Parasites from cod in two different localities, the Barents Sea and Øksfjord in the coastal region of northern Norway: a comparison

Ann Beate Løvland

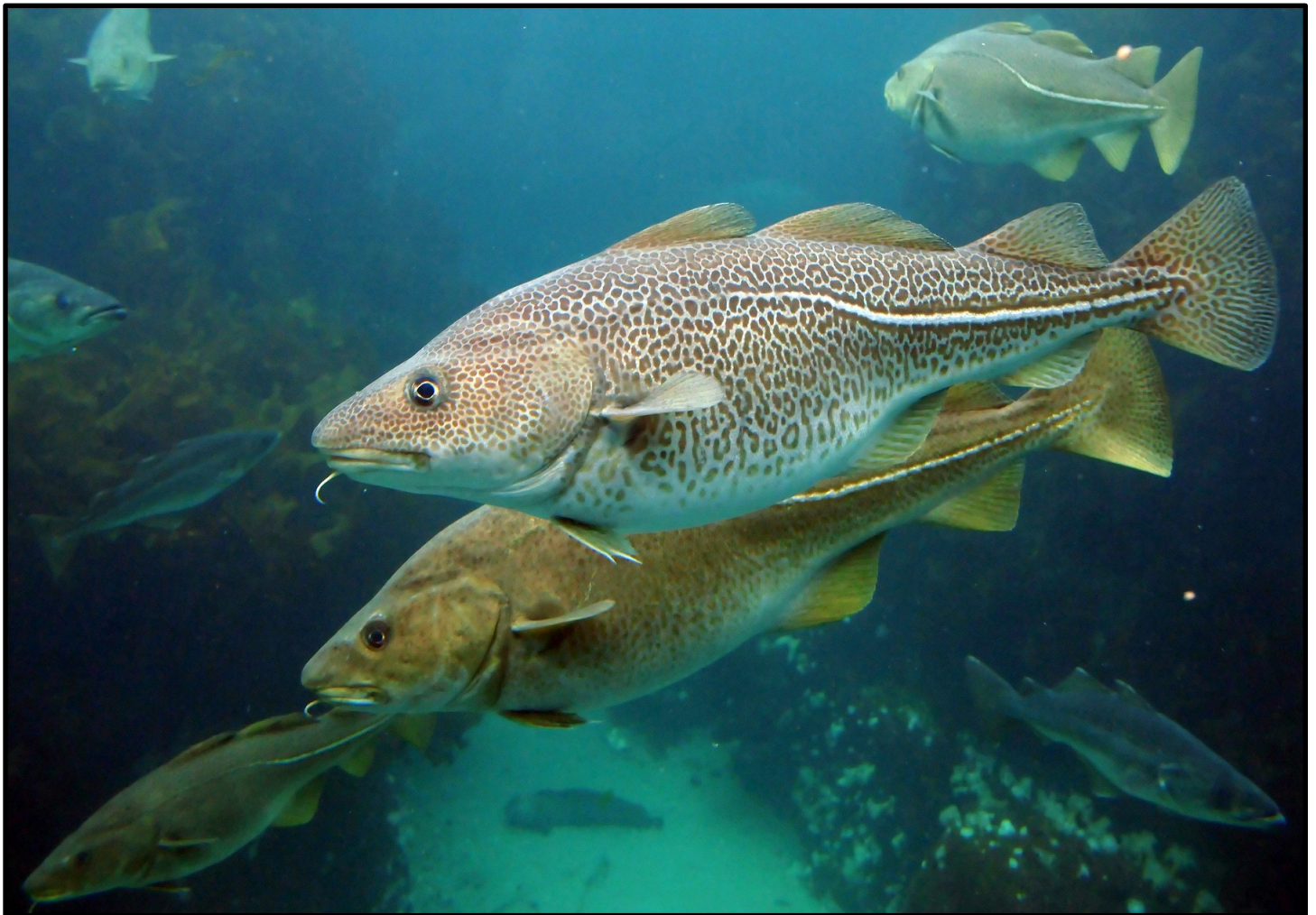*Bio-3906 Master thesis in Biology*
June 2017

Parasites from cod in two different localities, the Barents Sea and Øksfjord in the coastal region of northern Norway: a comparison

Ann Beate Løvland

Bio-3906 Master thesis in Biology
June 2017

Supervisor
Willy Hemmingsen, The Arctic University of Norway (UiT)

External supervisor
Per Arneberg, Institute of Marine Research (IMR)

Front page photo of Atlantic cod (*Gadus morhua*)

By Joachim S. Müller

Acknowledgements

First of all, I would like to thank my supervisors Willy Hemmingsen and Per Arneberg for excellent guidance and presence throughout this project, and especially for their patience and encouragements. They also contributed with their knowledge and valuable discussions that have been most inspiring and educational. I am very grateful for the opportunity to learn from them.

A big thanks goes out to my fellow students in the Science Teacher Education programme. They have helped me throughout this master programme with unlimited support, discussions and collaborations that are greatly appreciated. Special thanks to my fellow biology students, present and past, that have included me in their study colloquiums and friendships. I am very grateful!!

I would like to thank my wonderful office mates for their inspiring words, academic discussions, their good company, and for those moments when a coffee break was much needed.

Finally, I want to express my gratitude to family and friends for believing in me and always encouraging me to do my best, especially in times of frustration. Their unlimited support and encouragements throughout these years at UiT have been greatly appreciated.

Tromsø, June 2017
Ann Beate Løvland

Abstract

Parasites have been given a prominent role in ecology because of their potential to influence ecosystem dynamics. Parasite-host interactions are important in understanding host population dynamics and ecological processes. The marine environment is the largest ecosystem in the world, and between the coastal realm and the open water realm exists great ecological variances. Because parasites encompass a great influence on an ecological scale, studying parasites can bring out information about their role in food webs, and provide knowledge about occurrences of parasites between different types of habitats. In this study, a comparison of the level of parasite infection on the Atlantic cod (*gadus morhua*) from two different localities, the Barents Sea and Øksfjord in the coastal region of northern Norway are presented. The total number of parasite species was found to be higher on individual hosts of cod from the coastal region compared to the Barents Sea. Intensity of infestation of the parasites present in both localities is also higher in cod from the coastal region. These findings are consistent with the idea that parasites may mean less for the dynamics of the cod population in the open sea than at the coast. The observed different parasite diversity reflects the geographical distinct habitats, and demonstrates the importance of future studies on the subject.

Keywords: Fish parasites; Protozoa; Myxosporea; Nematoda; Digenea; Monogenea; Acanthocephala; Eucestoda; Parasitic copepods; Isopoda; The Barents Sea; Coastal region

Table of contents

Introduction

Parasites are of a great concern because of the importance they have in commercial interests, economical aspects, and the influence they encompass on an ecological scale (Marcogliese, 2002/2005; Rohde, 2005a; Sasal & Thomas, 2005). There are many definitions of parasitism and the one used in this thesis incorporates the ecological, immunological or physiological factors of parasites. The following definition stated by Webster´s Third New International Dictionary of the English Language unabridged (1961) is:

An organism living in or on another living organism obtaining from it part or all of its organic nutrient, and commonly exhibiting some degree of adaptive structural modification – such an organism that causes some degree of real damage to its host (p. 1639).

Scientists have given much attention to the role of parasites in ecology and assess parasites to have a prominent part in ecosystem functioning and ecosystem dynamics (Marcogliese, 2002; Hudson, 2005; Hudson et al., 2006; Amundsen et al., 2009). Parasite-mediated effects are proven to influence host population dynamics and interspecific competition, and further alter the structure of a food web by generating species diversity, increased connectance and nestedness (Hudson et al., 1998; Hudson et al., 2006; Lafferty et al., 2008). The host response to infection is loss of energy and higher energy demand, which could induce competition for limited resources or deprivation of physiological responses such as reproduction and growth, that eventually result in decreased fitness (Rynkiewicz et al., 2015). In this manner, parasites are capable of regulating and control population densities and abundance, for the purpose of increasing parasite transmission (Dobson, 1988). Hudson et al. (1998) reported from a long-term experiment done on Red grouse populations in Britain, that high parasite infections of the parasitic nematode *Trichostrongylus tenuis* were the main reason for population declines. The population growth rate and breeding production of the Red grouse were negatively related to the intensity of parasites. This illustrates the importance of parasites both on a community level and on an ecological scale, and further assesses parasites as a prominent part in ecosystem functioning and dynamics (Dobson, 1988; Marcogliese, 2002; Hudson et al., 2006). In many ecosystems parasitism, therefore, have been given a dominant role in ecological processes (Horwitz & Wilcox, 2005; Hudson, 2005).

Introduced host species is capable of escaping from the effects of natural enemies, such as parasites (Miura et al., 2006). Torchin et al. (2003) found that half the number of parasite species decreased when populations (of molluscs, crustaceans, fishes, birds, mammals, amphibians and reptiles) went from its native range to its introduced environment. Because of the complex life cycles of many parasites, the decrease in parasite abundance might be ascribed to host-specific limitations or to the host capability of better adapting to new environments than the parasites are (Torchin et al., 2003; Miura et al., 2006). For the reason that introduced species can escape from parasites, they are possible pest organisms. Mitchell & Power (2003) found that plant species with fewer parasites more often were reported as pest organisms, than plant species inhabited with many parasites. In lack of parasites the hosts fitness will enhance and make them capable of a higher growth rate, which further increases the population densities (Torchin et al., 2003). This points in the direction on how parasites can regulate population densities and strengthens the theory that parasites influence host population dynamics.

Parasite species are commonly host specific either with their final host or the intermediate host, and the distributional patterns of that host will contribute to prediction of the parasite distribution (Poulin & Morand, 2000; Marcogliese, 2002). Numerous animals within a wide range of phyla and living in different habitats may constitute as hosts to parasites. The largest and complex host species, the vertebrates, frequently inhabit the richest parasite fauna and provide an extensive number of niches to parasites (Rohde, 1993). Between tropical rainforests and the marine environment, the latter consist of the highest number of phyla and with considerable differences within the divergent habitats (May & Godfrey, 1994; Suchanek, 1994). The parasite diversity will therefore vary in different marine habitats depending on type of environment and habitat, along with species composition in the fish community. Within the marine environment fish species diversity vary between low and high latitudes, longitudinal gradients, and depth, which further can express the differences of the parasite distribution (Willig, 2001; Rohde, 2005b). There is for instance found to be less parasite species in cold-temperate environments, than in warmer regions, which might be due to the lower density of host populations in cold-temperate Seas (Rohde, 1993). Latitudinal gradients in species richness of parasites show different patterns for endoparasites and ectoparasites. The latter show an increase towards low latitudes, while the former appear

analogous at all latitudes but with higher diversity in the tropics (Rohde, 1992; Rohde, 2005b). Rohde & Hayward (2000) did a study on longitudinal patterns of parasite species. Results indicate that the diversity is occupied in centres within the western Pacific and western Atlantic, with decreasing diversity away from these centres. As the depth gradients constitute different marine fish species, potential intermediate and final hosts, it also inhabits differences in parasite diversity (Bray, 2005). The benthic fauna consist of many living species and have a higher biodiversity than the pelagic systems regarded both fish species and parasites species (Angel, 1993; Rohde, 1993; Gray, 1997; Marcogliese, 2002).

Further geographically differences in parasite diversity lies between inshore and open sea, and are connected to the infection of intermediate hosts (Rohde, 1993). Noble (1973) found that fish caught in habitats with many intermediate hosts, like coastal and pelagic Seas, had higher species diversity of parasites than fish caught in habitats with few intermediate hosts, such as the deep pelagic water (in: Rohde, 1993). Marine coastal ecosystems are considered the most productive on earth, with high biodiversity and diverse communities, and inhabit more habitats than pelagic Seas, despite the substantial realm of the latter (Angel, 1993; Poore & Wilson, 1993; Gray, 1997). However, the coastal food web contains substantially shorter food chain than the open ocean systems (Hairston & Hairston, 1993).

The Atlantic cod, *Gadus morhua* L., is among the most important commercial fishes that support valuable social and economic benefits to countries along the eastern and western coasts of the North Atlantic (Kurlansky, 1998). In the Northeast Atlantic, cod appear to be differentiated by small coastal stationary stocks to bigger migratory stock population, the coastal cod and the northeast Arctic cod respectively. However, there are no external features to distinguish between the stocks (Møller, 1968). The migratory movement of the Arctic cod follows a spawning and feeding migration, where the feeding migration are located in the Barents Sea north of Norway during summer, fall and winter. During spring, the Arctic cod migrate from the Barents Sea to spawning areas along the western coast of Norway (Stiansen et al., 2009). The Atlantic cod is a key species with predation on primary and secondary consumers (Marcogliese, 2002), and play an important role in parasitism as intermediate, paratenic or definitive host for many parasite species (Hemmingsen et al., 2001; Hemmingsen & MacKenzie, 2001). Hemmingsen & MacKenzie (2001) reported 107 named

species of parasites on cod, which illustrates the complexity of parasites within the food webs, and the importance of parasitism in cod ecology.

The marine environment is the largest ecosystem in the world, and between the coastal realm and the open sea exists great ecological variances (Marcogliese, 2002; Klimpel et al., 2006). Because parasites can have a great influence on ecosystem dynamics, an important question is whether occurrences of parasites between two different types of habitats are distinct. Since the coastal realms inhabit more habitats and higher marine biodiversity than the open sea, it is likely that the coastal realm inhabits more parasite species than the open sea. As a key species and important predatory fish, the Atlantic cod play an important role in parasitism and are therefore thought to be a good subject for investigation of parasite infection levels between two different habitats.

The main objective of the present study is to compare the level of parasite infection on the Atlantic cod from two different localities, the Barents Sea and Øksfjord in the coastal region of northern Norway. This will be assessed by looking at the number of parasite species on individual hosts of cod, and mean intensity of infestation on cod between the two habitats. In addition the paper examines differences of parasite intensities of the parasite species present in cod at both localities.

Material and methods

This master thesis is based on extensive fish sampling, parasite identification and counting in two large marine habitats, the Barents Sea and the coastal region of northern Norway. The collection and materials of two separate stocks of cod, the wild local cod and the Northeast Arctic cod, are obtained from the parasite screening programme (CodPar) (Heuch et al., 2011) and Trophic interactions in the Barents Sea – steps towards an Integrated Ecosystem Assessment (TIBIA) (P. Arneberg pers. comm.).
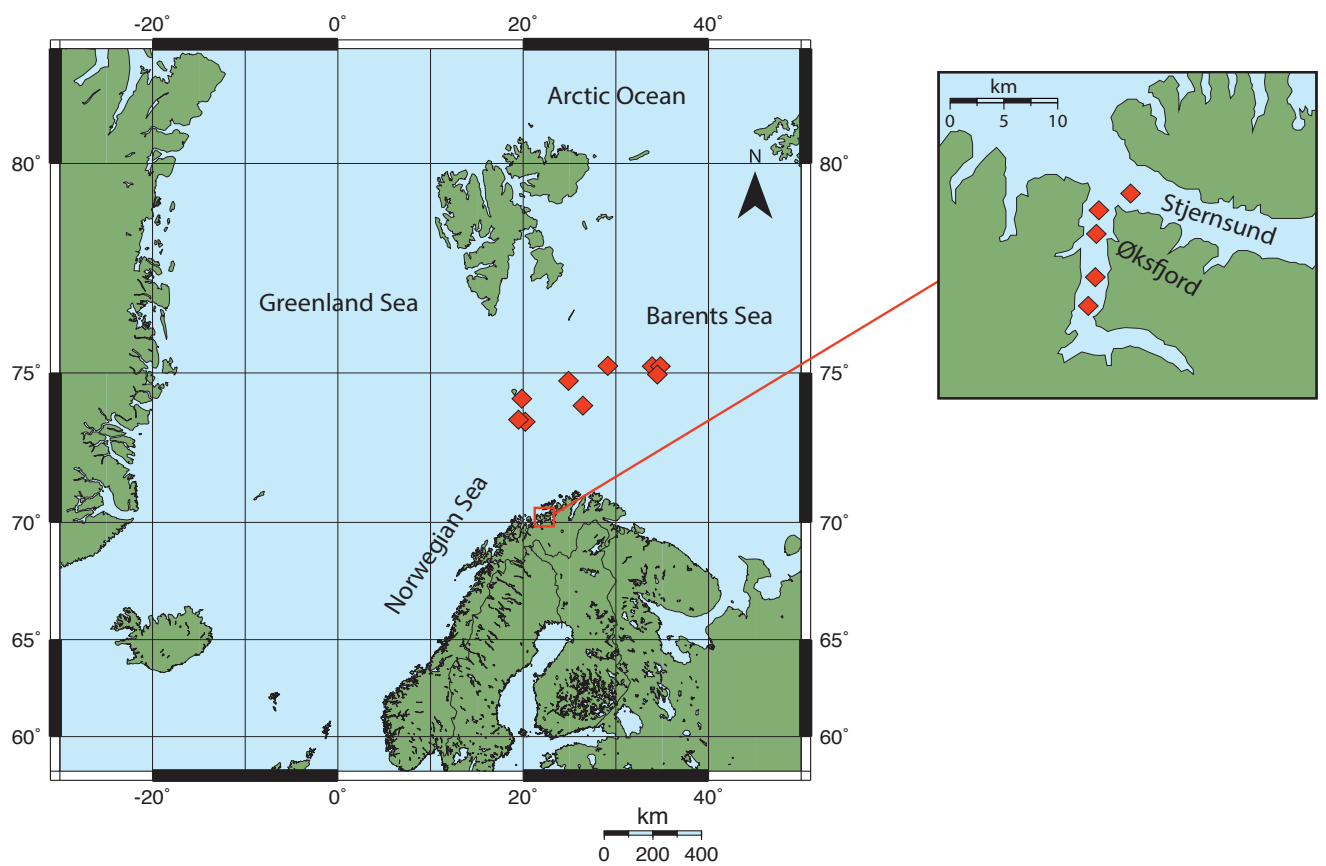
Fig. 1. Map of sampling stations in the Barents Sea (left) and Øksfjord, northern Norway (right) marked with red squares.

Study areas

The Barents Sea

The Barents Sea is located in the Arctic Ocean and makes up 4 ‰ of the world's total sea area. It is estimated to be about four times the area of Norway (Sakshaug et al., 1994). The Barents Sea belongs to the shallow continental shelf situated off the northern coasts of Norway and Russia (Sakshaug & Kovacs, 2009). The average depth is 230 meters with the largest depth being around 500 meters (Loeng, 1991). The water flows are influenced by the warm and high salinity Atlantic water coming from south and west, and the colder and low salinity Arctic water coming from north and east. These water flows makes up a current front, also known as the Polar front, and are found in the western Barents Sea (Ingvaldsen & Loeng, 2009; Loeng, 1991). The great biological production in the Barents Sea is mainly due to convections made by wind and currents, which continuously provide nutrient rich water for primary production (Sakshaug et al., 2009). The temperature varies between -1.9°C and +6°C depending upon seasonally changes in light, ice coverage, and current conditions (Sakshaug et al., 1994). The main types of species in the pelagic ecosystem are phytoplankton, zooplankton, fish, birds, and marine mammals such as seal and whales (Sakshaug et al., 1994). Large fish stocks in the area include capelin (*Mallotus villosus*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), and North-East Arctic cod (*Gadus morhua*) (Stiansen et al., 2009).

The coastal region of northern Norway

Northern Norway comprises three counties, Nordland, Troms and Finnmark, with the latter being the northernmost and adjacent to the Barents Sea. The continental shelf topography is formed by different banks separated by troughs. The shallowest bank has a mean depth of 61 meters and the deepest bank has a mean depth of 139 meters (Sundby, 1984). The coastal water is located between the coast and the Atlantic Ocean. It is comprised of low salinity water from the Baltic Sea mixed with Atlantic water, as well as freshwater from the coast (Sverdrup, 1952). The Norwegian coastal current moves north and the mixture of water evens out the salinity northwards (Sverdrup, 1952). Temperatures between air and water are highly correlated and with great variation in the northern coastline (Eilertsen & Skarðhamar, 2006). In the Finnmark county temperatures seldom reach above 10°C in summer and 4-6°C in winter (Ryvarden, 1997). The marine fauna is diverse and is comprised of different species of

phytoplankton, zooplankton, invertebrates and vertebrates (Ryvarden, 1997). The fish community is dominated by cod (*Gadus morhua*), herring (*Clupea harengus*), capelin (*Mallotus villosus*), saithe (*Pollachius virens*), blue whiting (*Micromestisius poutassou*), Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes mentella and Sebastes marinus*) and haddock (*Melanogrammus aeglefinus*) (Stiansen et al., 2009).

Sampling of cod

In 2006, material samples from the coastal region of Northern Norway were collected from Øksfjord, a fjord in Loppa municipality in the county of Finnmark. Wild local cod from this area were collected in April and October, and contributed to the CodPar project. The material form the Barents Sea was part of a different project, the TIBIA project, and collected a few years later. In 2015, Northeast Arctic cod from the Barents Sea were collected in May, June and November (Fig. 1). The fish both in TIBIA and CodPar was catched by the use of trawl. TIBIA used bottom trawl that works best for catches in deeper water, while CodPar applied Danish seines suited for relatively shallow water (Heuch et al., 2011 & P. Arneberg pers. comm.).

Examination and parasite identification

Examination and parasite identification in both cod stocks were performed by Heuch et al. (2011, p. 3-4) procedure:

Examination for parasites

The cod were held alive in tanks of aerated seawater until complete autopsies were carried out according to the following protocol.

1. Each fish was killed with a sharp blow to the head.
2. A blood smear taken from the caudal vein was air-dried, fixed in methanol, labelled and stored. For later microscopic examination, the slide was stained with Giemsa, a drop of DePeX mountant was placed on the smear, a 20×50 mm coverslip placed over it, and the entire surface was scanned at a magnification of 125×.

3. A skin smear was taken by scraping a microscope slide along the flank of the cod, which was then scanned under a compound microscope at 100 to 200 × magnifications.

4. The following organs were removed, placed in petri dishes under seawater, and scanned under a dissecting microscope at 20 to 40× magnification: the dorsal, ventral and tail fins, plus operculum and jaw from the left side; the nostril from the left side, complete with the olfactory rosette; the eye from the left side; the gill arches from the left side; and the pharynx. Any parasites found were removed and examined under higher magnifications where necessary.

5. A smear was taken from the gill filaments and scanned under a compound microscope at 200 to 400× magnifications.

6. The abdominal and pericardial cavities were opened and all internal organs, including the swim bladder, removed and isolated. Each organ was scanned under a dissecting microscope at 20 to 40×. Smears were taken from the liver, spleen, gonads, gall bladder, urinary ducts, and from any lesions observed, and examined at 200 to 400×. Samples of gall and urine were extracted with a syringe and scanned under a compound microscope at 200 to 400×. In addition, squash preparations were made from any abnormal tissue from the liver, spleen and gonads and examined at 200 to 400×.

7. The alimentary tract was divided into stomach, pyloric caeca, fore-, mid- and hind-intestine. Apart from the pyloric caeca, each section was opened longitudinally and examined under a dissecting microscope at 20 to 40×. Some of the contents of the pyloric caeca were squeezed into a slide and examined at 20 and 200×. Smears from the stomach and intestinal mucosa were examined at 200 to 400×. All metazoan parasites found were removed and placed in watch glasses of seawater. Any unidentified specimens were fixed in 10 % formalin for later examination.

8. Samples of head and rear kidney were squashed on a slide and examined at 200 to 400×.

9. A scraping from the swimbladder was examined at 200 to 400×.

10. The head was split longitudinally and the cranial cavity examined under a dissecting microscope at 20 to 40×. A smear was taken from the brain and surrounding fluid and examined at 200 to 400×.

11. The carcass was filleted and the left side fillets examined by eye over a light box for metazoan parasites or lesions.

12. The skin from the left side of the fish behind the head was examined for *Cryptocotyle lingua* metacercariae on a light box. The number of metacercariae within a standardised area was counted. If the skin was more than 9 cm wide, a circular area with this diameter was examined. In smaller fish 25 % of this area was examined and the count multiplied by 4. The counts were binned into 4 categories: 1 = 0; 2 = 1-10; 3 = 11-100; 4 = > 100 *C. lingua* metacercariae within the circle.

13. Representative specimens of each helminth species found were washed in seawater then fixed and preserved in either 10 % formalin (for morphological identification) or ethanol (for molecular study). Adult caligid copepods were identified to species in the field laboratory, whereas larvae of this family and all isopods were stored in ethanol for later examination. Only adult female *Clavella adunca* were counted.

14. The number of *Anisakis simplex* from the surface of the liver was noted. All compound microscope examinations were carried out using phase contrast.

Parasite identification

As far as possible the parasites were identified to species in the field laboratory using relevant literature. *Caligus* and isopod larvae (Crustacea) and specimens of *Gyrodactylus* (Monogenea) could not be identified to species in the field laboratory. Representative specimens of *Gyrodactylus* and larval *Caligus* and isopods in 96 % ethanol were brought back to the laboratory in the National Veterinary Institute for further characterisation.

Larval Caligus and isopods

Larval caligids were identified by DNA sequencing of fragments of the mitochondrial cytochrome oxidase 1 (CO1) gene and then comparing the obtained sequences to sequences in GenBank. DNA was extracted from 98 specimens using the GenMole DNA Tissue Kit on a Genemole extraction machine (Molegenetics) and the CO1 sequences were obtained following the protocols outlined by Øines & Heuch (2005). In instances where no sequences were obtained, the parasite was noted as *Caligus* sp. Attempts were made to identify the larval isopods morphologically.

Gyrodactylus

Ethanol preserved gills, fins and pharynx infected with *Gyrodactylus* specimens or individual specimens of *Gyrodactylus* preserved in ethanol were brought back to the laboratory for identification. A sub-sample of individual parasites from the different sites and organs were identified to species level using morphological criteria. The soft tissue of the haptor was digested following the protocol of Harris et al. (1999) and following digestion, the parasites were identified morphologically following Malmberg (1970).

Statistical analysis

Statistical terminology and measurements of infection rates

The statistical terminology prevalence, intensity, mean intensity and mean abundance used in this thesis follow the definitions of Bush et al. (1997):

Prevalence is the number of hosts in a sample that is infected with a given parasite species divided by the number of hosts infected by that parasite species, commonly expressed as a percentage. *Intensity* is the total number of a given parasite species in one host. *Mean intensity* is the total number of a given parasite species among the infected hosts in a sample, divided by the number of hosts infected. *Mean abundance* is the total number of a given parasite species in a sample, divided by the total number of hosts in that sample.

Intensity for each parasite species was estimated, and plotted for analysis and graphical presentation. Mean intensity, prevalence of infection and mean abundance was calculated for each parasite species in both cod stocks. Parasite infection on cod were determined by calculating the total number of parasite species in each cod stocks, and used for analysis and graphical presentation. Distribution pattern on body weight of cod were analysed and compared with regard to parasite infection on cod.

Shapiro-Wilk normality test

Shapiro-Wilk normality test calculate the mean and standard deviation of a complete data sample in order to statistically determine the normality of the population (Shapiro & Wilk,

1965). A p-value greater than 0.001, confirm that the sample comes from a population with normal distribution (Whitlock & Schluter, 2015).

Fisher's F-test

Measurements of two groups that are normally distributed can be tested with Fisher's F-test to determine whether two samples variances are equal. Both samples must require normal distributions in order for this test to be useful. To verify if the variances of two sample groups are homogenous, the p-value must be greater than 0.05 (Whitlock & Schluter, 2015).

Student's t-test

Student's t-test is used to describe the distribution relationship of two sets of independent populations. The test is applied on small samples and statistically estimates the means and standard deviation to determine if the populations are identical. Significant different samples reveal a p-value greater than 0.05 (Whitlock & Schluter, 2015).

Mann-Whitney U-test

If the data withdraw from normal distribution a non-parametric Mann-Whitney U-test is applied. It measures the frequency distribution of two samples when the normal distribution assumption is not met. This test compares the medians or means of two samples to test if the frequency distributions are the same. A p-value greater than 0.05 verify identical distributions of two samples and a p-value less than 0.05 confirms non-identical distributions (Whitlock & Schluter, 2015).

Spearman's-rank correlation

Spearman's rank correlation is a nonparametric statistical method that measures the linear association between paired data. By using the ranks of two variables the Spearman's rank correlation test the strength and direction between the data (Whitlock & Schluter, 2015). The statistical test gives two sets of values, rho-value and p-value. The rho-value represents the correlation between the data, and a p-value less than 0.05 indicates a statistical significant rho-value (correlation).

Fisher's exact test

The microparasites were noted as infected (1) or not infected (0). In order to statistically determine the deviation of two samples a Fisher's exact test was applied. It is a computer statistical package that examines the relationship in a 2x2 contingency table, and tests the independence of categorical small values (Whitlock & Schluter, 2015).

Software used

Calculations were carried out in Microsoft Excel, version 14.7.1 for Mac (Microsoft Corp., Redmond, WA, USA). Statistical analysis and graphs relied on RStudio, version 1.0.136 for Mac (Integrated Development for R. RStudio, Inc., Boston, MA). The map was made by Ørjan Garfjell (graphic designer at UiT).

Results

The total amount cod examined for parasites was 61, where 26 came from the Barents Sea and 35 from the coastal region in northern Norway, Øksfjord. The comparison analysis of the two populations did not reveal significant difference in body weight of cod (Student's t-test, $p \gg 0.05$). Body weight of the Barents Sea cod ranged from 199 to 4300 gram, with a mean of 2009 gram (SD$\pm$989.63). Body weight of the coastal cod ranged from 670 to 4400 gram, with a mean value of 2160 gram (SD$\pm$844.94) (Fig. 2).
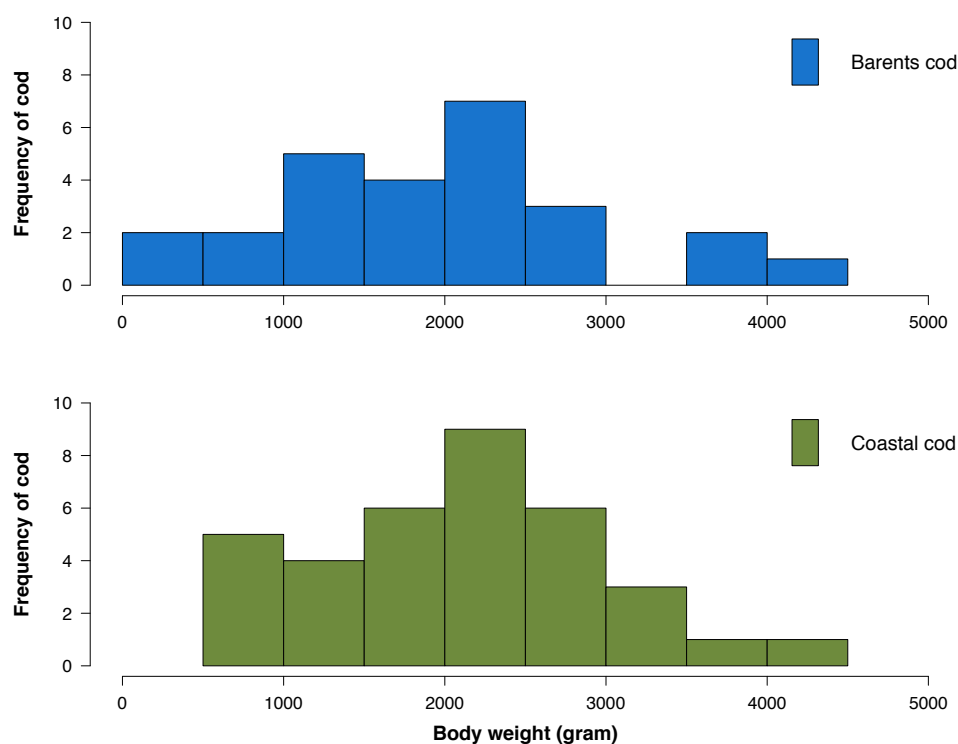
Fig. 2. Distribution of body weight of cod in the Barents Sea (top) caught in May, June and September 2015 and cod in the coastal region (bottom) caught in April and October 2006.

Parasites recorded from cod in the Barents Sea and coastal region of northern Norway

The total number of parasite species recorded from cod was highest in the coastal population with 36 compared to 13 in the Barents Sea population (Table 1). The majority of the parasite species (24 species) were found to have complex life cycles. Thirteen parasite species recorded had simple life cycle. They were: Undescribed *Trichodina* sp., Unidentified microsporidian, *Spironucleus torosa*, *Clavella adunca*, *Caligus* spp., *Caligus curtus*, *Caligus elongatus*, *Cresseyus confusus*, *Lernaeocera branchialis*, pranzia larvae, *Gyrodactylus callariatis*, *Gyrodactylus marinus* and *Gyrodactylus pharyngicus*. Among them, only two were found in the Barents Sea (Undescribed *Trichodina* sp. and *C. adunca*).

In both localities the parasite communities were dominated by digeneans and nematodes. The coastal region had additionally dominance of copepods and protozoans, and included three acanthocephalans, four myxosporeans, three monogeneans, one isopoda and one acanthocephalan. In the Barents Sea the component parasite communities further included one copepod, two eucestodes, one protozoan, and one acanthocephalan.

The average prevalence of parasites was higher in the Barents Sea at 34.1 %, compared to 26.8 % in the coastal region. Prevalence of infestations on cod showed large variations in both localities, ranging from 2.86 % to 100 % in the coastal region and 3.85 % to 84.62 % in the Barents Sea. The nematodes *Anisakis simplex*, *Hysterothylacium aduncum* (adult and larvae) and *Contracaecium osculatum* showed highest prevalence of infestation in the Barents Sea. In the coastal region the nematode *Anisakis simplex*, the digenea *Derogenes varicus* and the parasitic copepod *C. confusus* revealed highest prevalence of infestation. In both localities intensity of infestation of cod also revealed large variations, with most parasite species occurring at low intensities. Among the parasite species revealing high intensity in the Barents Sea, the nematodes *H. aduncum* (adult and larvae) and *A. simplex* were the most frequent occurring species. In the coastal region, the digenea *D. varicus*, the nematode *A. simplex* and the monogenea *G. pharyngicus* revealed highest intensity of infestations.

Table 1. Parasites collected from cod in the Barents Sea and coastal region with data of prevalence, mean intensity and mean abundance. Coastal cod was collected in April and October 2006 and the Barents Sea cod was caught in May, June and September 2015.

Parasite	Coastal cod (n=35)			Barents Sea cod (n=26)		
	Prevalence (%)	Mean intensity	Mean abundance	Prevalence (%)	Mean intensity	Mean abundance
Protozoa						
Undescribed *Trichodina* sp.	2.86	1.00	0.03	3.85	1.00	0.04
Digenea (adults)						
Lepidapedon rachion (Cobbold)	5.71	1.00	0.06	7.69	6.50	0.50
Hemiurus levinseni (Odhner)	31.43	6.00	1.89	23.08	25.17	5.81
Lecithaster gibbosus (Rudolphi)	5.71	1.00	0.06	3.85	1.00	0.04
Derogenes varicus (Müller)	100.00	21.11	21.11	23.08	12.00	2.77
Eucestoda (adults)						
Abothrium gadi (Van Beneden)	5.71	1.00	0.06	3.85	1.00	0.04
Nematoda (larvae)						
Anisakis simplex (Rudolphi)	91.43	26.97	24.66	80.77	5.14	4.15
Pseudoterranova decipiens (Krabbe)	5.71	1.00	0.06	7.69	3.00	0.23
Nematoda (adults)						
Hysterothylacium aduncum (Rudolphi)	42.86	9.07	3.89	84.62	40.27	34.08
Acanthocephala (adults)						
Echinorhynchus gadi (Zoega in Müller)	40.00	12.43	4.97	53.85	12.43	6.69
Copepoda						
Clavella adunca (Strøm)	40.00	2.36	0.94	11.54	2.00	0.23
Eucestoda (plerocercoids)						
Pyramicocephalus phocarum (Fabricius)	—	—	—	23.08	1.50	0.35
Nematoda (larvae)						
Hysterothylacium aduncum (Rudolphi)	—	—	—	65.38	24.12	15.77
Contracaecum osculatum (Rudolphi)	—	—	—	84.62	45.68	38.65
Protozoa						
Goussia spraguei (Morrison & Poynton)	2.86	1.00	0.03	—	—	—
Unidentified microsporidian	34.29	1.00	0.34	—	—	—
Spironucleus torosa (Morrison & Poynton)	65.71	1.00	0.66	—	—	—
Trypanosoma sp.	2.86	1.00	0.03	—	—	—
Myxosporea						
Myxidium oviforme (Parisi)	40.00	1.00	0.40	—	—	—
Myxidium bergense (Auerbach)	5.71	1.00	0.06	—	—	—

Gadimyxa sp.	34.29	1.00	0.34	—	—	—
Zschokkella hildae (Auerbach)	31.43	1.00	0.31	—	—	—
Monogenea						
Gyrodactylus callariatis (Malmberg)	17.14	15.00	2.57	—	—	—
Gyrodactylus marinus (Bychowsky & Polyansky)	20.00	10.14	2.03	—	—	—
Gyrodactylus pharyngicus (Malmberg)	11.43	49.25	5.63	—	—	—
Digenea (metacercariae)						
Cryptocotyle lingua (Creplin)	80.00	1.68	1.34	—	—	—
Digenea (adults)						
Lampitrema miescheri (Zschokke)	2.86	2.00	0.06	—	—	—
Lepidapedon elongatum (Lebour)	11.43	1.00	0.11	—	—	—
Eucestoda (plerocercoids)						
Grillotia erinaceus (Van Beneden)	8.57	1.00	0.09	—	—	—
Tetraphyllidea sp.	25.71	1.00	0.26	—	—	—
Nematoda (adults)						
Ascarophis filiformis (Polyansky)	2.86	1.00	0.03	—	—	—
Capillaria gracilis (Bellingham)	5.71	1.00	0.06	—	—	—
Cucullanus cirratus (Müller)	42.86	6.80	2.91	—	—	—
Copepoda						
Caligus spp.	11.43	1.00	0.11	—	—	—
Caligus curtus (Müller)	2.86	1.00	0.03	—	—	—
Caligus elongatus (Nordmann)	14.29	1.60	0.23	—	—	—
Cresseyus confusus (Stock)	77.14	4.41	3.40	—	—	—
Lernaeocera branchialis (Linnaeus)	14.29	1.00	0.14	—	—	—
Isopoda						
Praniza larvae	2.86	1.00	0.03	—	—	—

Infections of parasite species on cod from the Barents Sea and coastal region

Individual hosts of coastal cod showed significant higher number of parasite species consisting of 5 to 10 with a mean value of 9.60 (SD±3.05), compared to the Barents Sea cod that hosted between 1 to 8 parasite species with a mean value of 4.96 (SD±1.91) (Mann-Whiney U-test, $p \ll 0.001$) (Fig. 3). The total number of parasite species per fish did not vary with weight in both populations (Appendix A).
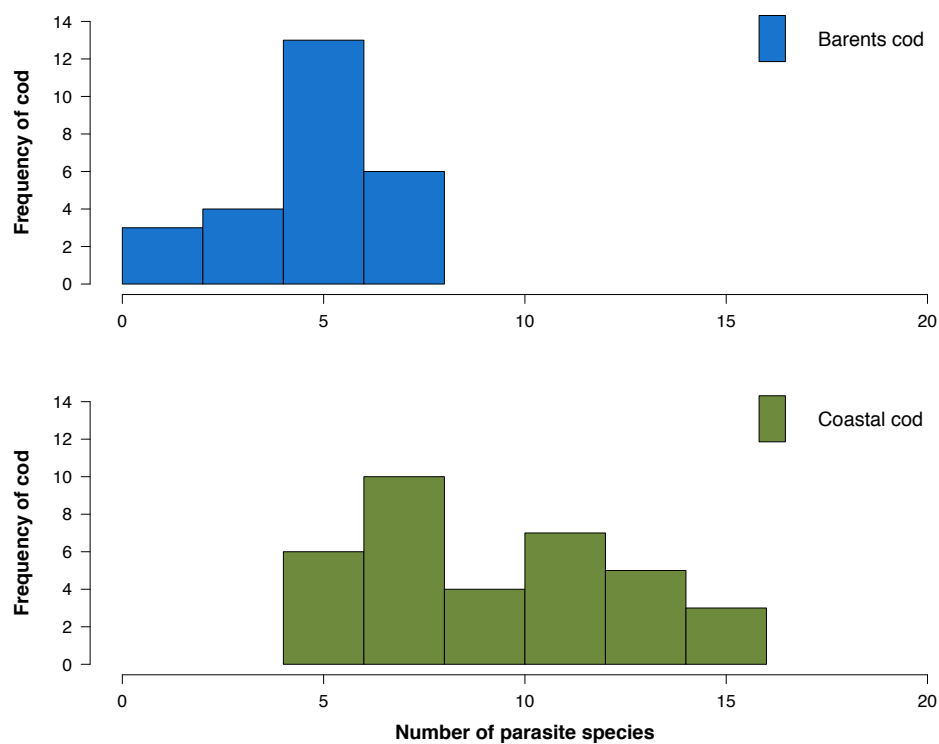
Fig. 3. Distribution of number of parasite species found on each host individual for cod sampled in the Barents Sea (top) and in the coastal region of northern Norway, Øksfjord (bottom).

Intensities of parasites present on cod in both habitats

Among the 11 parasite species present in both localities, four parasite species revealed significant differences of intensities (Table 2). They were: *C. adunca*, *A. simplex*, *H. aduncum* (adult) and *D. varicus* (Mann-Whitney U-test, $p < 0.05$). The remaining parasite species did not reveal significant intensity differences between the two localities, including the microparasite *Trichodina* sp. (Fisher's exact test, p-value < 0.05). Three parasite species exhibited significant variation in intensity with fish weight, although not in both cod stocks (Appendix B and C). The intensity of *A. simplex* correlated positively with fish weight whereas *H. levinseni* and *D. varicus* showed a negative correlation (Spearmans's rank correlation, $p < 0.05$).

Table 2. Mann-Whitney U-test comparing parasite intensities of individual species of macroparasites present in both coastal cod (n=35) and the Barents Sea cod (n=26).

Parasite	P-value
C. adunca	0.015
A. simplex	0.017
H. aduncum (adult)	$1.106*10^{-05}$
L. rachion	0.747
H. levinseni	0.796
L. gibbosus	0.756
D. varicus	$1.883*10^{-08}$
E. gadi	0.382
A. gadi	0.755
P. decipiens	0.747

The parasites *C. adunca*, *A. simplex* and *D. varicus* showed significant higher intensities in the coastal region (Fig. 4-6), while *H. aduncum* (adult) revealed significant higher intensities in the Barents Sea (Fig. 7).
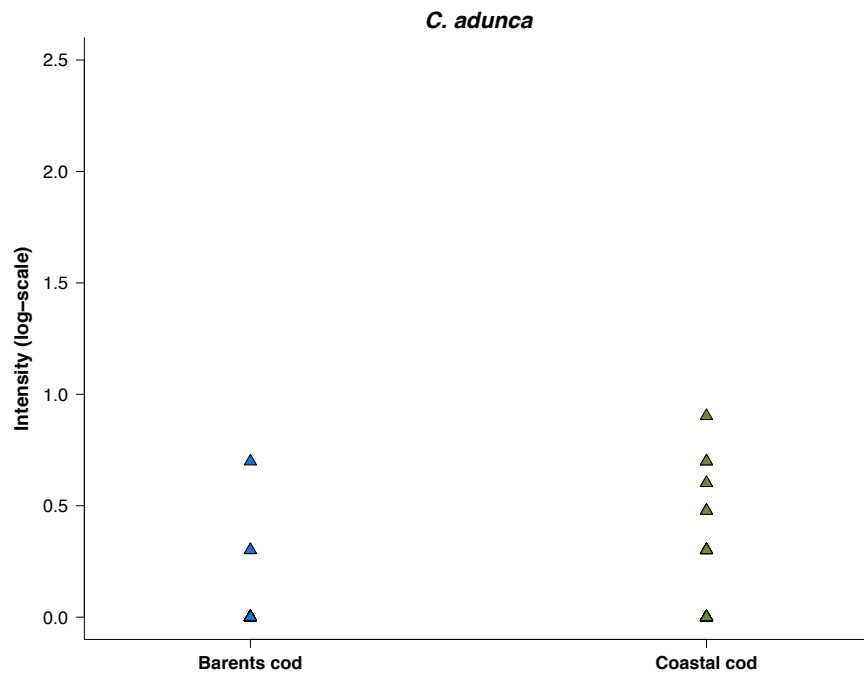
Fig. 4. Intensities of *C. adunca* on cod collected from the Barents Sea (left, n=26) and coastal region (right, n=35).
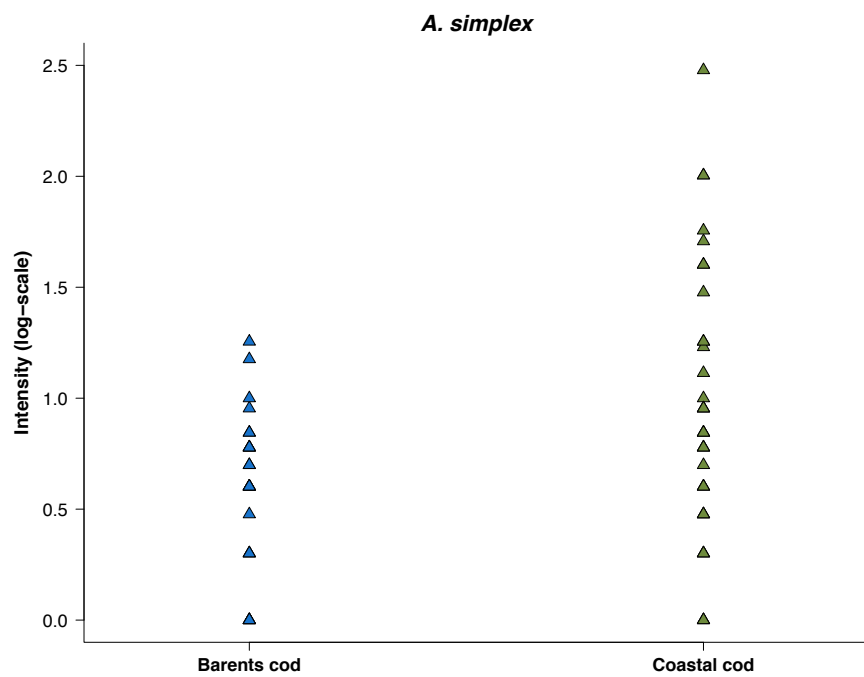
Fig. 5. Intensities of *A. simplex* on cod collected from the Barents Sea (left, n=26) and coastal region (right, n=35).
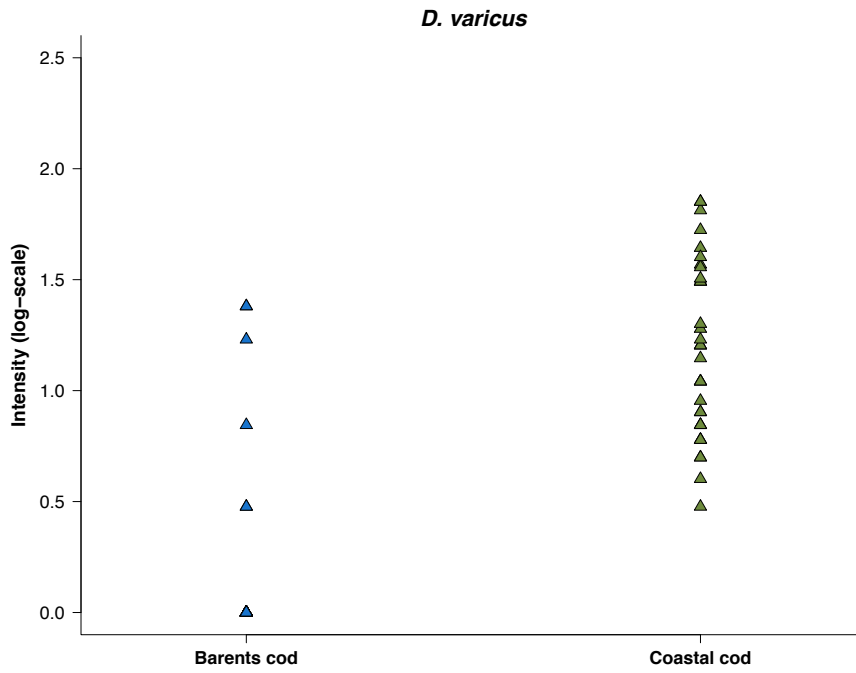
Fig. 6. Intensities of *D. varicus* on cod collected from the Barents Sea (left, n=26) and coastal region (right, n=35).

Fig. 7. Intensities of *H. aduncum* (adult) on cod collected from the Barents Sea (left, n=26) and coastal region (right, n=35).

Discussion

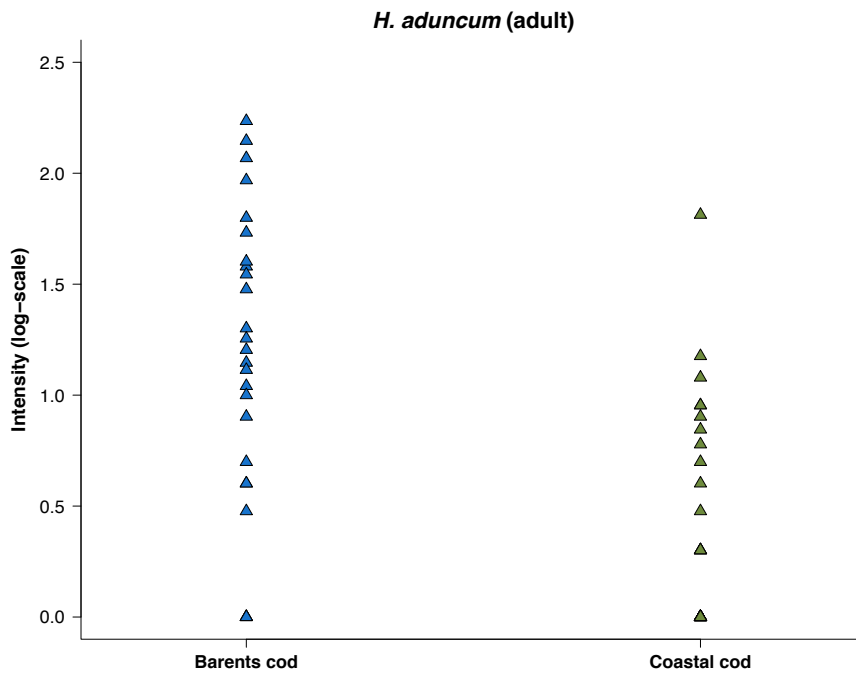The comparison of parasites from cod in two different habitats revealed that coastal cod had a significantly higher number of parasite species per host individual than the Barents Sea cod (Fig. 3). The average number of parasite species in individual hosts of coastal cod was 9.60, while the Barents Sea cod had an average number of 4.96. For the 11 parasite species present in both localities, the intensities were significantly higher between the coast and open sea for four of them (Table 2). Among these, three parasite species (*A. simplex, C. adunca* and *D. varicus*) displayed higher intensities in the coastal cod, and one parasite species (*H. aduncum*) displayed higher intensities in the Barents Sea cod. The two cod stocks displayed no difference in body weight, and for that reason was not a factor of significance in the present study (Fig. 2).

I will assume that there are no differences between the two cod stocks regarding susceptibility of parasites. The higher parasite burden per individual host of cod from the coastal region compared to the Barents Sea will therefore be discussed following the assumption that these differences have occurred by differences in parasite transmission.

The fact that there was a higher number of parasite species per individual host in cod from the coastal region could be explained by two main factors: (1) a great number of parasite species does not exist in the Barents Sea because of shortage or lack of intermediate hosts; (2) the average prevalence of parasite infection is lower in the Barents Sea compared to the coastal region.

Hosts influence on parasite transmission

The availability of intermediate hosts influences the parasite species composition in host population and varies between geographically distinct habitats (Rohde, 1993; Marcogliese, 2002). The present findings could be explained by shortage or lack of potential intermediate and final hosts in the Barents Sea, and this may contribute to certain parasite species not existing there. This corresponds with findings from Klimpel et al. (2006) that found demersal fish to have higher parasite diversity than deep-sea fishes. The authors suggested the available deep-sea intermediate and final hosts as not being suitable for completion of some of the parasite life cycles. Another explanation could be that there is not sufficient contact

31

between the intermediate hosts and the cod in the open ocean, as it appears to be in the coastal region. The threshold for parasite transmission requires the presence of enough parasites to establish themselves in a host population, otherwise the infection would cease (Dobson & May, 1987; Deredec & Courchamp, 2003). Another possible explanation could be the density of the host populations. The parasite persistence threshold depends upon the host population density and gives successful infection at large enough host populations (Deredec & Courchamp, 2003). It is easy to believe that the densities of cod in the Barents Sea are smaller than the densities in the coastal region. If that is the case, the present findings correspond well with empirical and theoretical works that display positive correlation with parasite infections and host density (Dobson & May, 1987; Arneberg et al., 1998). However, for parasite species with complex life cycles it is unclear which of the intermediate or final hosts densities determines successful infections (Hansen & Poulin, 2006).

Average lower number of parasite species in the Barents Sea

The present findings could be explained as a result of there being a generally lower prevalence of parasite species in the Barents Sea. If that is the case, then all parasite species appear with considerably lower prevalences in the Barents Sea and that would further generate an average lower number of parasite species on individual hosts in the Barents Sea. This occurs because of the number of parasite species per individual host equals the sum of prevalence of all the parasite species. However, as the present findings revealed, the average prevalence of parasites is higher in the Barents Sea at 34.1 %, compared to the coastal region at 26.8 %, so it was not evident to assess that as an adequate explanation.

Parasites only found in the coastal region

Protozoa

Protozoans are nucleated unicellular organisms that include both endo- and ectoparasites that commonly infect the skin, gills, fins, intestine or blood of fish (Möller & Anders, 1986). Among the protozoans recorded only in the coastal region, two were found to have a simple life cycle (Unidentified microsporidian and *S. torosa*), and two had a complex life cycle (*G. spraguei* and *Trypanosoma* sp.). Those with simple life cycles showed highest prevalence, with 43.29 % for the microsporidian and 65.71 % for *S. torosa*, while those with complex life cycles (*G. spraguei* and *trypanosome* sp.) revealed each a prevalence of 2.86 %. Microsporidians may have simple or complex life cycles depending upon the species. As

most fish-infecting microsporidians have simple life cycles (Lom & Nilsen, 2003; Moodie, 2005), the unidentified microsporidian in the present study is regarded as such. Transmission of the microsporidian occurs horizontally via ingestion of the infective spores by fish (Moodie, 2005), and transmission of the endoparasite *S. torosa* occurs directly through the aquatic environment (Nowak, 2005). The observed high prevalence of protozoans with direct life cycles could be a result of high host densities in the coastal region, as high stocking densities of fish are considered to increase infection of parasites with direct life cycles as a result of increased contact between the host and the infecting parasites (Heuch et al., 2011; Kent et al., 2014). This has been confirmed in an earlier study, where farmed fish showed higher infections of the microsporidian, *Loma branchialis*, compared with wild fish (Khan, 2005), and further illustrates host density as a factor of importance regarding parasite transmission. The absence of these protozoans in the Barents Sea could be explained as a result of difference in host densities between the two cod stocks, and that coastal cod acquire higher densities than the Barents Sea cod. Another explanation could be that environmental factors such as temperature, exposure to solar radiation and moisture condition are more favourable at the coast than in the open sea (Moodie, 2005), as the latter have a greater seasonal variety of those factors (Stiansen et al., 2009).

The two protozoans with indirect life cycles, *G. spraguei* and *Trypanosoma* sp., have a two-host life cycle that include leeches as vectors for transmission to fish (Möller & Anders, 1986; Goater et al., 2014). The protozoans infect a wide range of unrelated hosts including cod, and appear in a geographically wide range (Khan, 1977; Möller & Anders, 1986). Final hosts are therefore excluded as a factor of importance regarding the absence of these parasites in the Barents Sea. The leech vector, however, could be a factor of limitation. Findings of different species of fish leeches from several locations along the coast of Norway (Karlsbakk, 2005), could explain the presence of the parasites in the coastal cod population, as these leeches are potential hosts for the parasites. The leech uses the red king crab as a transport host, and a recent study by Hemmingsen et al. (2005), assessed the red king crab as indirectly responsible for the transmission of the parasite to cod by increasing the population of the vector. The crabs are present in shallow areas year-round, while in the Barents Sea there are seasonal migrations of the crabs (Falk-Petersen et al., 2011). A possible explanation for the absence of these parasites in the Barents Sea cod, could therefore be that the leech vector

responsible for transmission of these parasites are not appearing in high enough densities for the parasite to establish its presence there.

Copepoda

Most parasitic copepods are free-living ectoparasites that attach to skin and gills of fish, and the majority exploit only one host during their lifetime (Möller & Anders, 1986; Gunn & Pitt, 2012). A possible reason for the differences of the parasitic copepods between the two cod populations is best explained by the parasite life cycle, which comprises two phases: free-living nauplia and a parasitic copepodid (Möller & Anders, 1986). The free-living nauplius increases encountering with a potential host through larvae aggregation at suitable parts of the habitat (Boxshall, 2005). Host densities in shallow coastal regions have the possibility to become relatively high and aggregation of the infective larvae increases the possibility of locating a host (Rohde, 1993), which could increase the efficiency of parasite transmission and persistence (Dobson & May, 1987; Deredec & Courchamp, 2003). In the open ocean such as the Barents Sea potential hosts are restricted to bottom-living fish rather than pelagic, and limits species diversity of parasitic copepods (Boxshall, 2005). Recordings of high infections of parasitic copepods in cultivated fish in three coastal areas in northern Norway made by Strøm (2007), further assess that transmission with high host densities favour the completion of these parasites' life cycles. Another explanation for the absence of these parasitic copepods in the Barents Sea could be differences in temperatures between the two localities as population growth, infectivity and survival correlates positively with higher temperatures (Möller, 1978). Furthermore, three of the parasitic copepods found in the present study belong to the family Caligidae (*Caligus* spp., *C. curtus*, *C. elongatus*), and are sensitive to hydrographical conditions (Hahnenkamp & Fyhn, 1985; Schram et al., 1998; Tucker et al., 2000; Heuch et al., 2002), which are more profound in the Barents Sea where vertical salinity differences and seasonal variations in hydrographic conditions occur more frequently than in the coastal region (Stiansen et al., 2009).

Myxosporea

Myxosporeans have a two-host life cycle that includes invertebrates and vertebrates. Marine fishes are common intermediate hosts and become infected either by swallowing the multinucleated spores or by randomly encountering with spores (Möller & Anders, 1986; Lom & Dyková, 2006). Polychaetes for marine species function as final hosts, and in order to

complete the parasite life cycle the intermediate hosts have to be at close proximity when the spores are released (Lom & Dyková, 2006). In regard of that, higher host densities in the coastal region could explain the present findings, and that coastal cod have a greater chance of encountering the infecting spores. Hemmingsen et al. (1991) found great differences in myxosporean infection on cod between the Barents Sea and a coastal location of northern Norway, Ullsfjord, where the latter showed a higher prevalence of infection. This corresponds well with findings from the present study and could best be explained by the presence of final hosts. Myxosporeans infect fish gall bladders, urinary tract, blood or lymph systems, and are considered to persist in the host for a great length of time (Möller & Anders, 1986; Hemmingsen et al., 1991). Considering that, if myxosporeans were to be present in the Barents Sea they should have been recorded in the present study. Thus, findings of myxosporeans only in the coastal region could indicate that the coastal habitat is more suited for completion of the myxosporean life cycle.

Nematodes

In the present study nematodes dominated the parasite communities in both localities, which was not surprising given the broad range of host specificity that most of them possess (Polyanskii, 1966; Appy & Burt, 1982). Marine nematodes are endoparasites commonly living as adults or larvae in the intestinal tract or muscles of fish (Möller & Anders, 1986). The life cycle of nematodes typically consists of five developmental stages: four larval or juvenile stages (L1-L4) and the adult stage (Marcogliese, 1995; Goater et al., 2014). The three larval stages are considered long-lived and include both invertebrates and fish as intermediate hosts, with crustaceans common as first intermediate hosts (Appy, 1981; Hemmingsen et al., 1991; Bristow & Berland, 1992; Køie, 1993; Marcogliese, 2002). Depending on the parasite species the different final hosts comprise teleost fishes, marine mammals, elasmobranch or birds (Appy & Burt, 1982).

The three nematodes recorded from cod only in the coastal region were the adults: *A. filiformis*, *C. gracilis* and *C. cirratus*. As all of them have teleost fishes as final hosts (Appy, 1981), it was not possible to assess the absence of final hosts in the Barents Sea as a possible reason for the parasites not being there. Benthic crustaceans serve as intermediate hosts for *A. filiformis*, while small fish (e.g. gobies and cod fry) are intermediate hosts for *C. gracilis* and *C. cirratus* (Karasev et al., 1996; Køie, 2000; Køie & Nylund, 2001), all of which are present

in the Barents Sea (Stiansen et al., 2009). For distribution of larval nematodes in fish hosts, absence of invertebrate hosts is considered a limiting factor (Young, 1972). However, as the invertebrate hosts (e.g. crustaceans) are widely distributed and dispersion occurs mainly passively, they are not considered the most responsible for parasite distribution of nematodes (Young, 1972; Hemmingsen et al., 1992). Therefore, the present findings of the three nematodes only in the coastal region could not be attributed to the lack of intermediate or final hosts in the Barents Sea. A possible explanation could, however, be that the parasites have a northern limit to their ranges, as Polyanskii (1966) suggested when he found rare findings of the parasite *C. cirratus* in the Barents Sea (compared with present findings: 42.86 %). Both *C. gracilis* and *C. cirratus* have been recorded from cod in other coastal regions (e.g. Baltic Sea, Celtic Sea, Icelandic waters, Irish Sea, North Sea and Trondheimsfjorden) by Perdiguero-Alonso et al. (2008), which raises the possibility of them having a northern limit to their range. Another possibility is that they are evolutionarly adapted to coastal waters, and are not capable of surviving outside coastal areas. However, discussion of plausible reasons is problematic due to lack of research on that issue and the possibility of many factors being involved (e.g. salinity, currents, temperature, etc.).

Monogenea

Monogeneans are ectoparasites possessing a single definitive host, mostly teleost fishes, and are considered highly host-specific (Whittington et al., 2000). In the present study, monogeneans were only found in cod from the coastal region and not in cod from the Barents Sea, which was surprising given that their geographic distribution should reflect the distributional range of their specific host (Whittington et al., 2000; Whittington, 2005). The three monogeneans recorded in the coastal sample belonged all to the genus *Gyrodactylus* (*G. callariatis*, *G. marinus* and *G. pharyngicus*). Common for *Gyrodactylus* species is their reproductive strategy by viviparity that allows for rapid population growth on the infected host individual (Möller & Anders, 1986; Whittington, 2005). The importance of gyrodactylids coming in direct contact with the host for successful transmission has been well documented (Scott & Anderson, 1984; Kamiso & Olson, 1986; Bakke et al., 1992), and both theoretical and practical work have related increased parasite transmission with high stocking densities (Anderson, 1980; Kamiso & Olson, 1986). As mentioned earlier, it is likely that cod in the coastal region assess higher densities than in the Barents Sea, and thus could explain the absent of *Gyrodactylus* in the Barents Sea. However, earlier observations on cod in the

Barents Sea have found them obtaining seasonally high densities (P. Arneberg pers. comm.), and attributing high host densities as a possible explanation for the absence of monogeneans in the Barents Sea is less clear. A possible explanation for the presence of *Gyrodactylus* in the coastal region and not in the open sea could be explained by the biology of the genus. Transmissions of *Gyrodactylus* has been shown to correlate positively with increasing water temperature (Bakke et al., 1991; Appleby, 1996; Soleng et al., 1999) and could be the factor most responsible for the distribution of *Gyrodactylus* in cod from coastal waters. The temperature in both localities lies within the same scale with the exception of coastal water having an increase in summer months, while the Barents Sea temperatures are more constant throughout the year (Sakshaug et al., 1994; Ryvarden, 1997). Another aspect with the genus *Gyrodactylus* is that they are evolutionarly adapted to the host biology and thus to the host behaviour, physiology and biochemistry (Whittington et al., 2000), and could therefore be as adapted to the specific host as to the specific environment (e.g. coastal waters). As chemical sensors that these parasites use to find their host generate sensitivity for their habitat of choice, the stability of the environment could be important for these parasites, and changing climatic factors could be a limiting factor (Whittington et al., 2000). Thus, the coastal region could be best suited for the transmission and persistence of these parasites compared with the Barents Sea.

Digenea

It is common to find a great diversity of digenean parasites in fish due to their plasticity and complex life cycle. Digeneans are found in many groups of invertebrates and vertebrates (Cribb, 2005). Their life cycle includes many larval stages, both free-living and parasitic, and usually comprises two intermediate hosts. For most marine species of digeneans molluscs are the first intermediate hosts and vertebrates function as final hosts (Möller & Anders, 1986; Cribb et al., 2002). Poulin (1997) did not consider the type of habitat where digenean eggs were released as the most important factor for transmission of the parasite. The author suggested intermediate hosts as a factor of importance, which contributes to the theory that the abundance of intermediate or final hosts could explain the prevalence of the parasites. In Atlantic coastal waters fish are susceptible to an infection by the digenean *Cryptocotyle lingua*, commonly know as the "Black spot disease" (Möller & Anders, 1986). In the present study prevalence of *C. lingua* was 80 % in the coastal population, and was not recorded in the Barents Sea population. Galaktivonov & Bustnes (1999) did a study of digeneans in arctic

regions and suggested that decreased transmissions of digeneans with complicated life cycles correlated with a harsh climate, reduced prevalence of snails and moderate distribution of final hosts such as fish and birds. The authors found prevalence of infections of digeneans increased both in snails and fish caught in the western coast of Norway more than on the Russian coast. In the Barents Sea unpublished data on digeneans in molluscs show a decrease with increasing depth (P. Arneberg & W. Hemmingsen pers. comm.), and this could be the limiting factor for the absence of these digeneans in the Barents Sea. This further illustrates the importance of the presence of potential hosts for parasites and that declines in hosts densities correspond with declines in parasite transmission (Deredec & Courchamp, 2003). Furthermore, Möller (1978) considered development, survival and infectivity of the first larval stage of *C. lingua* to be negatively correlated with low temperatures. This corresponds with the temperature differences between the coastal region and the Barents Sea, where the former experiences greater temperature changes more suitable for completion of digenean life cycles (Sakshaug et al., 1994; Ryvarden, 1997).

Eucestoda

Eucestodes are exclusively endoparasitic with an indirect life cycle including two intermediate hosts and one final host (Möller & Anders, 1986). The eucestodes recorded only in the coastal region were plerocercoids of *G. erinaceus* and *Tetraphyllidea* sp. They have zooplankton, mainly copepods, as first intermediate hosts, fish as second intermediate hosts and elasmobranch (skates and rays) serving as final hosts (Marcogliese, 1995; Möller & Anders, 1986). As several elasmobranch species and other teleosts are present in the Barents Sea (Dolgov, 2005; Stiansen et al., 2009), the present findings of these eucestodes could not be attributed to lack of second intermediate or final hosts in the Barents Sea. The availability of first intermediate hosts, zooplankton, in the Barents Sea could be a limiting factor for the distribution of the parasites. In the Barents Sea zooplankton biomass shows great variation between years (Stiansen et al., 2009), and could cause an obstacle to successful parasite transmission when abundance is low, and further affect parasite transmission to both second intermediate and final hosts (Marcogliese, 1995). Considering the broad host specificity that both parasite species (*G. erinaceus* and *Tetraphyllidea* sp.) possess and that infections of plerocercoids are not restricted to cod (Polyanskii, 1966; Möller & Anders, 1986), the parasites are likely to occur in the Barents Sea. Therefore, an explanation could be that they are present in the Barents Sea and that the present result attributes to limitation of data in the

present study. Another explanation could be that infestations of larval eucestodes on cod are generally low, which corresponds with findings from an earlier study by Karasev et al. (1996).

Isopoda

The isopods recorded from cod only in the coastal region were the praniza larvae. The life cycle comprises two phases: the parasitic larvae that live on or in a host and the adult that is not parasitic and lives in tubes in muddy bottom (Möller & Anders, 1986). As the praniza larvae exploit fish or sea anemones and tunicates for food utilization (Möller & Anders, 1986), it is likely to believe that distribution of the parasite would be within the area of which these hosts reside. In the Barents Sea, abundance of sea anemones and tunicates declines with increasing depth (Stiansen et al., 2009), and thus could explain the absence of praniza larvae on cod from the Barents Sea. Furthermore, as the life cycle of this isopod includes both a benthic and a planktonic phase, another explanation could be that the depth of the Barents Sea is too large for transmission of the parasite. Thus, the Barents Sea might not be suited for the completion of the life cycle and transmission of the praniza larvae.

Differences of parasite intensity between two habitats

Among the 11 parasite species present in both localities, digeneans dominated with having four species present. This dominance corresponds with other findings (Karasev et al., 1996; Klimpel et al., 2006), and could be explained by their broad host specificity and wide distributional patterns (Cribb et al., 2002). However, *D. varicus* was the only species among them that showed significant higher intensity of infestation on coastal cod compared to the Barents Sea cod (Fig. 6). Karasev et al. (1996) found infestation of *D. varicus* on cod increasing with age, and argued this to be related to changes in food utilization of aging cod. The life cycle of *D. varicus* comprises planktonic and benthic intermediate hosts, including fish (Køie, 1979). The present findings could be explained by differences in food utilization of the two cod stocks, and that there is not enough contact between infected intermediate hosts and cod in the Barents Sea to keep the parasite transmission at higher levels. As mentioned earlier, molluscs are common first intermediate hosts for many digeneans (Möller & Anders, 1986; Cribb et al., 2002), and infected molluscs have shown to decrease with increasing depth (P. Arneberg & W. Hemmingsen pers. comm.), and infestations from molluscs are thus a limiting factor for the parasite transmission in the Barents Sea. Both cod

stocks are likely to obtain infestation by feeding on infected fish (Karasev et al., 1996). In the coastal region, the higher densities of cod could make them more susceptible to infection by eating infected fish or larger intermediate hosts infected by the parasite (Karasev et al., 1996). Another possibility is that the parasite are continuously present in the coastal region and that the Barents Sea cod get infected during spawning migrations to the coastal region, and thus obtain only small infestations of the parasite. The coastal cod that are continuously present in the coastal region would therefore obtain higher parasite intensities, as occurrence of the parasite species seem to be higher there.

Findings of the parasitic copepod *C. adunca* was not surprising, given that the parasite has been shown to have broad host specificity (Karasev et al., 1996). Karasev et al. (1996) recorded high prevalence with low intensity of infestation of *C. adunca* from the Barents Sea. This corresponds with the present findings of significant higher intensity of infestation on cod from the coastal region compared with the Barents Sea. There is insufficient evidence to assess possible reasons for these differences in intensity. One explanation could be that the potentially higher host densities in the coastal region favour parasite transmission, and that leads to higher intensities. It is worth accentuating that *C. adunca* was the only parasitic copepod found from the Barents Sea, and earlier recordings of the parasite by Perdiguero-Alonso et al. (2008) viewed *C. adunca* from different areas, even from areas with low salinity. This could point in the direction that *C. adunca* is highly tolerant against environmental changes, and therefore has the ability of sustaining at different habitats. Furthermore, the present findings could indicate that the environment in the coastal region could be the most preferred, as higher intensities indicates higher population growth (Deredec & Courchamp, 2003).

As mentioned earlier, nematodes dominated the parasite communities on cod in both the coastal region and the Barents Sea. The high prevalence (> 80 %) of larval *A. simplex* and *H. aduncum* in both cod stocks was not surprising given the widespread geographical distribution of these generalist parasite species (Möller & Anders, 1986; Køie, 1993; Mattiucci et al., 1997). However, with significant differences of parasite intensity between the two habitats, both nematodes seem to have an environment that suits completion of the parasite life cycles best. That could be explained by differences of feeding behaviour of the two cod stocks (Karasev et al., 1996). The present findings could also be explained by the

appearance of final hosts, as marine mammals and fish, have large geographical distributions and are considered active dispersers of the parasite eggs (Young, 1972; Hemmingsen et al., 1992). The coastal cod revealed significant higher intensity of infestation with *A. simplex* (26.97) compared to the Barents Sea cod (5.14). High infestation of *A. simplex* indicates pelagic feeding on crustaceans (Karasev et al., 1996), and the lower intensity of infestation in the Barents Sea cod could be explained by benthic feeding behaviour. For *A. simplex* mammals serving as final hosts are commonly whales and occasionally seals (Young, 1972). Strømnes & Andersen (2000) found distinct seasonal variation in infection of larval *A. simplex* on cod in Norwegian coastal waters. The authors argued that northward-migrating whales accompanied with spring bloom of plankton, as most responsible for the clear infection peak in April. This was due to whales supplying parasite eggs at the same time as abundance of potential intermediate host rose in the same areas. Given that whales occur in both habitats (Stiansen et al., 2009), the present findings could further be explained by the size differences of the two habitats. As the open sea constitute a considerable larger habitat in comparison with areas within the coastal region, distribution of the parasite eggs in coastal regions are more likely to be spread at close proximity to potential intermediate hosts in comparison to distribution of the eggs in the Barents Sea. Therefore, coastal cod would obtain higher transmission rate compared with the Barents Sea cod, which leads to higher intensities in the coastal cod.

Intensity of infestation of *H. aduncum* (adult) was higher in the Barents Sea cod (40.27) compared to the coastal cod (9.07). Larval *H. aduncum* was only recorded from the Barents Sea cod, which was surprising given that the larval stage is found on cod from other areas in the coastal region (Heuch et al., 2011). However, since both prevalence and intensity of infestation were higher in the Barents Sea, the present findings indicate that *H. aduncum* could be best suited to the habitat of the open sea. As high infestations with larval *H. aduncum* also indicate feeding on pelagic crustaceans (Karasev et al., 1996), high infestation of adult *H. aduncum* could indicate feeding on fish infected with these larval nematodes. Teleost fish serve as both intermediate and final hosts for *H. aduncum*. Contrary to the adult nematodes found only in the coastal region, *H. aduncum* has a great variety of fish species that could serve as final hosts (Køie, 1993), whereas the adult nematodes only found in the coastal region are mainly restricted to gadoid fish (Polyanskii, 1966; Køie & Nylund, 2001). This is important because parasite transmission rate is directly related to host densities

(Dobson & May, 1987), and the Barents Sea assesses a great variety of fish stocks suitable as potential hosts for the parasite species (Stiansen et al., 2009). Furthermore, the migratory movement of cod in the Barents Sea could be important for transmission of *H. aduncum*, whilst the stationary cod stock in the coastal region could limit transmission of the parasite species and thus obtain lower intensities of infestation.

The statistics in the present study must be viewed with caution, as possibilities of type 1 error could be present. That means that conclusions of connection between independent and dependent variables have been made, even if the opposite was true (Keppel & Wickens, 2004). In the present study a lot of statistical tests were conducted, and type 1 errors could have been inflated. The p-value represents an estimate of the probability for making a type 1 error, and the probability of making the wrong conclusions increases with increasing p-value.

In summary, infestation of parasites on individual hosts between two distinct habitats could be a result of ecological variations (Rohde, 1993; Marcogliese, 2002; Klimpel et al., 2006), the availability of potential hosts, and differentiation of factors facilitating parasite transmission (Dobson & May, 1987; Deredec & Courchamp, 2003). Benthic faunas and depth gradients are important for the abundance and prevalence of parasites with complex life cycles, as parasite diversity decreases with increasing depth (Campbell et al., 1980; Dobson & May, 1987; Klimpel et al., 2006). The coastal region encompasses a diverse marine fauna that high parasite abundance and prevalence directly depend upon (Campbell et al., 1980; Ryvarden, 1997; Marcogliese, 2002). Intermediate hosts in the open water realm of the Barents Sea might be restricted due to environmental variations and biomass distributions (Campbell et al., 1980; Hamre, 1994; Sakshaug, 1997), which could cause restriction of the prevalence and intensity of parasites. The present study shows that the total number of parasite species was highest on individual hosts of cod from the coastal region compared with the Barents Sea, and that intensity of infestation was highest in the coastal region. There are a great number of unanswered questions regarding causes of this disposition. However, the results are consistent with the idea that parasites may mean less for the dynamics of the cod population in the Barents Sea than at the coast. Further studies of parasites in the Barents Sea and the coastal region of northern Norway are essential in advancing our knowledge about the parasite distribution, parasite-host relationship and the influence they encompass on an ecological scale.

References

Amundsen P. A., Lafferty, K. D., Knudsen, R., Primicerio, R., Klemetsen, A., & Kuris, A. M. (2009). Food web topology and parasites in the pelagic zone of a subarctic lake. *Journal of Animal Ecology, 78*(3), 563-572.

Anderson, R. M. (1980). Depression of Host Population Abundance by Direct Life Cycle Macroparasites. *Journal of Theoretical Biology, 82*(2), 283-311.

Angel, M. V. (1993). Biodiversity of the Pelagic Ocean. *Conservation Biology, 7*(4), 760-772.

Appleby, C. (1996). Seasonal occurrence, topographical distribution and transmission of *Gyrodactylus callariatis* (Monogenea) infecting juvenile Atlantic cod in the Oslo Fjord, Norway. *Journal of Fish Biology, 48*(6), 1266-1274.

Appy, R. G. (1981). Species of *Ascarophis* van Beneden, 1870 (Nematoda: Cystidicolidae) in North Atlantic fishes. *Canadian Journal of Zoology, 59*(11), 2193-2205.

Appy, R. G., & Burt, M. D. B. (1982). Metazoan parasites of cod, *Gadus morhua* L., in Canadian Atlantic waters. *Canadian Journal of Zoology, 60*(7), 1573-1579.

Arneberg, P., Skorping, A., Grenfell, B., & Read, A. F. (1998). Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London B: Biological Sciences, 265*(1403), 1283-1289.

Babcock, P. G., & The Merriam-Webster editorial staff. (Ed.). (1961). *Webster's Third New International Dictionary of the English language unabridged.* Massachusetts: Merriam-Webster incorporated.

Bakke, T. A., Harris, P. D., Jansen, P. A., & Hansen, L. P. (1992). Host specificity and dispersal strategy in gyrodactylid monogeneans, with particular reference to *Gyrodactylus salaris* (Platyhelminthes, Monogenea). *Diseases of Aquatic Organisms, 13*(1), 63-74.

Bakke, T. A., Jansen, P. A., & Hansen, L. P. (1991). Experimental transmission of *Gyrodactylus salaris* Malmberg, 1957 (Platyhelminthes, Monogenea) from the Atlantic salmon (*Salmo salar*) to the European eel (*Anguilla anguilla*). *Canadian Journal of Zoology, 69*(3), 733-737.

Boxshall, G. (2005). Crustacean parasites. In K. Rohde (Ed.), *Marine Parasitology* (p. 123-138). Wallingford, UK: CABI Publishing.

Bray, R. A. (2005). Deep-sea parasites. In K. Rohde (Ed.), *Marine Parasitology* (p. 366-369). Wallingford, UK: CABI Publishing.

Bristow, G. A., & Berland, B. (1992). On the ecology and distribution of *Pseudoterranova decipiens* (Nematoda: Anisakidae) in an intermediate host, *Hippoglossoides platessoides*, in northern Norwegian waters. *International Journal for Parasitology, 22*(2), 203-208.

Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology Meets Ecology on Its Own Terms: Margolis et al. Revisited. *The Journal of Parasitology, 83*(4), 575-583.

Campbell, R. A., Haedrich, R. L., & Munroe, T. A. (1980). Parasitism and Ecological Relationships Among Deep-Sea Benthic Fishes. *Marine Biology, 57*(4), 301-313.

Cribb, T. H. (2005). Digenea (endoparasitic flukes). In K. Rohde (Ed.), *Marine Parasitology* (p. 76-87). Wallingford, UK: CABI Publishing.

Cribb, T. H., Chisholm, L. A., & Bray, R. A. (2002). Diversity in the Monogenea and Digenea: does lifestyle matter?. *International Journal for Parasitology, 32*(3), 321-328.

Deredec, A., & Courchamp, F. (2003). Extinction thresholds in host-parasite dynamics. *Annales Zoologici Fennici, 40*(2), 115-130.

Dobson, A. P. (1988). The Population Biology of Parasite-Induced Changes in Host Behavior. *Quarterly Review of Biology, 63*(2), 139-165.

Dobson, A. P., & May, R. M. (1987). The effects of parasites on fish populations – theoretical aspects. *International Journal for Parasitology, 17*(2), 363-370.

Dolgov, A. V. (2005). Feeding and Food Consumption by the Barents Sea Skates. *Journal of Northwest Atlantic Fishery Science, 35*(1), 495-503.

Eilertsen, H. C., & Skarðhamar, J. (2006). Temperatures of north Norwegian fjords and coastal waters: Variability, significance of local processes and air-sea heat exchange. *Estuarine, Coastal and Shelf Science, 67*(3), 530-538.

Falk-Petersen, J., Renaud, P., & Anisimova, N. (2011). Establishment and ecosystem effects of the alien invasive red king crab (Paralithodes camtschaticus) in the Barents Sea – a review. *ICES Journal of Marine Science, 68*(3), 479-488.

Galaktionov, K. V., & Bustnes, J. O. (1999). Distribution patterns of marine bird digenean larvae in periwinkles along the southern coast of the Barents Sea. *Diseases of Aquatic Organisms, 37*(3), 221-230.

Goater, T. M., Goater, C. P., & Esch, G. W. (2014). *Parasitism: The diversity and ecology of animal parasites* (2nd ed.). Cambridge, UK: Cambridge University Press.

Gray, J. S. (1997). Marine biodiversity: patterns, threats and conservation needs. *Biodiversity & Conservation, 6*(1), 153-175.

Gunn, A., & Pitt, S. J. (2012). *Parasitology: An integrated Approach.* Chichester, UK: John Wiley & Sons, Ltd.

Hahnenkamp, L., & Fyhn, H. J. (1985). The osmotic response of salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae), during the transition from sea water to fresh water. *Journal of Comparative Physiology B, 155*(3), 357-365.

Hairston Jr, N. G., & Hairston Sr, N. G. (1993). Cause-Effect Relationships in Energy Flow, Trophic Structure, and Interspecific Interactions. *The American Naturalist, 142*(3), 379-411.

Hamre, J. (1994). Biodiversity and exploitation of the main fish stocks in the Norwegian – Barents Sea ecosystem. *Biodiversity & Conservation, 3*(6), 473-492.

Hansen, E. K., & Poulin, R. (2006). Spatial covariation between infection levels and intermediate host densities in two trematode species. *Journal of Helminthology, 80*(03), 255-259.

Harris, P. D., Cable, J., Tinsley, R. C., & Lazarus, M. (1999). Combined ribosomal DNA and morphological analysis of individual gyrodactylid monogeneans. *The Journal of Parasitology, 85*(2), 188-191).

Hemmingsen, W., Lile, N., & Halvorsen, O. (1992). The parasite fauna of cod (*Gadus morhua* L.) in Balsfjord, North Norway. *Polar biology, 12*(8), 739-742.

Hemmingsen, W., Lombardo, I., & MacKenzie, K. (1991). Parasites as biological tags for cod, *Gadus morhua* L., in northern Norway: a pilot study. *Fisheries Research, 12*(4), 365-373.

Hemmingsen, W., & MacKenzie, K. (2001). The parasite fauna of the Atlantic cod, Gadus morhua L. *Advances in Marine Biology, 40*, 1-80.

Hemmingsen, W., Jansen, P. A., & MacKenzie, K. (2005). Crabs, leeches and trypanosomes: an unholy trinity?. *Marine Pollution Bulletin, 50*(3), 336-339.

Heuch, P. A., Jansen, P. A., Hansen, H., Sterud, E., MacKenzie, K., Haugen, P., & Hemmingsen, W. (2011). Parasite faunas of farmed cod and adjacent wild cod populations in Norway: a comparison. *Aquaculture Environment Interactions, 2*(1), 1-13.

Heuch, P. A., Knutsen, J. A., Knutsen, H., & Schram, T. A. (2002). Salinity and temperature effects on sea lice over-wintering on sea trout (*Salmo trutta*) in coastal areas of the Skagerrak. *Journal of the Marine Biological Association of the United Kingdom, 82*(5), 887-892.

Horwitz, P., & Wilcox, B. A. (2005). Parasites, ecosystems and sustainability: an ecological and complex systems perspective. *International Journal for Parasitology, 35*(7), 725-732.

Hudson, P. (2005). Parasites, diversity, and the ecosystem. In F. Thomas, F. Renaud & J.-F. Guégan (Eds.), *Parasitism & Ecosystems* (p. 1-12). New York: Oxford University Press.

Hudson, P. J., Dobson, A. P., & Lafferty, K. D. (2006). Is a healthy ecosystem one that is rich in parasites?. *Trends in Ecology & Evolution, 21*(7), 381-385.

Hudson, P. J., Dobson, A. P., & Newborn, D. (1998). Prevention of Population Cycles by Parasite Removal. *Science, 282*(5397), 2256-2258.

Ingvaldsen, R., & Loeng, H. (2009). Physical oceanography. In E. Sakshaug, G. Johnsen & K. Kovacs (Eds.), *Ecosystem Barents Sea* (p. 33-64). Trondheim: Tapir Academic Press.

Kamison, H. N., & Olson, R. E. (1986). Host-Parasite Relationships between Gyrodactylus stellatus (Monogenea: Gyrodactylidae) and Parophrys vetulus (Pleuronectidae: English Sole) from Coastal Waters of Oregon. *The Journal of Parasitology, 72*(1), 125-129.

Karasev, A. B., Mitenev, V. K., & Shulman, B. S. (1996). Ecological peculiarities of the parasite fauna of cod and Pollock in the vicinity of the kislaya inlet tidal power plant, Western Murman (the Barents sea). *Sarsia, 80*(4), 307-312.

Karlsbakk, E. (2005). Occurrence of leeches (Hirudina, Piscicolidae) on some marine fishes in Norway. *Marine Biology Research, 1*(2), 140-148.

Kent, M. L., Shaw, R. W., & Sanders, J. L. (2014). Microsporidia in Fish. In L. M. Weiss & J. J. Becnel (Eds.), *Microsporidia: Pathogens of Opportunity* (1st ed., p. 493-520). Chichester: John Wiley & Sons, Inc.

Keppel, G., & Wickens, T. D. (2004). Simultaneous comparisons and the control of type 1 errors. *Design and analysis: A researcher´s handbook. (4th ed.). Upper Saddle River (NJ): Pearson Prentice Hall.* p, 111-130.

Khan, R. A. (1977). Susceptibility of marine fish to trypanosomes. *Canadian Journal of Zoology, 55*(8), 1235-1241.

Khan, R. A. (2005). Prevalence and Influence of Loma branchialis (Microspora) on Growth and Mortality in Atlantic Cod (Gadus morhua) in Coastal Newfoundland. *The Journal of Parasitology, 91*(5), 1230-1232.

Klimpel, S., Palm, H. W., Busch, M. W., Kellermanns, E., & Rückert, S. (2006). Fish parasites in the Arctic deep-sea: Poor diversity in pelagic fish species vs. heavy parasite load in a demersal fish. *Deep Sea Research Part 1: Oceanographic Research Papers, 53*(7), 1167-1181.

Kurlansky, M. (1998). *Cod. A biography of the fish that changed the world.* London: Jonathan Cape.

Køie, M. (1979). On the Morphology and Life-History of *Derogenes varicus* (Müller, 1784) Loss, 1901 (Trematoda, Hemiuridae). *Parasitology Research, 59*(1), 67-78.

Køie, M. (1993). Aspects of the life cycle and morphology of *Hysterotylacium aduncum* (Rudolphi, 1802) (Nematoda, Ascaridoidea, Anisakidae). *Canadian Journal of Zoology, 71*(7), 1289-1296.

Køie, M. (2000). Life cycle and seasonal dynamics of *Cucullanus cirratus* O.F. Müller, 1777 (Nematoda, Ascaridida, Seuratoidea, Cucullanidae) in Atlantic cod, *Gadus morhua* L.. *Canadian Journal of Zoology, 78*(2), 182-190.

Køie, M., & Nylund, A. (2001). The life-cycle of *Capillaria gracilis* (Capillariidae), a nematode parasite of gadoid fish. *Sarsia, 86*(4-5), 383-387.

Lafferty, K. D., Allesina, S., Arim, M., Briggs, C. J., De Leo, G., Dobson, A. P., … & Thieltges, D. W. (2008). Parasites in food webs: the ultimate missing links. *Ecology letters, 11*(6), 533-546.

Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. *Polar Research, 10*(1), 5-18.

Lom, J., & Dyková, I. (2006). Myxozoan genera: definition and notes on taxonomy, life-cycle terminology and pathogenic species. *Folia Parasitologica, 53*(1), 1-36.

Lom, J., & Nilsen, F. (2003). Fish microsporidia: fine structural diversity and phylogeny. *International Journal for Parasitology, 33*(2), 107-127.

Malmberg, G. (1970). The excretory systems and the marginal hooks as a basis for the systematics of Gyrodactylus (Trematoda, Monogenea). *Arkiv for Zoologi, 23*(1/2), 1-235.

Marcogliese, D. J. (1995). The role of zooplankton in the transmission of helminth parasites to fish. *Reviews in Fish Biology and Fisheries, 5*(3), 336-371.

Marcogliese, D. J. (2002). Food webs and the transmission of parasites to marine fish. *Parasitology, 124*(7), 83-99).

Marcogliese, D. J. (2005). Transmission of marine parasites. In K. Rohde (Ed.), *Marine Parasitology* (p. 280-286). Wallingford, UK: CABI Publishing.

Mattiucci, S., Nascetti, G., Cianchi, R., Paggi, L., Arduino, P., Margolis, L., … & Bullini, L. (1997). Genetic and Ecological Data on the Anisakis simplex Complex, with Evidence for a New Species (Nematoda, Ascaridoidea, Anisakidae). *The Journal of Parasitology, 83*(3), 401-416.

May, R. M., & Godfrey, J. (1994). Biological Diversity: Differences between Land and Sea [and Discussion]. *Philosophical Transactions: Biological Sciences, 343*(1303), 105-111.

Mitchell, C. E., & Power, A. G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature, 421*(6923), 625-627.

Miura, O., Torchin, M. E., Kuris, A. M., Hechinger, R. F., & Chiba, S. (2006). Introduced cryptic species of parasites exhibit different invasion pathways. *Proceedings of the National Academy of Sciences, 103*(52), 19818-19823.

Moodie, E. (2005). Microsporidia (microsporans). In K. Rohde (Ed.), *Marine Parasitology* (p. 30-34). Wallingford, UK: CABI Publishing.

Møller, D. (1968). *Studies on genetic diversities in Arctic and coastal cod in Norwegian waters*. Oslo: Universitetsforlaget.

Möller, H. (1978). The effects of salinity and temperature on the development and survival of fish parasites. *Journal of Fish Biology, 12*(4), 311-323.

Möller, H., & Anders, K. (1986). *Diseases and parasites of marine fishes*. Kiel: Verlag Möller.

Nowak, B. F. (2005). ´Sarcomastigophora´(amoebae and flagellates). In K. Rohde (Ed.), *Marine Parasitology* (p. 17-20). Wallingford, UK: CABI Publishing.

Perdiguero-Alonso, D., Montero, F. E., Raga, J. A., & Kostadinova, A. (2008). Composition and structure of the parasite faunas of cod, *Gadus morhua* L. (Teleostei: Gadidae), in the North East Atlantic. *Parasites & Vectors, 1*(1), 1-23.

Polyanskii, Yu. I. (1966). *Parasites of the fish of the Barents Sea*. Washington, D.C.: Israel Program for Scientific Translations Ltd.

Poore, G. C. B., & Wilson, G. D. F. (1993). Marine species richness. *Nature, 361*(6413), 597-598.

Poulin, R. (1997). Egg production in adult trematodes: adaptation or constraint?. *Parasitology, 114*(2), 195-204.

Poulin, R., & Morand, S. (2000). The Diversity of Parasites. *The Quarterly Review of Biology, 75*(3), 277-293.

Rohde, K. (1992). Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. *Oikos, 65*(3), 514-527.

Rohde, K. (1993). *Ecology of Marine Parasites: An Introduction to Marine Parasitology.* (2nd ed.). Wallingford: Cab International.

Rohde, K. (2005a). Definitions, and adaptations to a parasitic way of life. In K. Rohde (Ed.), *Marine Parasitology* (p. 1-6). Wallingford, UK: CABI Publishing.

Rohde, K. (2005b). Latitudinal, longitudinal and depth gradients. In K. Rohde (Ed.), *Marine Parasitology* (p. 348-351). Wallingford, UK: CABI Publishing.

Rohde, K., & Hayward, C. J. (2000). Oceanic barriers as indicated by scombrid fishes and their parasites. *International Journal for Parasitology, 30*(5), 579-583.

Rynkiewicz, E. C., Pedersen, A. B., & Fenton, A. (2015). An ecosystem approach to understanding and managing within-host parasite community dynamics. *Trends in parasitology, 31*(5), 212-221.

Ryvarden, L. (1997). *Kysten: Landskap, flora og fauna langs Norges kyst.* Oslo: Teknologisk Forlag.

Sakshaug, E. (1997). Biomass and productivity distributions and their variability in the Barents Sea. *ICES Journal of Marine Science, 54*(3), 341-350.

Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H., & Mehlum, F. (Eds.). (1994). *Økosystem Barentshavet.* Oslo: Universitetsforlaget.

Sakshaug, E., Johnsen, G., Kristiansen, S., Quillfeldt, C. V., Rey, F., Slagstad, D., Thingstad, F. (2009). Phytoplankton and primary production. In E. Sakshaug, G. Johnsen & K. Kovacs (Eds.), *Ecosystem Barents Sea* (p. 167-208). Trondheim: Tapir Academic Press.

Sakshaug, E., & Kovacs, K. M. (2009). Introduction. In E. Sakshaug, G. Johnsen & K. Kovacs (Eds.), *Ecosystem Barents Sea* (p. 9-32). Trondheim: Tapir Academic Press.

Sasal, P., & Thomas, F. (2005). Behavioural aspects of parasitism. In K. Rohde (Ed.), *Marine Parasitology* (p. 259-264). Wallingford, UK: CABI Publishing.

Schram, T. A., Knutsen, J. A., Heuch, P. A, & Mo, T. A. (1998). Seasonal occurrence of *Lepeophtheirus salmonis* and *Caligus elongatus* (Copepoda: Caligidae) on sea trout (*Salmo trutta*), off southern Norway. *ICES Journal of Marine Science, 55*(2), 163-175.

Scott, M. E., & Anderson, R. M. (1984). The population dynamics of *Gyrodactylus bullatarudis* (Monogenea) within laboratory populations of the fish host *Poecilia reticulata*. *Parasitology, 89*(1), 159-194.

Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika, 52*(3-4), 591-611.

Soleng, A., Jansen, P. A., & Bakke, T. A. (1999). Transmission of the monogenean *Gyrodactylus salaris*. *Folia Parasitologica, 46*(3), 179-184.

Stiansen, J. E., Korneev, O., Titov, O., Arneberg, P. (Eds.), Filin, A., Hansen, J. R., Høines, Å., Marasaev, S. (Co-eds.). (2009). *Joint Norwegian-Russian environmental status 2008. Report on the Barents Sea Ecosystem. Part II – Complete report.* IMR/PINRO Joint Report Series, 2009(3), 375 pp. ISSN 1502-9928.

Strøm, M. (2007). *Parasitter hos oppdrettstorsk i Nord-Norge*. Masteroppgave i fiskehelse, Universitetet i Tromsø.

Strømnes, E., & Andersen, K. (2000). "Spring rise" of whaleworm (*Ansakis simplex*; Nematoda, Ascaridoidea) third-stage larvae in some fish species form Norwegian waters. *Parasitology Research, 86*(8), 619-624.

Suchanek, T. H. (1994). Temperate Coastal Marine Communities: Biodiversity and Threats. *American Zoologist, 34*(1), 100-114.

Sundby, S. (1984). Influence of bottom topography on the circulation at the continental shelf off northern Norway. *Fiskeridirektoratets skrifter, Serie Havundersøkelser, 17*(14), 501-519.

Sverdrup, H. U. (1952). *Havlære: alminnelig havlære, vannmasser og strømforhold utenfor norskekysten*. Oslo: Fabritius.

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J., & Kuris, A. M. (2003). Introduced species and their missing parasites. *Nature, 421*(6923), 628-630).

Tucker, C. S., Sommerville, C., & Wooten, R. (2000). The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L.. *Journal of Fish Diseases, 23*(5), 309-320.

Whitlock, M. C., & Schluter, D. (2015). *The Analysis of Biological Data* (2nd ed.). Colorado: Roberts and Company Publishers, Incorporation.

Whittington, I. D. (2005). Monogenea Monopisthocotylea (ectoparasitic flukes). In K. Rohde (Ed.), *Marine Parasitology* (p. 63-72). Wallingford, UK: CABI Publishing.

Whittington, I. D., Cribb, B. W., Hamwood, T. E., & Halliday, J. A. (2000). Host-specificity of monogenean (platyhelminth) parasites: a role for anterior adhesive areas?. *International Journal for Parasitology, 30*(3), 305-320.

Willig, M. R. (2001). Latitude, common trends within. *Encyclopedia of biodiversity, 3*(1), 701-714.

Young, P. C. (1972). The Relationship Between the Presence of Larval Anisakine Nematodes in Cod and Marine Mammals in British Home Waters. *Journal of Applied Ecology, 9*(2), 459-485.

Øines, Ø., & Heuch, P. A. (2005). Identification of sea louse species of the genus *Caligus* using mtDNA. *Marine Biological Association of the United Kindom. Journal of the Marine Biological Association of the United Kindom, 85*(1), 73-79.
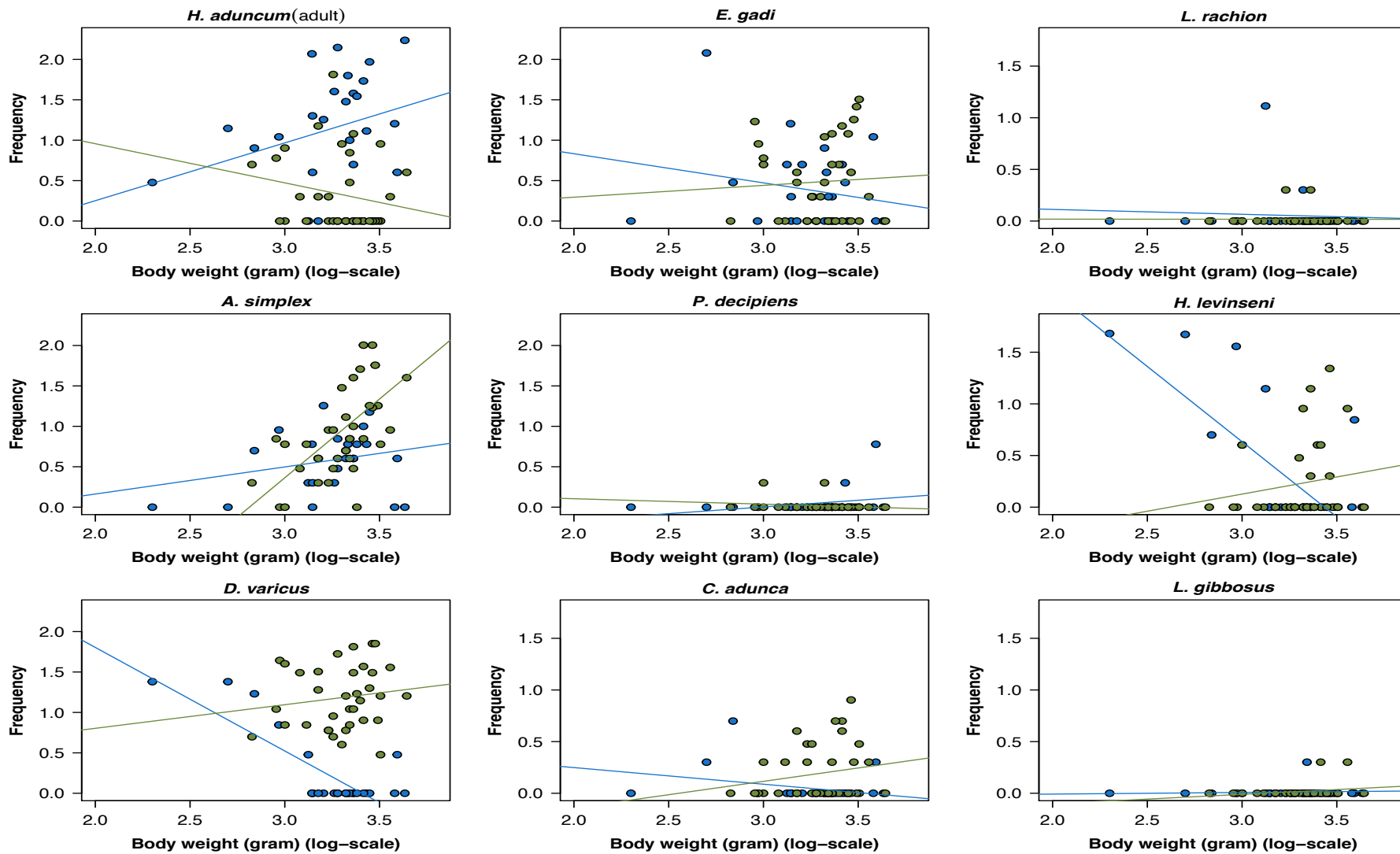
Appendix

Appendix A. Number of parasite species per host individual body weight of cod in the Barents Sea (blue) and coastal region (green), with associated regression lines.
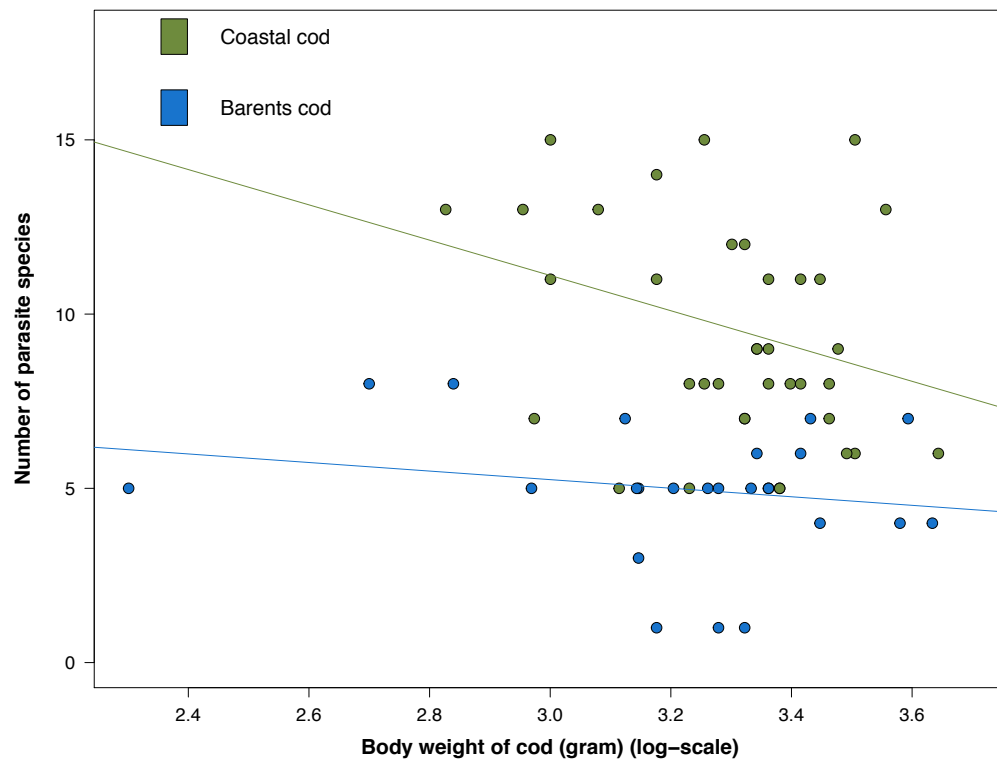
Appendix C. Frequency distribution of individual parasite species per host individual body weight of cod from the Barents Sea (blue) and coastal region (green), with associated regression lines.

Appendix C. Spearman's rank correlation analysis of parasite intensity of individual parasite species compared to individual body weight of cod. Parasite species included are present in both the Barents Sea and coastal region. Body weight of cod was log-transformed (log10).

Parasite species	Coastal cod (n=35)		Barents Sea cod (n=26)	
	P-value	Rho-value	P-value	Rho-value
C.adunca	0.3564	0.161	0.375	- 0.181
A.simplex	$1.806*10^{-05}$	0.657	0.368	0.184
H.aduncum (adult)	0.178	- 0.233	0.088	0.341
L.rachion	0.754	- 0.055	0.461	- 0.151
H.levinseni	0.334	0.168	0.005	- 0.531
L.gibbosus	0.095	0.287	0.650	0.093
D.varicus	0.265	0.194	0.004	- 0.545
E.gadi	0.561	0.102	0.441	- 0.158
P.decipiens	0.293	- 0.182	0.051	0.387