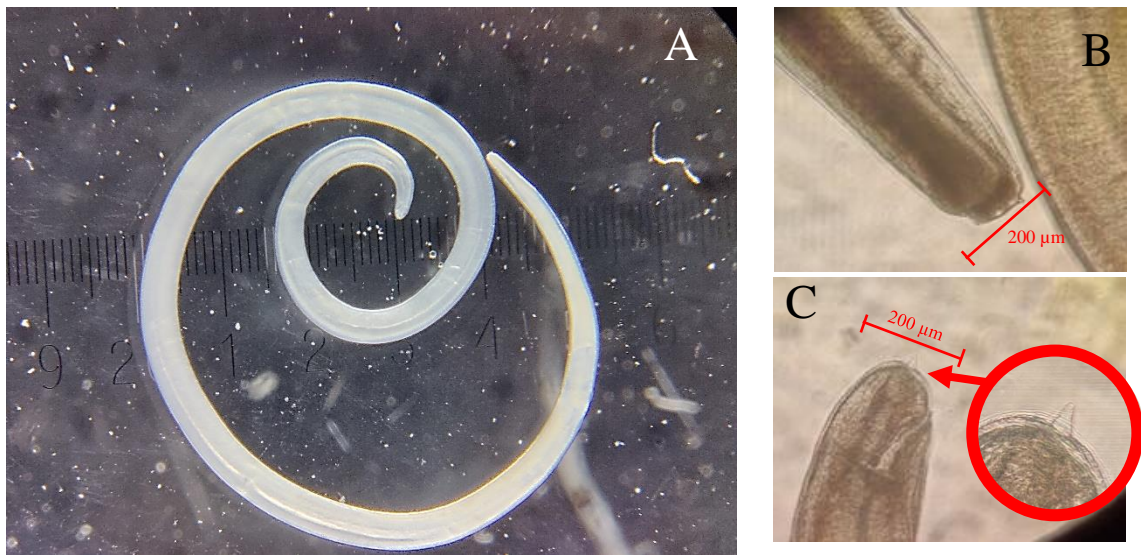
**Family Hymenolepididae**

Notation: All three pictures show an individual of Family Hymenolepididae. In picture A, one sees the whole body of the cestode, while in B and C, shows off the hooks of this taxa.



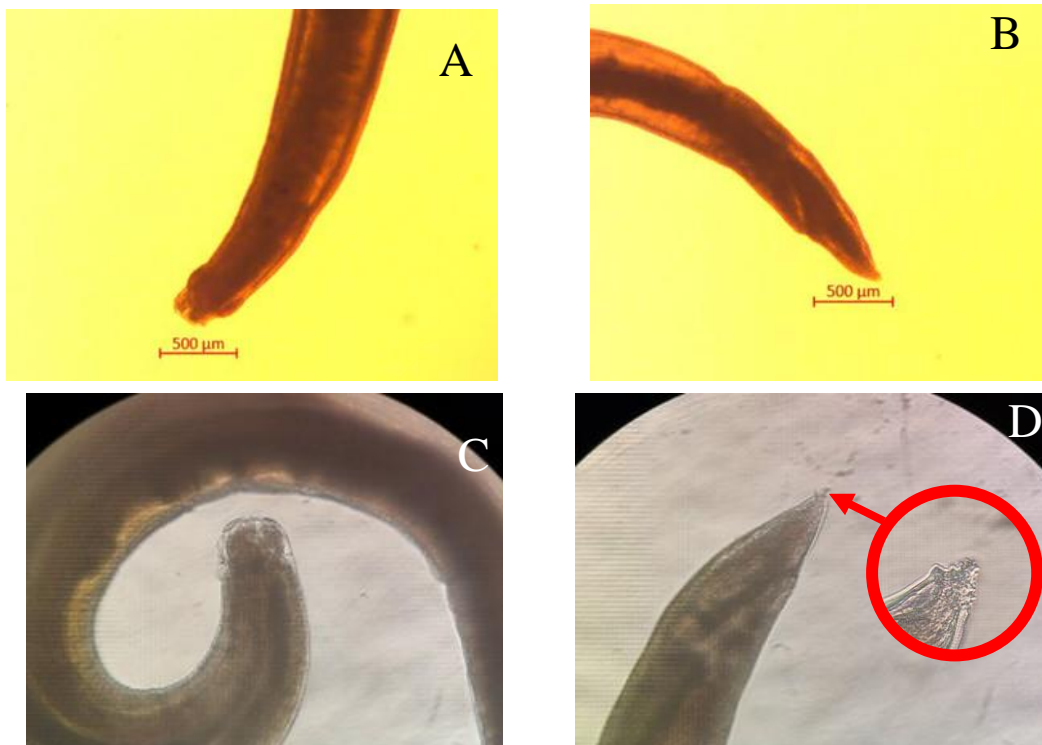
*Anisakis simplex*

Notation: Picture A gives of a picture of a *Anisakis simplex* encysted in a curl. In the background there are a scalebar in millimetres. Head of the *Anisakis* is visible in picture B, while in picture C one sees the tail of *A. simplex* with a zoom in on the cuticular spike.



*Hysterothylacium auduncum*

Notation: Picture A and C shows the head of a *H. auduncum*, while Picture B and D shows the tail of the same nematode. The tail has a “brush”-like tail, covered in granulated cuticle.



## 6.2 Models for selected taxa

Table 5: Separate models of the selected taxa

Coefficients	Estimate	Std. error	z value	Pr(> z )
<b><i>Lecithaster gibbosus</i></b>				
a) <i>zeroinfl(formula = L_gibbosus ~ Location * Length, dist = "poisson") AIC: NA</i>				
<b>Count model coefficients (poisson with log link):</b>				
(Intercept)	5.77	1.37	4.195	<b>2.7e-05</b>
LocationVaranger	-5.46	3.11	-1.76	0.079
Length	-0.006	0.002	-2.07	<b>0.039</b>
LocationVaranger:Length	0.01	0.01	1.32	0.187
<b>Zero-inflation model coefficients (binomial with logit link):</b>				
(Intercept)	1.73	5.43	0.32	0.751
LocationVaranger	-0.85	8.57	-0.09	0.921
Length	-0.002	0.01	-0.21	0.831
LocationVaranger:Length	-3.7e-04	0.02	-0.02	0.984
Number of iterations in BFGS optimization: 18, Log-likelihood: -178.7 on 8 Df				
<b><i>Scolex pleuronectis</i></b>				
b) <i>zeroinfl(formula = S_pleuronectis ~ Location * Length, dist = "poisson") AIC: NA</i>				
<b>Count model coefficients (poisson with log link):</b>				
(Intercept)	2.362	0.070	33.9	<b>&lt;2e-16</b>
LocationVaranger	4.36	3.27	1.33	0.183
Length	0.01	1.3e-04	74.84	<b>&lt;2e-16</b>
LocationVaranger:Length	-0.02	0.01	-0.295	<b>0.003</b>
<b>Count model coefficients (poisson with log link):</b>				
(Intercept)	-2.81	6.71	-0.42	0.675
LocationVaranger	-1.87	9.47	-0.20	0.844
Length	0.003	0.01	0.20	0.844
LocationVaranger:Length	0.009	0.02	0.42	0.672
Number of iterations in BFGS optimization: 14. Log-likelihood: -3.505e+04 on 8 Df				
<b><i>Derogenes varicus</i></b>				
c) <i>glm(formula = D_varicus ~ 1, family = quasipoisson) AIC: NA</i>				
(Intercept)	5.282	0.161	32.890	<b>&lt;2e-16</b>
Null deviance: 12008 on 51 degrees of freedom, Residual deviance: 12008 on 51 degrees of freedom				
<b><i>Hemiurus levinseni</i></b>				
d) <i>glm(formula = H_levinseni ~ 1, family = quasipoisson) AIC: NA</i>				
(Intercept)	1.202	0.521	2.309	<b>0.025</b>
Null deviance: 632.48 on 51 degrees of freedom. Residual deviance: 632.48 on 51 degrees of freedom				
<b><i>Hemiurus communis</i></b>				
e) <i>glm(formula = H_communis ~ 1, family = quasipoisson) AIC: NA</i>				
(Intercept)	4.964	0.705	7.037	<b>4.6e-9</b>
Null deviance: 42470 on 51 degrees of freedom, Residual deviance: 42470 on 51 degrees of freedom				
<b><i>Anisakis simplex</i></b>				
f) <i>glm(formula = A_simplex ~ 1, family = quasipoisson) AIC: NA</i>				
(Intercept)	1.644	0.131	12.510	<b>&lt;2e-16</b>
Null deviance: 243.49 on 51 degrees of freedom, Residual deviance: 243.49 on 51 degrees of freedom				
<b><i>Hysterothyliacium aduncum</i></b>				
g) <i>glm(formula = H_auduncum ~ 1, family = quasipoisson) AIC: NA</i>				
(Intercept)	4.006	0.154	26.010	<b>&lt;2e-16</b>
Null deviance: 2401.2 on 51 degrees of freedom, Residual deviance: 2401.2 on 51 degrees of freedom				





