Nematode infestation in flatfish in the outer Oslofjord

by

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Abstract

Nematodes from 361 fish from 15 species were collected between August 2010 and March 2012 at Langøya and at Torbjørnskjær in the outer Oslofjord. The study focused on the infection levels of the three most abundant nematode species, *Hysterothylacium aduncum*, *Anisakis simplex* and *Contracaecum osculatum*, in the three flatfish species American plaice (*Hippoglossoides platessoides*), witch flounder (*Glyptocephalus cynoglossus*) and common dab (*Limanda limanda*).

When all nematode and fish species were pooled the percentage of infected fish (i.e prevalence), the average number of nematodes per fish (i.e. abundance) and the average number of nematodes per infected fish (i.e. the intensity) were significantly higher at Langøya than at Torbjørnskjær. While *H. aduncum* and *C. osculatum* had higher abundances at the western site, *A. simplex* was more abundant at the eastern site. Among the three flatfish species, American plaice had a relatively high prevalence both at Langøya and at Torbjørnskjær (55 and 53 % respectively). Witch flounder was only infected at Langøya (59 %) and mainly with *H. aduncum* (53 %). Common dab had a high prevalence at Langøya (80%) and rather low at Torbjørnskjær (15 %). However, since the sample size was small for witch flounder at Torbjørnskjær (n = 4) and for common dab at Langøya (n = 5), these results are likely to be biased.

This study also supports the general view that there is a large fluctuation in the nematode populations in the outer Oslofjord. The previously observed decrease of *A. simplex* seems to continue. *C. osculatum* and *H. aduncum* are getting more widespread in the Oslofjord. In addition, my data contain the first recording of the flatfish nematode *Cucullanus heterochrous* at Langøya, suggesting that also this species is expanding in the Oslofjord.

The lengths of the nematodes were used to investigate whether the three flatfishes are suitable hosts for the three nematode species. American plaice and witch flounder are good transport and final hosts for *H. aduncum*. American plaice seemed to be suitable

transport host for *C. osculatum* as well. Despite the fact that *A. simplex* is known to have a pelagic life-cycle with Atlantic herring (*Clupea harengus*) as the main transport host, my observations show that it can also use the benthic common dab as transport host in the outer Oslofjord.

The number of nematodes per witch flounder and common dab had a random distribution (Poisson distribution). However, the number of *Pseudoterranova decipiens* per American plaice was highly over-dispersed. It is likely that a combination of different factors, especially the feeding ecology and habitat preferences of the fish, is the cause for the observed infestation patterns. In addition, American plaice and witch flounder harboured a more diverse parasite fauna than common dab. Finally, the length measurements indicate that there may be some interspecific interaction between the nematodes.

Table of Contents

1 Introduction

This study is part of a larger project on seal nematodes conducted by Karl Inne Ugland at the Marine Biology Research Program of the Department of Biology at the University of Oslo. Two master theses have already been completed: Emma Lähdekorpi (2011) investigated seal worm (*Pseudoterranova decipiens*) infections in shorthorn sculpins (*Myoxocephalus scorpius*) at Hvaler and at Koster, and Julie Døvle Johansen (2012) studied nematode infections in harbour seals (*Phoca vitulina*) at Sandøy and at Hvaler.

Marine fish are known to be infected by many different parasites including viruses, bacteria, fungi, protozoa, coelenterata, plathelminthes, nemathelminthes, hirudinea and crustacea (Möller & Anders 1986). One group of nemathelminthes (Nematoda) are endoparasites in marine mammals, sea birds and fish (Anderson 2000; Berland 2006). These are thin, elongated, round worms without segmentation. In contrast to most endoparasites, nematodes have a complete digestive tract with mouth, oesophagus, intestine and anus (Berland 2006). There are five main nematode species that are known to infect marine fish in the Norwegian coastal waters: *Anisakis simplex* (commonly called herring worms or whale worms), *Pseudoterranova decipiens* (commonly called cod worms or seal worms), *Contracaecum osculatum, Hysterothylacium aduncum* and *Cucullanus heterochrous* (Anderson 2000; Berland 2006). The first three of these species use fish as transport hosts and reproduce in marine mammals. In contrast, the latter two species have fish as their final hosts (Möller & Anders 1986; Berland 1989).

Nematode larvae, called '*kveis*' in Norwegian, are common in most marine teleost fish and have always been well known to coastal people (Berland 1961, 1989). The larvae of stomach worms are found encapsulated in the liver, mesenteries and flesh. They can be very numerous and are easily spotted (Anderson 2000). This creates a hygienic problem, so nematodes represent serious problems for the fishing industry.

The ecology of the nematodes maturing in marine mammals has been investigated by several students at the University of Oslo. Aspholm (1991) found that the infection of *P.*

decipiens in Atlantic cod (*Gadus morhua*) in the outer Oslofjord decreased with increasing distance from the haulout places. He also observed that *A. simplex* constituted more than 90 % of the stomach worms found in the Oslofjord some of this *A. simplex* even matured in harbour seals. Jensen & Idås (1992) found that there was a negligible occurrence of nematodes in cod fish living in areas with practically no harbour seals. There was also evidence that the abundance level of *A. simplex* had declined in the 1980's. However, Hansen & Malmstrøm (2006) concluded that while the abundance of *P. decipiens* was increasing, *A. simplex* had a decreasing trend. They also made the first record of *C. heterochrous* in the inner Oslofjord and suggested that the lower abundance of nematodes might be connected with changes in populations of first intermediate hosts. Damsgaard Jensen (2009) investigated liver spots and their impact on the general condition of the seals in the outer Oslofjord and at Sandøy. She studied the lungworms *Otostrongylus circulitus*, *Parafilaroides gymnurus* and heartworm *Acanthocheilonema spirocauda*. This was the first recording of these nematodes in Norwegian seals. In the Oslofjord she found further evidence that *A. simplex* had a declining trend and matured in harbour seals.

It is clear from the previous investigations in the Oslofjord that there is a substantial variability in the nematode populations. These parasites have rather complex life cycles involving different invertebrate and vertebrate species as their intermediate and final hosts. As a result the abundance of each species is influenced by many factors. This was demonstrated by the findings of Lähdekorpi (2011) which showed that the number of nematodes per fish was either randomly distributed or over-dispersed. Two factors in particular have a large influence on the stochastic parasitic burden: (1) nematodes with seals as final host are naturally dependent on the distance to the seal skerries (Aspholm *et al*. 1995), and (2) since the worms move up the food chain, a change in the foraging habit or behaviour of fish or seals may significantly influence the nematode abundance.

In their thesis work, Hansen and Malmstrøm (2006) found that flatfish were only infected with nematodes at Torbjørnskjær and in the inner part of the Oslofjord. However, according to local fishermen there was also a substantial infestation on the western side of the outer Oslofjord. My part of the ongoing project at the University of Oslo was therefore to investigate whether there really is a marked difference between the two sides of the outer Oslofjord. Two study areas were chosen, Langøya on the western side and Torbjørnskjær on the eastern side. The study focused on (but was not restricted to) the parasitic infection levels of three flatfish species: American plaice (*Hippoglossoides platessoides*), witch flounder (*Glyptocephalus cynoglossus*) and common dab (*Limanda limanda*). The following questions were raised for my investigation:

1. What is the parasitic burden at Langøya and at Torbjørnskjær?
2. Do different nematode species have preferable hosts at these two sites?
3. Does the number of nematodes per fish deviate from a random distribution (the Poisson distribution) at the two areas?
4. Is the condition of the fish influenced by the nematode burden?

Harbour seals and fish were sampled under the leadership of Morten Bronndal in 2010 and 2012. Professor Emeritus Bjørn Berland from the University of Bergen taught us the techniques for fixing and identifying the nematodes. I was part of a team of three students collecting data at Torbjørnskjær in the outer Oslofjord and at Sandøy on the western coast of Norway. I identified the stomach parasites from the fish and harbour seals and determined the age of the fish (reading otoliths annual rings). However, during our investigation we decided that I should focus on the nematode infections in fish, so I did not perform any analysis of the nematodes found in the harbour seals. My species identification of the seal nematodes is here reported in Appendix VII. These data were given to Døvle Johansen (2012) who should focus on the infection in seals.

1.1 The biology of the nematodes

1.1.1 *Hysterothylacium aduncum* (Rudolphi, 1802)

H. aduncum is the most widespread and abundant nematode in North Atlantic fish (Berland 1961, 2006; Möller & Anders 1986; Andersen 1993; Balbuena *et al*. 1998). In Norwegian waters *H. aduncum* is the only species of the genus *Hysterothylacium* (Berland 1961, 1989; Køie 1993; Balbuena *et al*. 1998; Anderson 2000). It is a "cold" parasite since the third stage larvae occur encapsulated in the fish viscera, and they also mature in the fish.

The life-cycle of *H. aduncum* involves many invertebrates as the first (transport/paratenic) hosts for the young larvae (Figure 1.1). Fish can be either transport hosts when the third-stage larvae are found in the body cavity and viscera, or final hosts when adult worms occur in the digestive tract. Maturation and reproduction occur in a variety of fish species with different foraging patterns. In the Northwest Pacific an herbivorous fish *Siganus fuscescens* has recorded to be a definitive host for *H. aduncum* (Shih & Jeng 2002). Eggs are shed in the faeces of the definite host. The first two moults take place in the egg (Køie 1993; Berland 1998; Anderson 2000). Eggs with developed third stage larvae are taken up by small crustaceans where they invade the haemocoel. Larvae are carried up to larger crustaceans, polychaetes, chaetognats, ctenophores, medusa and fishes through the food chain. In fish, the larvae become encapsulated in the viscera. These larvae are also found in plankton-eating fish such as Atlantic herring and European sprat (*Sprattus sprattus*; Køie 1993; Berland 1989; Klimpel & Rückert 2005).

When the larvae reach a suitable intermediate host it will grow. Berland (1989) assumed that the larvae must reach a certain size or physiological maturity before it can moult twice to become mature. Køie (1993) found that the size of the developing worms seems important in deciding their fate. She found that larvae less than 2 mm do not survive in fish. Larvae 2 – 3 mm in length survive; they penetrate into the fish's body cavity, where they become encapsulated. But larvae having reached 3 mm or more in crustaceans or other invertebrates will, when ingested by their host fish, migrate to the gut. There they grow and moult twice to reach the adult fifth stage. Unlike most parasitic nematodes which are restricted to particular sections of the digestive tract, *H. aduncum* occurs in the entire gut and can move freely throughout the digestive tract (Berland 1998, 2006; Anderson 2000).

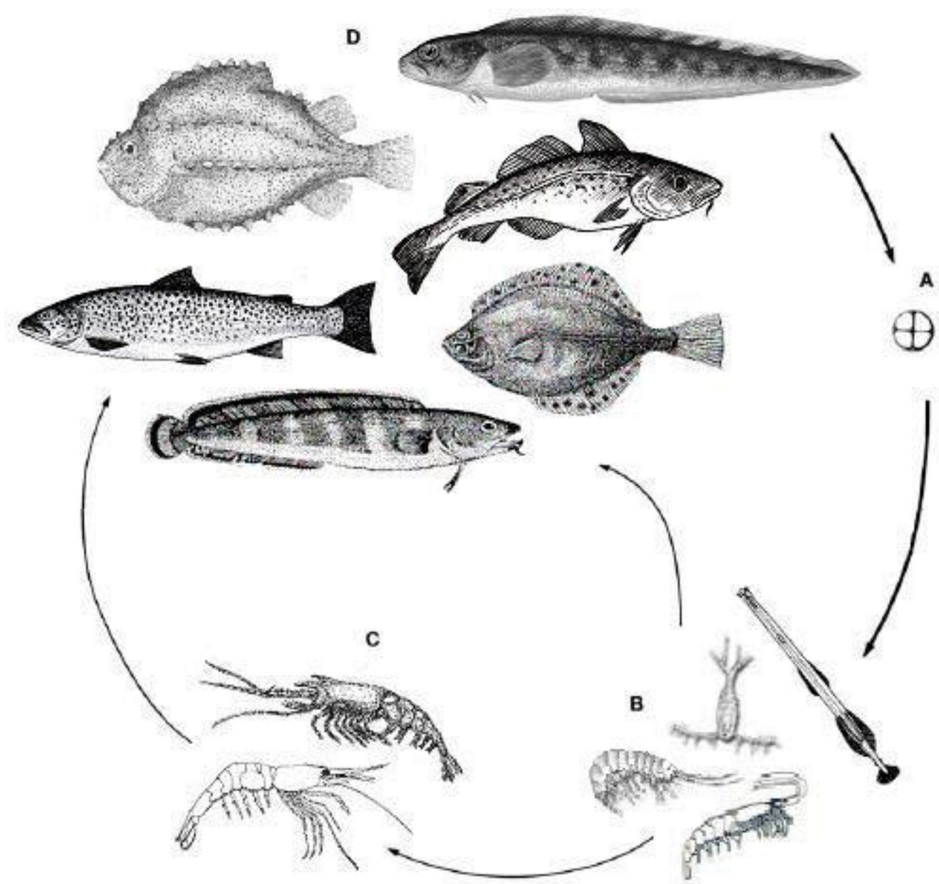

Figure 1.1. Life-cycle of *H. aduncum*. **A** Egg; **B** First transport/paratenic host (crustaceans and other zooplankton); **C** Second transport/paratenic host (larger crustaceans, zooplankton and fish); **D** Final host (fish). Reproduced from Hansen & Malmstrøm (2006)

1.1.2 *Anisakis simplex* (Rudolphi, 1809)

Adult *Anisakis* are parasites in the stomach and intestine of whales primarily, though occasionally seals as well. Their immature stages have been reported in a wide range of marine and anadromous teleosts in cool-temperate and polar waters (Berland 1989;

Anderson 2000). According to Mattiucci & Nascetti (2008) there are nine valid species in this genus. Since the larvae in fish are morphologically indistinguishable, molecular methods are needed for identification (Berland 2006). The nine species include the *A. simplex* species-complex with three sibling species: *A. simplex* (*s.s.*), *A. pegreffii* and *A. simplex* C. Only the first two of them can be found in North East Atlantic and as *A. pegreffii* has only been recorded in the Mediterranean (Mattiucci & Nascetti 2007), all *Anisakis* found in the Oslofjord are classified as *A. simplex* (*s.s.*).

A. simplex is also called herring worm since the development stages follow a pelagic food chain (Figure 1.2) and is especially abundant in Atlantic herring and saithe (*Pollachius virens*: Karl Inne Ugland *pers. comm.*). Eggs are shed in the faeces of the final host. It develops to second stage larva in the sea water. After hatching, the free-swimming larvae are taken up by a pelagic crustacean, generally a Euphausid (the first intermediate host). The larvae invade the haemocoel where they moult into the third stage and grow until they are transferred to various pelagic fish or directly to marine mammals that have been foraging on krill (Berland 1989; Anderson 2000). In fish the larvae become encapsulated in tight flat coils on or in the viscera (Berland 1961). The larvae may be transported upwards in the food chain, so large fish may accumulate enormous numbers of larvae (Berland 1989). In whale stomachs the worm moults twice, matures, mates, reproduces and dies (Berland 2006).

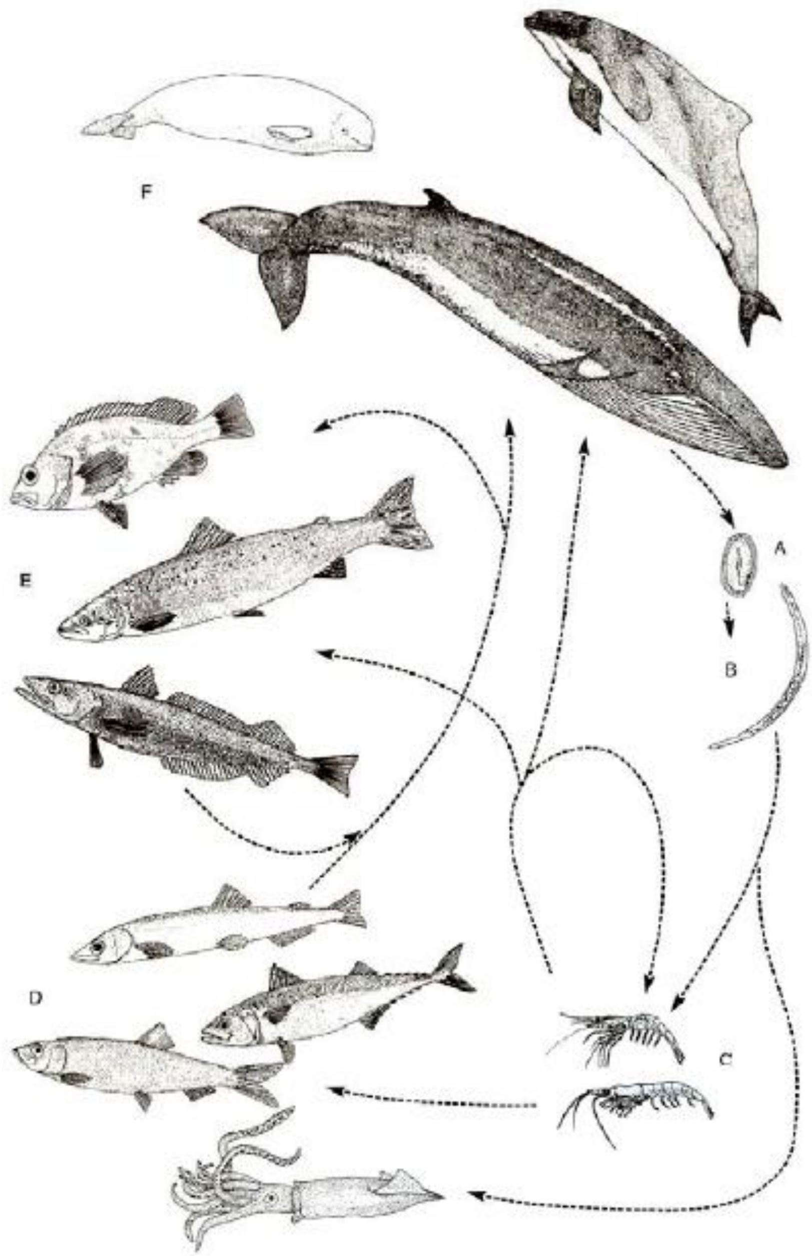

Figure 1.2. Life-cycle of *A. simplex*. **A** Embryonated egg; **B** Free-living second-stage larva; **C** Euphausiid intermediate hosts in which the third stage is attained with marked growth; **D** & **E** various fish and squid paratenic and transport hosts in the food chain of; **F** The definitive cetacean host. Reproduced from Anderson (2000)

1.1.3 *Pseudoterranova decipiens* (Krabbe, 1878)

Adult *Pseudoterranova* are parasites in the stomach and intestine of seals primarily. Immature stages have been reported in a wide range of marine benthic fish in temperate and polar regions of the world (Berland 1989; Anderson 2000). The genus

Pseudoterranova consists of at least seven species (Nadler *et al*. 2005), of which five species, including *P. decipiens*, have a cosmopolitan distribution (Berland 2006). Molecular methods have revealed that the specie *P. decipiens* is actually a complex of four species: *P. decipiens*, *P. krabbei*, *P. bulbosa* and *P. azarasi* (Nadler *et al*. 2005). The first three have been reported from the North Atlantic (Paggi *et al*. 1991; Mattiucci & Nascetti 2008). *P. bulbosa* matures in the bearded seal (*Erignathus barbatus*) in the Pacific, but its larva occurs in the liver of American plaice in northern Norwegian waters (Bristow & Berland 1992). *P. krabbei* matures in the grey seal (*Halichoerus grypus*; Berland 1961, 2006). *P. decipiens* (*s.s.*) matures mainly in the harbour seal. Therefore all *Pseudoterranova* observed in the Oslofjord is classified as *P. decipiens* (*s.s.*).

The life-cycle of *P. decipiens* involves several hosts (Figure 1.3). The eggs sink to the bottom after they have been shed in seal faeces. Hatched second stage larvae are ingested by the first intermediate host which usually is an isopode, benthic harpacticoide or cyclopoide copepode, or a polychaete (McClelland 1990). The larvae are then transmitted to larger invertebrate or fish hosts. Small fish become infected after feeding on benthic invertebrates. After ingestion, the yellow-brown larvae bore into the dorsal somatic muscle of the fish where it becomes encapsulated. Cod-fish, flatfish and sculpins are important transport/paratenic hosts. Since cod-fish tend to be highly infected near colonies of grey seals, *P. decipiens* is also called cod worm. When the fish is consumed by a seal the larvae start to grow, completing their third and fourth moults to reach the sexually mature fifth stage.

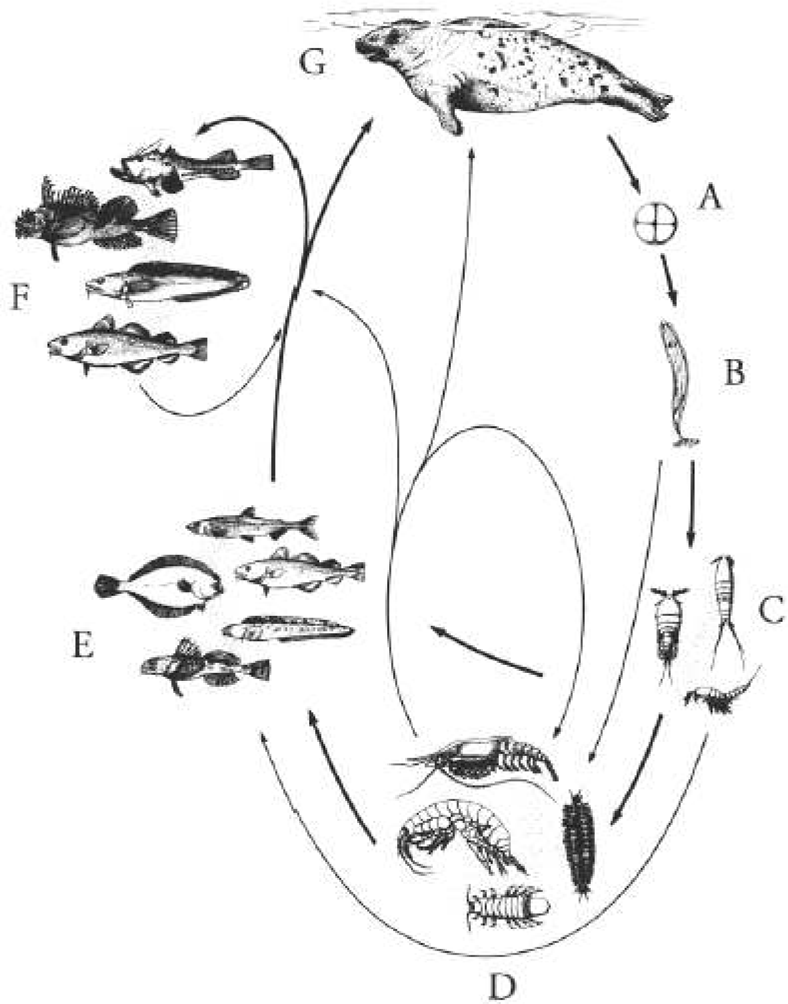

Figure 1.3. Life cycle of *P. decipiens* and *C. osculatum*. **A** Egg; **B** Free-living second stage larvae; **C** Small benthic copepods (intermediate hosts); **D** Larger benthic macroinvertebrates (mysids, amphipods, isopods and errant polychaetes; transport hosts); **E** Primary benthophagous fish (transport/paratenic hosts); **F** Secondary demersal piscivorous fish (transport/paratenic hosts); **G** Third and fourth moults and development to adult in stomach of a pinniped final host. Reproduced from McClelland *et al*. (1990)

1.1.4 *Contracaecum osculatum* (Rudolphi, 1802)

There are 10 species in the genus *Contracaecum*. Five subspecies of *C. osculatum* are recorded in the northern hemisphere, three of which are found in several species of seals and fish in the Atlantic Arctic-Boreal region (Anderson 2000; Berland 2006; Mattiucci & Nascetti 2007, 2008). These species have similar morphology and can only be distinguished by molecular methods (Berland 1989, 2006). All the larvae in the outer Oslofjord are classified as *C. osculatum*.

Most species of the genus *Contracaecum* are found in aquatic environments (Berland 1989, 2006). Seabirds function as their transport or final hosts. The exception is *C. osculatum* which has a life cycle almost equal to *P. decipiens* (Køie & Fagerholm 1995; Anderson 2000; Figure 1.3). In the waters around Greenland and Iceland, *Contracaecum* larvae are very abundant in several fish species. Sporadically it also occurs in fish along the Norwegian coast (Berland 1989, 2006).

The life-cycle of *C. osculatum* is described by Berland (1989, 2006) and Anderson (2000). Thin-shelled, unembryonated eggs are passed out in the faeces of the warm-blooded host. In water, eggs embryonate and moult to second stage larvae. After hatching in the water they are ingested by the first invertebrate host, usually copepods. In this host they move to the haemocoel where they grow until a vertebrate host consumes the invertebrate host. Once in the fish the larvae become encapsulated in the viscera and undergo substantial growth. When a marine mammal or bird eats the infected fish the worms grow, moulting twice and reach maturity, mate, reproduce and die.

1.1.5 *Cuccullanus heterochrous* (Rudolphi, 1802)

Parasites of the family Cucullanidae are intestinal parasites of fish and occasionally turtles. The family is characterized by a highly developed buccal cavity formed from the oesophagus (Berland 1970). Details of the development and transmission of the cucullanids are still not well known (Anderson 2000). Two species are found in North-East Atlantic: a gadiform fish parasite *C. cirratus* and flatfish parasite *C. heterochrous* (Køie 2000a; 2000b). Accordingly all the individuals of *Cucullanus* in American plaice are classified as *C. heterochrous*.

The life-cycle of *C. heterochrous* is described by Køie (2000a) and shown below in Figure 1.4. The eggs, which are discharged in fish faeces, develop into embryos, but do not hatch until a transport host has eaten them. In the egg, larvae undergo three development stages, so it is the third larval stage which hatches (Køie 2000b). In the North Atlantic it seems that only polychaetes, mainly *Nereis diversicolor*, are infected with larvae of *C. heterochrous*. The larvae grow in the polychaete, but do not develop any further. The life cycle is completed when the polychaete is eaten by a flatfish. After ingestion, the larva develops into its fourth and fifth sexually mature stage (Køie 2000a). *C. heterochrous* lives in the stomach and intestines of the fish where they eat both the stomach contents and the abdominal wall (mucosa; Anderson 2000). European flounder (*Platichthys flesus*) is the main final host for *C. heterochrous* (Køie 2000a).

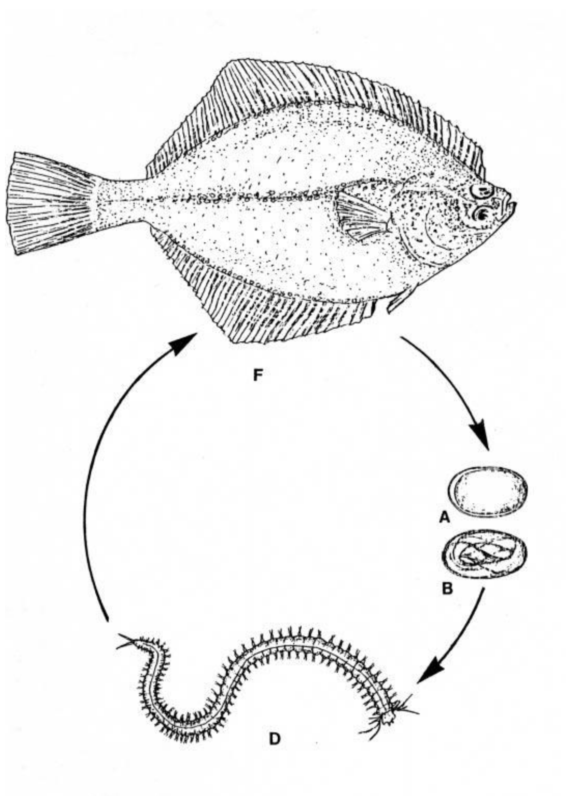

Figure 1.4. The life-cycle of *C. heterochrous*. **A** Fertilized newly shed egg; **B** Embryonated, infective egg; **D** Intermediate host, plychaetes; **F** Final host. Reproduced and modified from Køie (2000a)

1.1.6 Fish

In this investigation I focused on three species of flatfish: American plaice (Fabricius, 1780), witch flounder, (Linnaeus, 1758) and common dab (Linnaeus, 1758).

These three benthic species live on soft bottoms. Witch flounder has the deepest vertical distribution (down to 1460 m) and common dab has the shallowest distribution (down to 150 m). American plaice is generally found between 10 and 400 m. All three species have a variable diet, but on average their food preferences are rather similar: various kinds of crustaceans, molluscs, worms, brittle stars and even a few small fish (Cargnelli *et al*. 1999; Johnson 2004).

2 Materials and Methods

2.1 Study area

2.1.1 Oslofjord

The Oslofjord is 110 km long and located in the south eastern part of Norway (Figure 2.1). It ranges from 59°01' N to 59°55' N and from 10°15' E to 11°10' E (Andersen *et al.* 1970). Five main sections may roughly be identified: (1) The outer Oslofjord from Færder to Horten/Moss, (2) the central basin, Breiangen, from north of Horten to Drøbak, (3) the Drøbak Sound, (4) the inner Oslofjord, including the waters north of Håøya, the Vestfjord and the Bunnefjord and (5) the Drammenfjord, which forms a separate system, connected to the western area of Breiangen. Only the first two parts were investigated in this project.

According to Gade (1963, 1970) and Andersen *et al*. (1970) the outer Oslofjord is separated from Skagerrak by a ridge that is located from the Hvaler islands in the east to Tjøme in the west with a sill depth of 100 – 120 m. This threshold represents the first barrier for water transport in and out of the fjord. Inside the ridge, the fjord deepens to more than 360 m. Breiangen, the widest section of Oslofjord, reaches depths of more than 200 m. It is separated from the outer Oslofjord by a narrow sound between Jeløy and Horten and a ridge of about 110 m depth. It also connects with the Drammenfjord to its west via a 10 m deep sill and with the inner Oslofjord to its east via the Drøbak Sound, which has a maximum depth of 19.5 m.

Samples for this study were collected at two sites of the outer Oslofjord: in an area around Langøya and in an area around Torbjørnskjær. These areas were selected for practical reasons. They are both trawling locations for fishermen. The decision to focus on flatfish and the nematode *H. aduncum* was made after the initial days in the laboratory. Differences in nematode infection levels between these two areas in flatfish were already seen at this early stage.

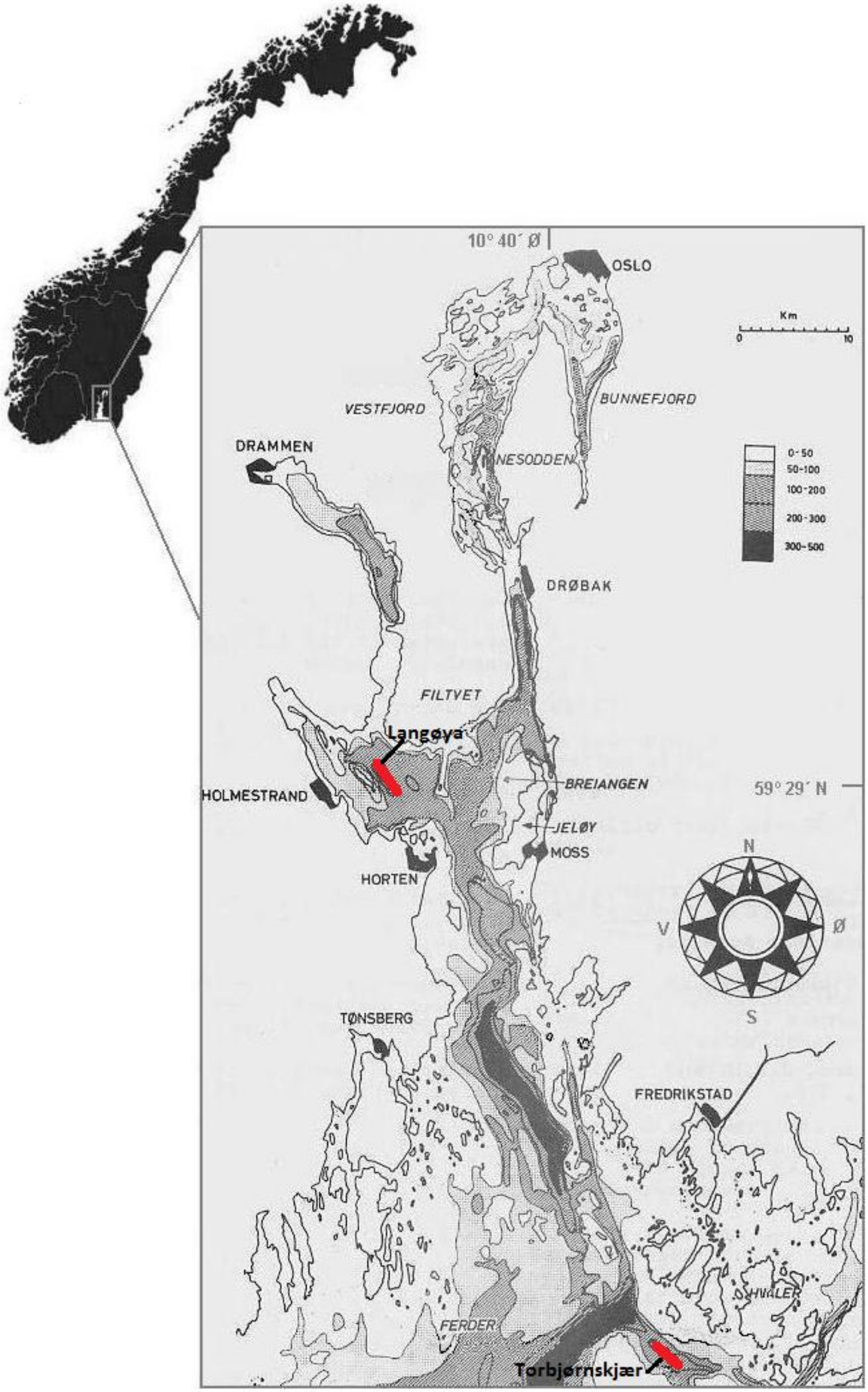

Figure 2.1. Bathymetric map of the Oslofjord with two study areas. Reproduced and modified from Andersen *et al*. (1970)

2.1.2 Torbjørnskjær

The Torbjørnskjær archipelago (Figure 2.1) is based on a plateau situated on the east side of the outer Oslofjord. This plateau is about 2 km wide in the south, Heia skerry, narrowing to about 1 km in the north, near Torbjørnskjær lighthouse. Approximately 50 % of the area is shallower than 20 m and there are a number of gorges and depressions that cut into the plateau in various directions (Aspholm 1991). Between the Torbjørnskjær archipelago and the mainland is a 10 km wide stretch of open sea that contains a channel with a depth declining from 150 m in the south to 250 m in the northern part (Aspholm *et al.* 1995).

The Torbjørnskjær archipelago is highly exposed, with the formation of waves up to 2 m by northwestern and southeastern winds of low strengths. Water masses with low salinity are prevailing in the upper layer due to the influence from the Glomma River, which has an average flow of 680 m^3/s as measured at the Solberg power plant. The water flow is greatest in May and June when the major floods occur in connection with the melting snow. Some years there may also be relatively large flows associated with the autumn rains (Pettersson 2002). Since there are no significant thresholds[1] to prevent the deep-water replacement between Skagerrak and outer Oslofjord the deep water is almost homogenous having quite uniform salinities of 33 – 34 ‰ (Gade 1968; Andersen *et al*. 1970; Pederstad *et al*. 1993; Lekve *et al*. 1999).

Fish were collected by trawling between August 2010 and October 2011 at 90 – 100 m on the east side of Heia Island (Figure 2.1).

2.1.3 Langøya

Langøya is situated on the west side of Breiangen (Figure 2.1) and ranges between 100 and 200 m deep. In this area the surface water is highly influenced by inflow from the Drammen River and variation in precipitation. The annual discharge of the Drammen

[1] There are no significant thresholds for this study since the trawling was held above the ridge.

River is reported to about $5.5*10^9$ m^3, with seasonal variation spanning from 22 % in January to 309 % in May of the yearly 30 day-average (Gade 1968). The deeper layer is almost homogenous due to water exchange with the outer Oslofjord (Andersen *et al*. 1970; Gade 1970; Lekve *et al*. 1999; Baalsrud & Magnusson 2002).

Fish were collected by trawling between August 2011 and February 2012 at depths between 80 and 90 m in the eastern and northern areas around Langøya Island (Figure 2.1).

2.2 Fish sampling

In the period from August 2010 to March 2012 local fishermen brought in 361 fish from trawling in the outer Oslofjord. Depending on the bottom topography all catches were obtained at depths of 80 to 100 m. In the laboratory the weight was measured to the nearest gram and the fork length (Figure 2.2) was measured to the nearest millimetre. The sex of the fish was determined by examining the gonads. While mature individuals have clearly recognisable gonads (males having sperm and females having visible eggs), it is a combination of form and colour that separates the sexes among immature individuals (the female gonads being more dark pink or even red in colour, while males having almost white gonads). Age determination was based on the largest otoliths, sagitta, as explained below. All nematodes were removed from the digestive tract, liver and body cavity (Figure 2.3).

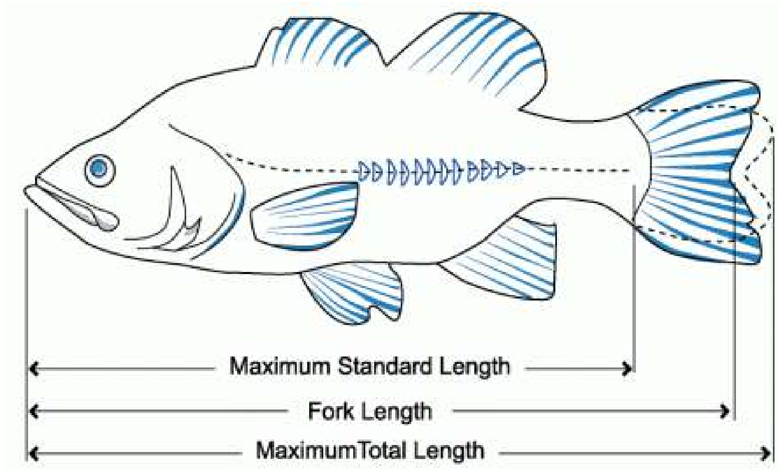

Figure 2.2. Measuring fish length. Reproduced form FishXing (http://www.fsl.orst.edu/geowater/FX3/help/FX3_Help.html#9_Fish_Performance/Measures_of_Fish_Length.htm)

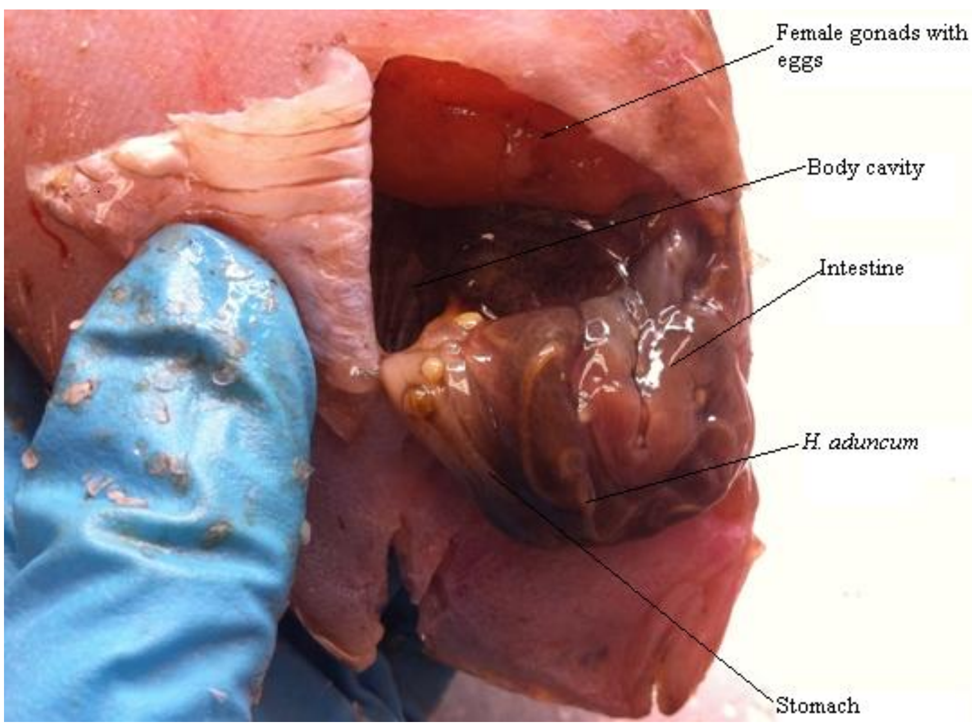

Figure 2.3. Dissection of the fish, liver is placed on the other side of the stomach in the picture. Taken by Karin Raamat

2.2.1 Age determination

Teleost fish have three pairs of otoliths called lapillus, asteriscus and sagitta, which lie in three cranial cavities filled with endolymph within the scull. These small bones are composed primarily of crystallized calcium carbonate in the form of aragonite and of otoline, a fibrous, collagen-like protein (Degens *et al*. 1969; Campana 1999). In temperate areas the deposition of inorganic matter into otoliths growth varies throughout the year due to large changes in water temperature and availability of food. This seasonal variation induces formation of two different annual growth rings or annulae. The two types of annulae are: a wide transparent zone formed during times of good nutrition, which is comprised of inorganic compounds; and a rather narrow opaque zone, formed during the season with little prey availability, which contains both calcium compounds and organic matter (Dannevig 1956; Christensen 1964; Morales-Nin 1992; Figure 2.4). These alternating zones form year rings which may be used for age determination of the fish. It is most usual to count the rings in sagitta since this is the largest otoliths. Therefore the terms ‘otolith’ and ‘sagitta’ are frequently treated as synonymous, and I will follow this praxis here.

Figure 2.4. Reading the year rings from a sagitta otoliths. Reproduced from Lähdekorpi (2011)

To be used for age estimation the otoliths must first be cleaned in water and, after drying, stored into small paper envelopes. Counting the annual zones may then be performed with a light microscope. In some fish species (*Gadus morhua, Melanogrammus aeglefinus, Merlangius merlangus, Merluccius merluccius, Pollachius pollachius,*

Pollachius virens, Trisopterus esmarkii) the otoliths were so thick that the zones were not readily visible. It is then necessary to burn the otoliths carefully for two minutes (I used a Bohning alcohol burner) and afterwards crack the otoliths along the mid-line using a scalpel (Christensen 1964; Asbjørn Vøllestad *pers. comm.*). Since the fish were caught from late summer to late winter, the proper age would be the number of growth zones plus 0.5 years. However since an accuracy of a half year is not needed for the analysis of the nematode community, the age was simply determined as the number of growth zones in the otoliths.

2.2.2 Nematode identification

I learned the methods for preparing and identifying the nematodes from Professor Emeritus Bjørn Berland from the University of Bergen. All nematodes were fixed in Berland's fluid, which consists of 1 part of 40 % formalin and 19 parts of glacial acetic acid (Berland 1984). This fluid kills nematodes very quickly. They uncoil and increase in length. However, the great advantage with Berland's fluid is that the nematodes become so transparent that identification and handling is easy. After a few minutes the nematodes must be transferred to 75 % ethanol for preservation.

In order to get the clearly visible internal organs, different colouring liquids with different refractive indices (RI) were used. According to Berland (1984, 2005) there are three different types of colouring liquids that are useful for identifying nematodes. For the smallest nematodes, the best choice is lacto phenol (lactic acid, phenol, water and glycerol with the ratio of 1:1:1:1; RI = 1.44). For the medium size nematodes, the best choice is glycerol – benzyl alcohol (with a ratio 1:1; RI = 1.49). For the large individuals, the best choice is benzyl alcohol (RI = 1.54).

In the laboratory the nematodes were first placed in acetic acid to make the tissue more permeable for the colouring liquid. After one to thirty minutes (depending on the size of the nematode) they were placed on the microscopy glass with the colouring liquid.

Having experimented with the three different colouring liquids in the laboratory I concluded that lacto phenol was sufficient the purposes of this study, even for the largest nematodes. After identification the nematodes were cleansed of the colouring liquid in acetic acid and the length was measured to the nearest millimetre. To avoid the error that is caused by the Berland's fluid all the nematodes were handled identically for the length measurements**.** Finally, the nematodes were brought back to 75 % ethanol.

Many characteristics are used for identifying nematodes. Overall, the larvae in fish have a relative simple morphology since they possess a boring tooth and lack lips. Nematodes maturing in marine mammals (genera *Contracaecum*, *Anisakis* and *Pseudoterranova*) have no visible reproductive organs. In contrast, the morphological characters of the digestive tract, shape of oesophagus and ventricle, presence or absence of ventricular appendix and intestinal caecum, are similar to those of the adults. The classification of these worms is based on the morphology of the sexually mature adults: head and lip structure, oesophagus and intestine, excretory system including position of excretory pore, and reproductive system, with emphasis on male tail with its papillae and spicules. More detailed descriptions about the species and genera which are central in this investigation are given in the subsequent sections (See Table 2.1 for an overview).

2.2.2.1 Identification of *Hysterothylacium aduncum*

The morphology and anatomy of *H. aduncum* are described in detail by Berland (1961, 1998) and Anderson (2000). While most parasitic nematodes are restricted to particular sections of the digestive tract, the adult *H. aduncum* occurs throughout the entire gut. This is possible because of the cervical wings, alae, which permit them to swim freely through the length of the digestive tract. They are never attached to the mucosa lining in the gut. However, in dead fish, *H. aduncum* frequently leave the host through the mouth and gills and those in the intestine leave through the anus (Berland 2006; Figure 2.5). In comparison to the adult specimens in this genus, the third stage larvae are found mainly in the body cavity and viscera. Since the *H. aduncum* matures in fish, all the stages L3, L4 and sexually mature L5 are found in fish.

Figure 2.5. Adult *H. aduncum* leaving the dead fish host through the gills and mouth. Taken by Karin Raamat

The most typical character for *H. aduncum* is the conical “cactus tail” (Figure 2.6) which is present in the L4 and L5 stage. In the third stage the body tapers gradually to the end as a blunt, thin tail bearing a long spine, cactus tail can be seen under the cuticle (Berland 1961; Weerasooriya *et al*. 1986). Other distinguishable traits in the L3, L4 and L5 stages are (1) a rather long oesophagus with a posterior ventricular appendix and (2) anterior intestinal caecum. In contrast to the other species, the *H. aduncum* larvae have the excretory pore at the level of the nerve ring. In the third stage larvae the head is provided with four small elevations and a boring tooth situated ventral to the mouth opening. During the fourth and fifth stage, *H. aduncum* has three lips with 3 semi-interlabia (Berland 1961). Males have equal spicules and a number of caudal papillae.

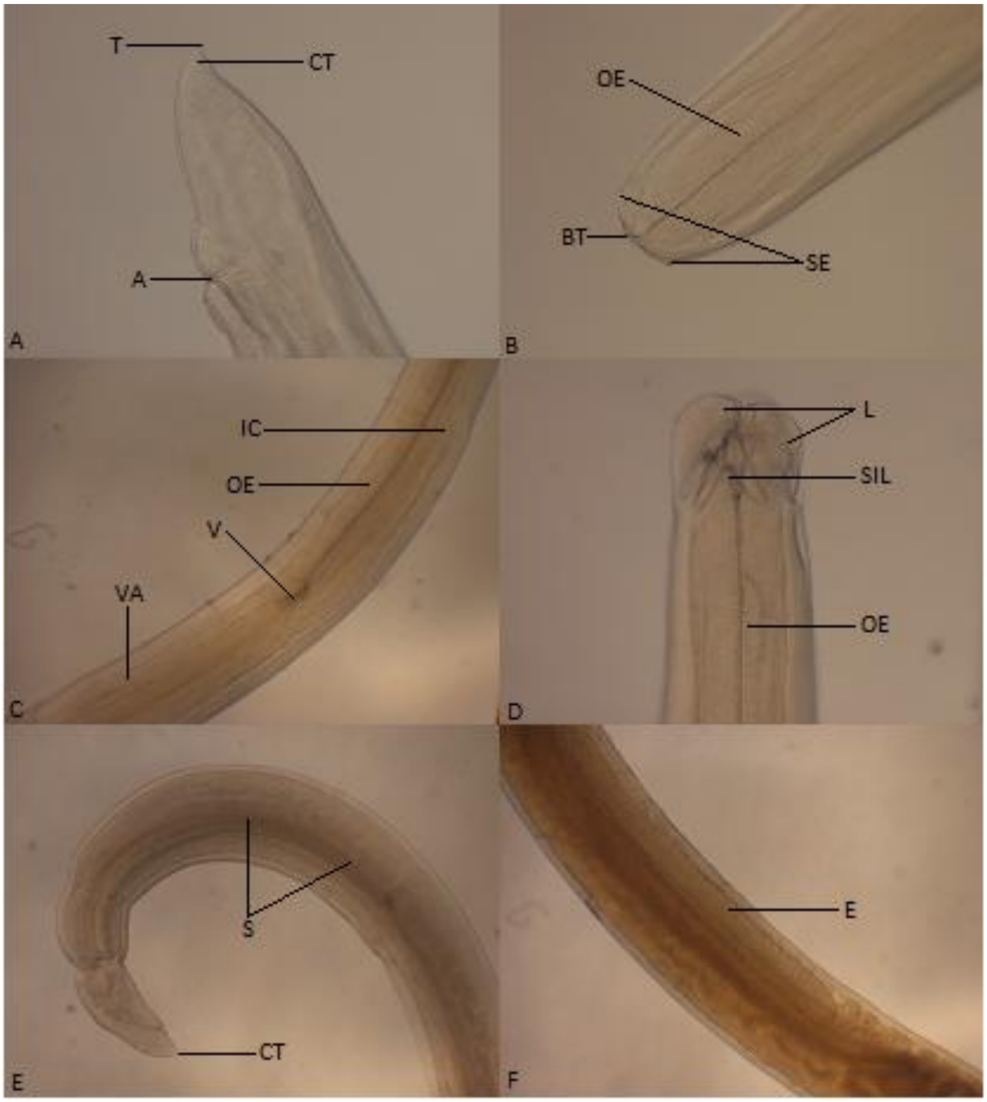

Figure 2.6. Various developmental stages of *H. aduncum*. **A** Posterior part of third stage larva with cactus tail (CT) that is seen under the cuticle, tail (T) and anus (A), 20 x magnification; **B** Anterior part of third stage larva with boring tooth (BT), oesophagus (OE) and two of four visible small elevations (SE), 20 x magnification; **C** Anterior part of fourth stage larva, showing oesophagus (OE) and opposed ventricular appendix (VA) and anterior intestinal caecum (IC), 4 x magnification; **D** Head of an adult with two visible labia (L), one visible semi-interlabia (SIL) and the beginning of oesophagus (OE), 10 x magnification; **E** Tail of an adult male with characteristic cactus tail (CT) and spicules (S), 4 x magnification; **F** Female adult with eggs (E). Taken by Karin Raamat

2.2.2.2 Identification of *Contracaecum osculatum*

Anderson (2000) provided a detailed description of the morphology and anatomy of *C. osculatum*. These nematodes have their third stage in fish and mature in the stomachs of seals. The third stage is mainly found encapsulated in the viscera of the fish.

Like *H. aduncum*, *C. osculatum* have a rather long oesophagus with a short ventricle, anterior intestinal caecum and posterior ventricular appendix (Figure 2.7). However, the tail of these worms narrows conically and is lacking a spine at the top (i.e. no cactus tail as in *H. aduncum*). The excretory organ is a long band ventral to the anterior intestine and has a pore at the level of the boring tooth. In the third stage the boring tooth is located ventrally and projected inwards (Weerasooriya *et al*. 1986). Adult specimens have three lips that are squarer compared to the other species having the anterior corners drawn out. Between the lips, well-developed interlabia are present. In adult males, the spicules are long and nearly equal.

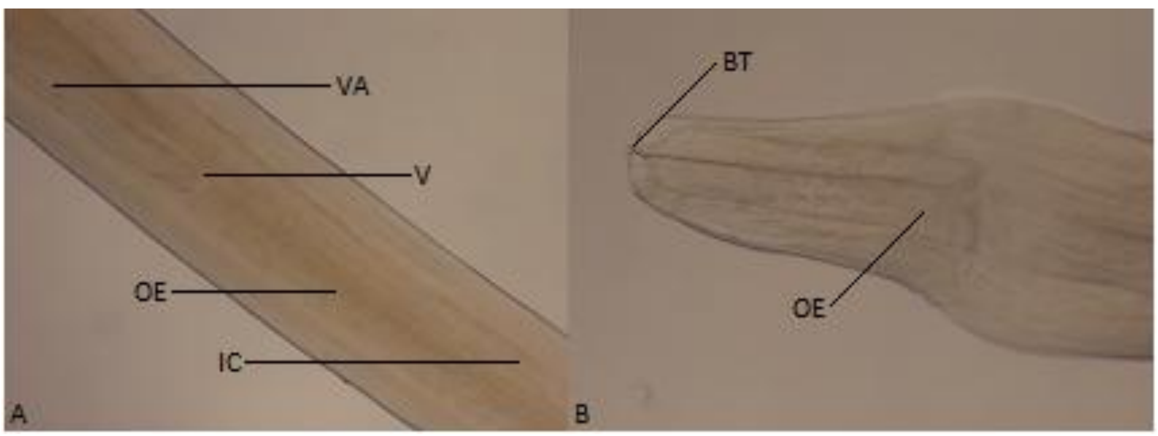

Figure 2.7. Third stage *C. osculatum* larva. **A** Anterior part of the body with ventricle (V), oesophagus (OE) ventricular appendix (VA) and intestinal caecum (IC), 10 x magnification; **B** The head with boring tooth (BT) and oesophagus (OE), 10 x magnification. Taken by Karin Raamat

2.2.2.3 Identification of *Anisakis simplex*

Berland (1961, 2006) and Anderson (2000) give a detailed description of the morphology and anatomy of *A. simplex*. This species has its third stage in fish and matures in the stomachs of pinnipeds and cetaceans. Larvae of *A. simplex* form tight coils with diameter 3 – 4 mm in the viscera, on the surface of the liver or even in the belly flaps.

A. simplex is characterized by a very long oesophagus with a large glandural ventricle that is S-shaped in adults (Figure 2.8). Intestinal caecum and ventricular appendix are lacking. A straight or weakly curved small pointy spine is present at the top of the tail in the third stage (Weerasooriya *et al*. 1986), and a triangular ventral boring tooth is directed outward. The excretory organ is well developed with a pore ventrally below the boring tooth. Compared to the other genera the transversal striation on the cuticle is much more marked and it appears serrated in optical sections. *A. simplex* larvae can also be distinguished from other species by the very thick muscle layer which is clearly visible under a microscope. In the fourth and fifth stage the developed lips are "broad shouldered" and no interlabia are present. Adult males have unequal spicules; the right one being the shorter.

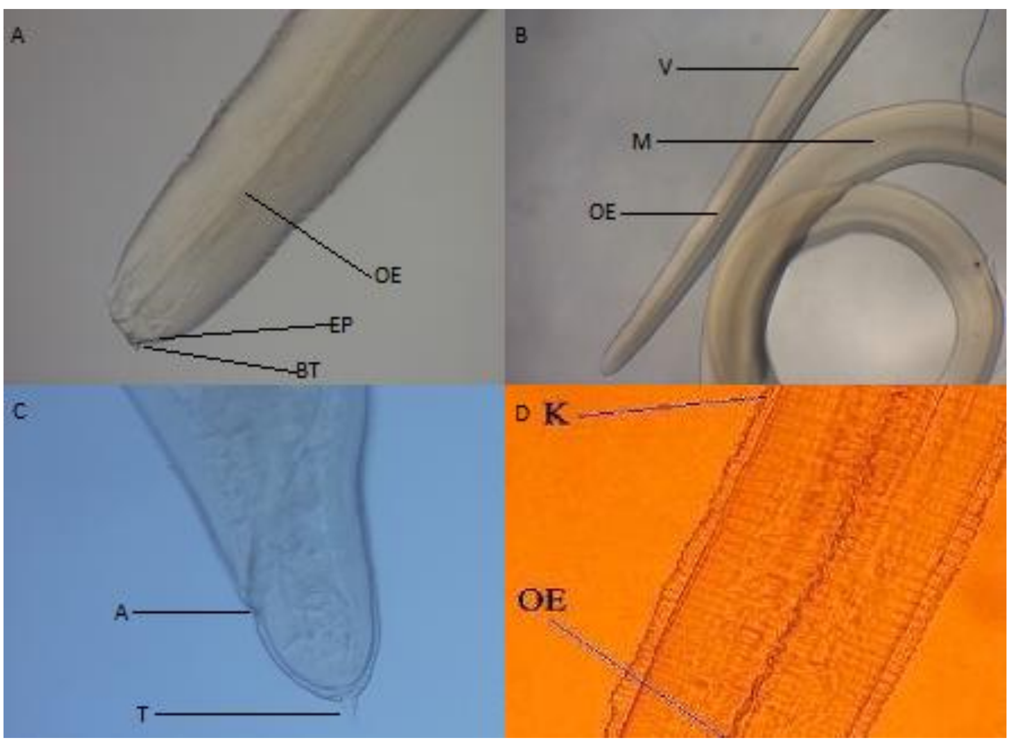

Figure 2.8. Third stage larva of *A. simplex* **A** Head with the boring tooth (BT), excretory pore (EP) and oesophagus (OE), 20 x magnification; **B** Spirally coiled larva with marked ventricle (V), long and thin oesophagus (OE) and thick muscle layer (M), 4 x magnification; **C** The posterior end of the body with the tail (T) and anus (A), 20 x magnification; **D** Fourth stage larva with striated cuticle of the body (K) and oesophagus (OE), 20 x magnification. A, B and C taken by Karin Raamat; D reproduced from Damsgaard Jensen (2009)

2.2.2.4 Identification of *Pseudoterranova decipiens*

Berland (1961) and Anderson (2000) give a detailed description of the morphology and anatomy of *P. decipiens*. This species has its third larval stage in fish and matures in the stomachs of pinnipeds. *P. decipiens* larvae are yellowish-brown in colour and are most often found in the dorsal part of the fish flesh where they are irregularly coiled.

P. decipiens have a characteristic short and stout oesophagus and a large glandular ventricle that is not bent. While the ventricular appendix is absent, an intestinal caecum is present and located dorsal to the ventricle. Compared to *A. simplex*, the striation of the cuticle is much finer, giving the body an almost smooth look. The excretory organ is well developed with an excretory pore ventrally below the boring tooth (Figure 2.9). *P. decipiens* have a rather long pointy spine in the end of the tail (Weerasooriya *et al*. 1986). Similar to *A. simplex*, the boring tooth is ventrally positioned, triangular in shape and directed outwards. In the fourth and the fifth stage, the lips are "broad shouldered" and no interlabia are present. In males the spicules are equal in length and longer than in *A. simplex*.

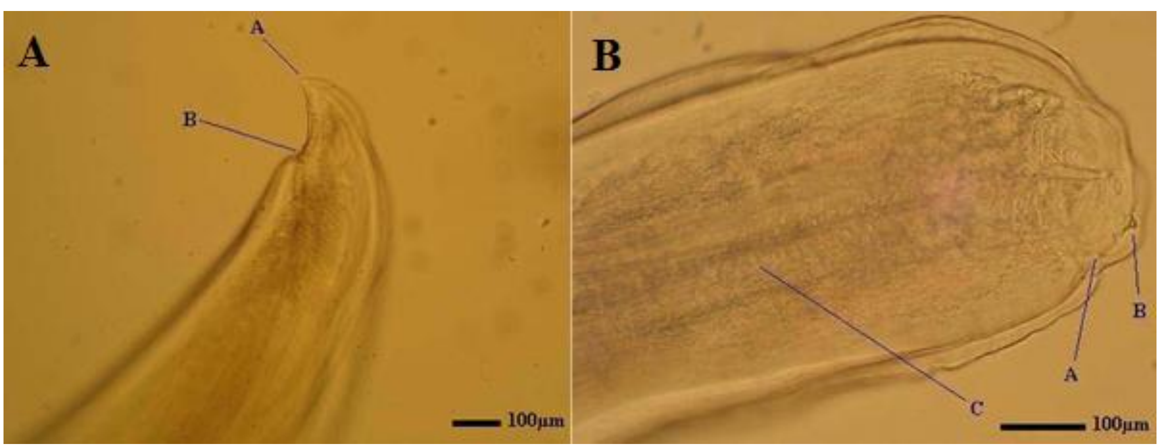

Figure 2.9. Third stage *P. decipiens* larva **A** The curved tail from anus (B) to the tip of the tail (A); **B** The head with the boring tooth (B) oesophagus (C) and the excretory pore (A). Reproduced from Hansen and Malmstrøm (2006)

Table 2.1. Summary of the characteristics of the four nematode genera.

	Hysterothylacium	*Contracaecum*	*Anisakis*	*Pseudoterranova*
Oesophagus	Long	Long	Long	Short and stout
Ventricle	Small	Small	Large S-shaped	Large
Intestinal caecum	Present	Present	Absent	Present
Ventricular appendix	Present	Present	Absent	Absent
Boring tooth	Ventral, four elevations	Ventral, inwards	Ventral, outwards	Ventral, outwards
Tail	"Cactus tail"	No spine	Shorter spine	Longer spine
Cuticle	–	Folds behind the head	Pronounced striation	Smoother look
Excretory pore	By the nerve ring	By the boring tooth	By the boring tooth	By the boring tooth
Lips	Semi-interlabia	Interlabia	Broad shouldered no interlabia	Broad shouldered no interlabia
Spicules	Long, equal	Long, equal	Unequal, short	Long, equal

2.3 Statistical methods

2.3.1 Characterization of infection rate

Margolis *et al*. (1982) recommended the following standard terminology for describing the infestation rate of nematodes in fish. Prevalence is defined as the fraction of infected fish, that is, the number of fish containing at least one parasite divided by the total number of fish investigated. Prevalence is usually given as the percentage of infected fish. Abundance is defined as the average number of nematodes per investigated fish, and obtained by dividing the total number of parasites by the total number of investigated fish. Intensity is defined as the average number of nematodes per infested fish and obtained by dividing the total number of parasites by the total number of fish found to have at least one parasite.

An ordinary T-test using Microsoft Office Excel 2007 was applied to analyse the differences in nematode length. The prevalences were analysed with Chi-Square tests on Microsoft Office Excel 2007. In samples providing 4 or more individuals per category, comparison of abundances were performed with the Mann-Whitney U-tests in SPSS

Statistics 17.0. For samples containing fewer individuals the differences in prevalences were checked with the G-test/Likelihood Ratio test in SPSS Statistics 17.0. All intensities were tested with the same statistical program (G-test/Likelihood Ratio test in SPSS).

2.3.2 Condition factor

According to Williams (2000) the well-being of fish is best described by the condition factor, which is defined as $K = 100\ W/L^3$ where W is total body weight (g) and L is the total length (cm; Ricker 1975). It is therefore of interest to investigate whether there was a relationship between the number of nematodes and the condition of the fish.

3 Results

The samples in the outer Oslofjord contained 361 individuals from 15 different species, of which 136 fish from 12 species were infected with nematode parasites (Appendix II). A complete list of the examined individuals is given in Appendix I. The species composition was markedly different at the two sites (Figure 3.1; Appendix III). On the western side American plaice constituted 76 % (116 ind.) and witch flounder 11 % (17 ind.). The remaining 6 species: common dab, European flounder, Norway pout (*Trisopterus esmarkii*), European hake (*Merluccius merluccius*), starry ray (*Amblyraja radiata*), rabbit fish (*Chimaera monstrosa*) occurred between 1 and 4 % (1 – 6 ind.). On the eastern side the most common species were almost equally represented: common dab 21 % (41 ind.), European plaice (*Pleuronectes platessa*) 16 % (34 ind.), whiting (*Merlangius merlangus*) 15 % (32 ind.), American plaice 14 % (30 ind.) and Atlantic cod 14 % (30 ind.). All the remaining species: witch flounder, shorthorn sculpin, European hake, haddock (*Melanogrammus aeglefinus*), goldsinny-wrasse (*Ctenolabrus rupestris*), grey gurnard (*Eutrigla gurnardus*) occurred between 0 and 9 % (1 – 18 ind.).

Due to their larger abundances in the two sampling areas, site comparison was predominantly based on American plaice, witch flounder and common dab (Figure 3.1). Of these three species 100 of 213 individuals were infected with nematodes (Appendix II). Data from the remaining species were used as supplementary information.

Since *P. decipiens* and *C. heterochrous* were only found in one individual at the eastern site and three individuals at the western site, these species were not included in the main analysis.

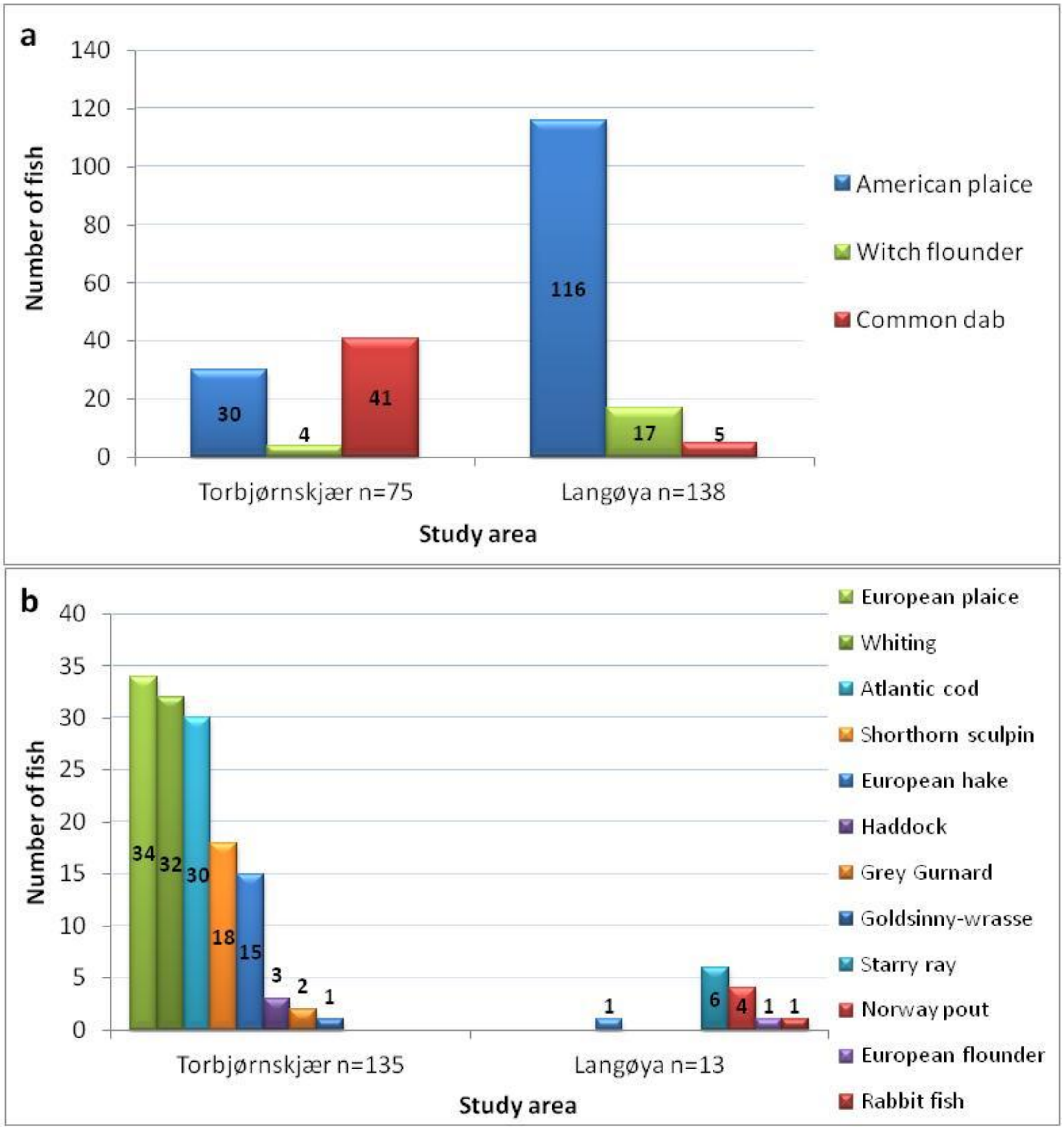

Figure 3.1. Number of fish sampled at Torbjørnskjær and at Langøya: **A** American plaice, witch flounder and common dab; **B** The remaining fish species. The number of sampled fish (n) is given for each species at both study sites.

3.1 Infestation rate

3.1.1 Prevalence

At Langøya the percetance of infected fish was about two times higher than at Torbjørnskjær and the prevalence differed significantly for all nematode species. On the western side *H. aduncum* was responsible for the largest infection of fish, on the eastern side it was *C. osculatum*. American plaice had a relatively high prevalence at

both locations. Witch flounder was only infected at Langøya, mainly with *H. aduncum*. Common dab had a high prevalence at Langøya and rather low at Torbjørnskjær. There might be a sampling error for the last two flatfish species due to small sample sizes.

The prevalence at Langøya was about twice as high as at Torbjørnskjær, 55 % and 25 % respectively (Appendix II). At the western site 83 fish out of 151 were infected with stomach nematodes while at the eastern site only 53 out of 210 were. This was a significant difference (Chi-Square test, df = 1, P < 0.001). At Langøya the prevalence ranking of the nematodes was *H. aduncum* (41.1 %), *C. osculatum* (21.9 %), *A. simplex* (2.6 %); compared to that of Torbjørnskjær, which was *C. osculatum* (11 %), *H. aduncum* (9.5 %) and *A. simplex* (8.6 %). The number of infected fish differed significantly in all three nematode species (Chi-Square test, df = 1, P < 0.001 for *H. aduncum*, P = 0.005 for *C. osculatum* and P = 0.020 for *A. simplex*).

Of the three flatfishes American plaice had a relatively high prevalence at both locations: 55 % at Langøya and 53 % at Torbjørnskjær (Table 3.1). At the western site 64 out of 116 fish were infected with stomach nematodes, while at the eastern site 16 out of 30 were infected (Appendix II). However this was not a significant difference (Chi-Square test, df = 1, P = 0.857). At Langøya 44 % of this fish species was infected with *H. aduncum*, 22 % with *C. osculatum* and none with *A. simplex*. At Torbjørnskjær the prevalences were 30 % with *C. osculatum*, 20 % with *H. aduncum* and 10 % with *A. simplex*. For the two latter species the number of infected fish differed significantly between the sites (Chi-Square test, df = 1, P = 0.016 for *H. aduncum* and G-test/Likelihood Ratio, P = 0.002 for *A. simplex*). Number of fish with *C. osculatum* did not differ between sites (Chi-Square test, df = 1, P = 0.386).

Witch flounder sampled in the Langøya area also had a high prevalence (59 %) while those sampled at Torbjørnskjær were free of any nematode infection (Table 3.1). However, it should be kept in mind that only 4 witch flounder were caught on the eastern side. At the western site 10 out of 17 fish were infected with nematodes (Appendix II). The difference between the sites was significant (G-test/Likelihood Ratio, P = 0.014). At Langøya 53 % of this fish species were infected with *H. aduncum*, 12 % with *C. osculatum* and none with *A. simplex*. The number of fish infected with *H. aduncum* differed significantly between two sites (G-test/Likelihood Ratio, P = 0.023) but fish infected with *C. osculatum* did not (G-test/Likelihood Ratio, P = 0.345).

Common dab had a much higher prevalence at Langøya (80 %) than at Torbjørnskjær (15 %; Table 3.1). At the western site 4 out of 5 fish were infected with nematodes, compared to the eastern site's 6 out of 41 (Appendix II). This difference was significant (G-test/Likelihood Ratio, P = 0.003). At Langøya 40 % of common dab were infected with *H. aduncum*, none with *C. osculatum* and 40 % with *A. simplex*. At Torbjørnskjær the prevalences were 15 % with *A. simplex* and 0 % with *H. aduncum* and *C. osculatum*. For *H. aduncum* the number of infected fish was significantly different between sites (G-test/Likelihood Ratio, P = 0.002) while for *A. simplex* the difference was not significant (G-test/Likelihood Ratio, P = 0.200). As for witch flounder there may be sampling error due to the small number of fish collected at Langøya (n = 5).

Table 3.1. Prevalences (percentage of infected fish) in American plaice, witch flounder and common dab at Torbjørnskjær and at Langøya. Separate tables are given for *H. aduncum* (*H.a.*), *A. simplex* (*A.s.*) and *C. osculatum* (*C.o.*). Number of examined fish (n) is given in parenthesis.

Total prevalence	American plaice	Witch flounder	Common dab
Langøya	55 % (116)	59 % (17)	80 % (5)
Torbjørnskjær	53 % (30)	0 % (4)	15 % (41)
Total	**55 % (146)**	**48 % (21)**	**22 % (46)**

Prevalence ***H.a.***	American plaice	Witch flounder	Common dab
Langøya	44 % (116)	53 % (17)	40 % (5)
Torbjørnskjær	20 % (30)	0 % (4)	0 % (41)
Total	**39 % (146)**	**43 % (21)**	**4 % (46)**

Prevalence ***A.s.***	American plaice	Witch flounder	Common dab
Langøya	0 % (116)	0 % (17)	40 % (5)
Torbjørnskjær	10 % (30)	0 % (4)	15 % (41)
Total	**2 % (146)**	**0% (21)**	**17 % (46)**

Prevalence ***C.o.***	American plaice	Witch flounder	Common dab
Langøya	22 % (116)	12 % (17)	0 % (5)
Torbjørnskjær	30 % (30)	0 % (4)	0 % (41)
Total	**24 % (146)**	**10 % (21)**	**0 % (46)**

3.1.2 Abundance

At Langøya the number of nematodes per fish was about triple as high as that at Torbjørnskjær and the abundances differed significantly for all nematode species. At the western site the most abundant nematode was *H. aduncum*, while at the eastern site it was *C. osculatum*. The abundance in American plaice was almost twice as high at Langøya as at Torbjørnskjær. No comparison between the two sites was done for witch flounder since this species was not infected with nematodes at Torbjørnskjær. For common dab the abundance was five times higher at Langøya than at Torbjørnskjær. However, the analysis for witch flounder and common dab may be highly influenced by the small sample sizes.

At Langøya the abundance was about triple the level at Torbjørnskjær (1.59 and 0.46 respectively; Appendix II). The difference was statistically significant (Mann-Whitney U test, P < 0.001). At Langøya the abundances were 1.07 for *H. aduncum*, 0.48 for *C. osculatum* and 0.03 for *A. simplex*. At Torbjørnskjær the abundances were much lower: 0.19 for *C. osculatum*, 0.15 for *H. aduncum* and 0.12 for *A. simplex*. The abundance of the three nematode species also differed significantly between two sites (Mann-Whitney U test, P < 0.001 for *H. aduncum*, P = 0.004 for *C. osculatum* and P = 0.020 for *A. simplex*).

The abundance level for American plaice was almost twice as high at Langøya as at Torbjørnskjær, 1.64 and 0.87 respectively (Table 3.2). But this difference was not statistically significant (Mann-Whitney U test, P = 0.303). At Langøya the abundances were 1.22 for *H. aduncum*, 0.42 for *C. osculatum* and 0 for *A. simplex*. At Torbjørnskjær the ranking of the nematodes in American plaice was *C. osculatum* (0.43), *H. aduncum* (0.30) and *A. simplex* (0.13). For the two latter species the difference was statistically significant (respectively Mann-Whitney U test, P = 0.010 and P = 0.001). *C. osculatum* had no significant variation between the sites (Mann-Whitney U test, P = 0.417).

The total abundance for witch flounder at Langøya was 1.24 and no fish from Torbjørnskjær were infected with nematodes (Table 3.2). This difference was not significant (Mann-Whitney U test, P = 0.051). At the western site the abundances were 1.06 for *H. aduncum* and 0.18 for *C. osculatum* and 0 for *A. simplex*. The number of the three nematode species per fish did not differ significantly between two sites (Mann-Whitney U test, P = 0.120 for *H. aduncum*, P = 0.763 for *C. osculatum* and P = 1.000 for *A. simplex*).

The abundance level for common dab was five times higher at Langøya than at Torbjørnskjær, respectively 1.20 and 0.24 (Table 3.2). This difference was significant (Mann-Whitney U test, P = 0.001). At Langøya the abundances were 0.60 for *H. aduncum*, 0.60 for *A. simplex* and 0 for *C. osculatum*. At Torbjørnskjær the ranking of the nematodes in common dab was *A. simplex* (0.24), *C. osculatum* (0.00) and *H. aduncum* (0.00). The latter species varied significantly between sites (Mann-Whitney U test, P <

0.001). The number of *A. simplex* and *C. osculatum* per fish did not differ between the two sites (Mann-Whitney U test, P = 0.164 for *A. simplex* and P = 1.000 for *C. osculatum*).

Table 3.2. Abundances (number of nematodes per examined fish) in American plaice, witch flounder and common dab at Torbjørnskjær and at Langøya. Separate tables are given for *H. aduncum* (*H.a.*), *A. simplex* (*A.s.*) and *C. osculatum* (*C.o.*). Number of examined fish (n) is given in parenthesis.

Total abundance	American plaice	Witch flounder	Common dab
Langøya	1.64 (116)	1.24 (17)	1.20 (5)
Torbjørnskjær	0.87 (30)	0.00 (4)	0.24 (41)
Total	**1.48 (146)**	**1.00 (21)**	**0.35 (46)**

Abundance *H.a.*	American plaice	Witch flounder	Common dab
Langøya	1.22 (116)	1.06 (17)	0.60 (5)
Torbjørnskjær	0.30 (30)	0.00 (4)	0.00 (41)
Total	**1.03 (146)**	**0.86 (21)**	**0.07 (46)**

Abundance *A.s.*	American plaice	Witch flounder	Common dab
Langøya	0.00 (116)	0.00 (17)	0.60 (5)
Torbjørnskjær	0.13 (30)	0.00 (4)	0.24 (41)
Total	**0.03 (146)**	**0.00 (21)**	**0.28 (46)**

Abundance *C.o.*	American plaice	Witch flounder	Common dab
Langøya	0.42 (116)	0.18 (17)	0.00 (5)
Torbjørnskjær	0.43 (30)	0.00 (4)	0.00 (41)
Total	**0.42 (146)**	**0.14 (21)**	**0.00 (46)**

3.1.3 Intensity

The number of parasites per infected fish was significantly higher at Langøya than at Torbjørnskjær. *H. aduncum* had the highest intensity at Langøya while *C. osculatum* had the highest intensity at Torbjørnskjær. However the intensities for the three nematode species did not differ significantly between the two sampling sites. American plaice had an intensity almost two-times higher at Langøya than at Torbjørnskjær. No comparison between the two sites was done for witch flounder since this species was not infected with nematodes at Torbjørnskjær. Common dab

had low intensities at both locations. As remarked for the abundances, the analysis might be biased for the last two flatfish species due to small sample sizes. The number of the various nematode species found in the fish varied remarkably between Langøya and Torbjørnskjær. For the three flatfishes the number of nematodes found at Langøya was more than six times higher than at Torbjørnskjær, although the number of fish at Langøya was about the double of that caught at Torbjørnskjær.

The intensities were 2.89 and 1.83 nematodes per infected fish at Langøya and at Torbjørnskjær respectively (Appendix II). This difference was statistically significant (G-test/Likelihood Ratio, P = 0.004; Grouping tables used for analyzing are given in Appendix IV). The variation in the intensities of the three nematode species between the sampling areas was similar to the differences observed in the prevalence and abundance. At Langøya *H. aduncum* had the highest intensity (2.61) followed by *C. osculatum* (2.21) and *A. simplex* (1.25). At Torbjørnskjær *C. osculatum* had the highest intensity (1.70) followed by *H. aduncum* (1.60) and *A. simplex* (1.44). The intensities did not differ significantly between sampling sites for any of the nematodes (G-test/Likelihood Ratio, P = 0.069 for *H. aduncum*; P = 0.325 for *A. simplex*; P = 0.391 for *C. osculatum*).

American plaice had a high intensity at Langøya (2.93) and remarkably low intensity at Torbjørnskjær (1.63; Table 3.3). The difference in number of nematodes per infected fish was statistically significant (G-test/Likelihood Ratio, P = 0.021). At Langøya *H. aduncum* had the highest intensity (2.76); followed by *C. osculatum* (1.88). No American plaice were infected with *A. simplex* at the western site. At Torbjørnskjær the intensity was 1.50 for *H. aduncum*, 1.44 for *C. osculatum* and 1.33 for *A. simplex*. The number of *H. aduncum* and *C. osculatum* per infected fish did not differ significantly between the sites (G-test/Likelihood Ratio, P = 0.161 for *H. aduncum* and P = 0.417 for *C. osculatum*). Thus no one species of nematode dominated at the eastern site.

Witch flounder at Torbjørnskjær were not infected with any of the three main nematode species (Table 3.3). Therefore no statistical analyses were possible. At Langøya the intensities were 2.00 *H. aduncum* and 1.50 *C. osculatum* per infected fish. No witch flounder at Langøya were infected with *A. simplex*.

For common dab the intensities were somewhat lower than for the other two flatfishes. It was 1.50 at Langøya and 1.67 at Torbjørnskjær (Table 3.3). The number of nematodes per infected fish did not differ significantly between sites (G-test/Likelihood Ratio, P = 0.599). At Langøya the intensities were 1.50 *H. aduncum* and 1.50 *A. simplex* specimens per infected fish. At Torbjørnskjær common dab were only infected by *A. simplex* with an intensity of 1.67. The number of *A. simplex* per infected fish did not differ significantly between sites (G-test/Likelihood Ratio, P = 0.676).

Table 3.3. Intensities (number of nematodes per infected fish) in American plaice, witch flounder and common dab at Torbjørnskjær and at Langøya. Separate tables are given for *H. aduncum* (*H.a.*), *A. simplex* (*A.s.*) and *C. osculatum* (*C.o.*). Number of examined fish (n) is given in parenthesis.

Total intensity	**American plaice**	**Witch flounder**	**Common dab**
Langøya	2.93 (64)	2.10 (10)	1.50 (4)
Torbjørnskjær	1.63 (16)	0.00 (0)	1.67 (6)
Total	**2.70 (80)**	**2.10 (10)**	**1.60 (10)**

Intensity *H.a.*	**American plaice**	**Witch flounder**	**Common dab**
Langøya	2.76 (51)	2.00 (9)	1.50 (2)
Torbjørnskjær	1.50 (6)	0.00 (0)	0.00 (0)
Total	**2.63 (57)**	**2.00 (9)**	**1.50 (2)**

Intensity *A.s.*	**American plaice**	**Witch flounder**	**Common dab**
Langøya	0.00 (0)	0.00 (0)	1.50 (2)
Torbjørnskjær	1.33 (3)	0.00 (0)	1.67 (6)
Total	**1.33 (3)**	**0.00 (0)**	**1.63 (8)**

Intensity *C.o.*	**American plaice**	**Witch flounder**	**Common dab**
Langøya	1.88 (26)	1.50 (2)	0.00 (0)
Torbjørnskjær	1.44 (9)	0.00 (0)	0.00 (0)
Total	**1.77 (35)**	**1.50 (2)**	**0.00 (0)**

Figure 3.2 shows the number of the various nematodes found in the fish. For the three flatfishes the number of nematodes found at Langøya (217) was more than six times higher than at Torbjørnskjær (36), although the number of fish at Langøya (138) was about the double of that caught at Torbjørnskjær (75).

It is also remarkable that the total number of *H. aduncum* in the three flatfishes was 18 times higher at Langøya than at Torbjørnskjær, 162 and 9 respectively (Figure 3.2). This difference was the same or greater for the various developmental stages of *H. aduncum*. For *C. osculatum* the difference between Langøya and Torbjørnskjær was also large (about four times); 52 and 13 respectively. On the other hand *A. simplex* had about five times lower number at Langøya (3) than at Torbjørnskjær (14) even though the sample size at Langøya was much larger.

Among the remaining species at Langøya (Norway pout, European flounder, European hake, starry ray, rabbit fish) and Torbjørnskjær (European plaice, whiting, Atlantic cod, shorthorn sculpin, European hake, haddock, goldsinny-wrasse, grey gurnard) the infection pattern of nematodes were quite different (Figure 3.2). While no *H. aduncum* was found at Langøya, 23 were found at Torbjørnskjær. Further, two *A. simplex* was sampled at Langøya and 12 at Torbjørnskjær. Finally about the same number of *C. osculatum* was found in the two areas, 21 and 26 at Langøya and Torbjørnskjær respectively. However, it should be kept in mind that these results are probably strongly biased because the sample size was approximately 10 times larger at the eastern site (135) than at the western site (13).

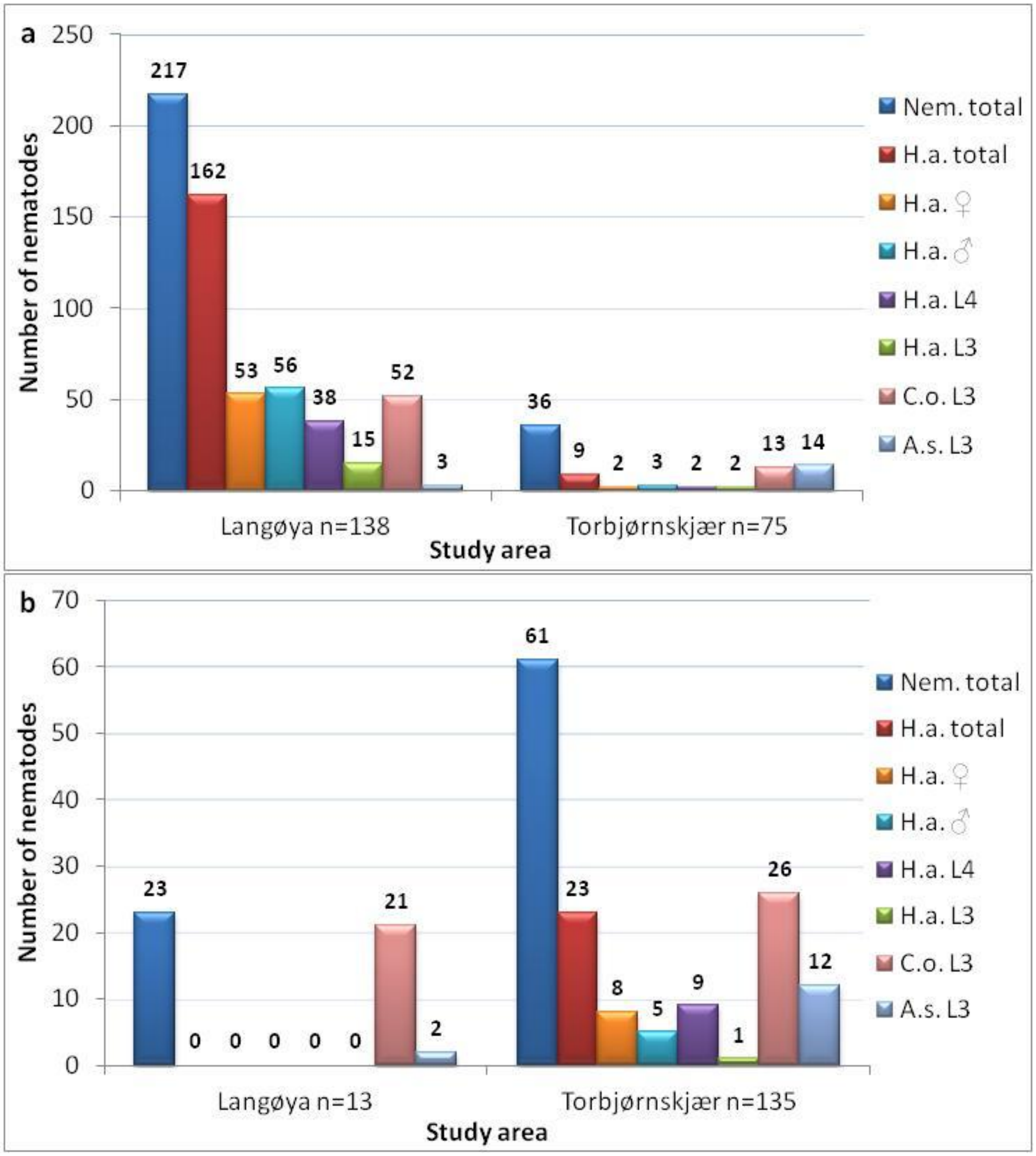

Figure 3.2. Total number of nematodes (Nem. total), number of *H. aduncum* (H.a.) with different stages, *C. osculatum* (C.o.) and *A. simplex* (A.s.) **A** In American plaice, witch flounder and common dab; **B** In the remaining fish at the two sites in the outer Oslofjord. The number of sampled fish (n) is given next to the study area.

3.2 Nematode length

The average length of *A. simplex* and *H. aduncum* was longer at Langøya than at Torbjørnskjær. In contrast, *C. osculatum* achieved the longest average length at

Torbjørnskjær. The nematodes found In American plaice, witch flounder and common dab caught at the western site were slightly longer.

Length measurements of all nematodes in all fish species are given in Appendix V. The average length of *A. simplex* from all infected fish varied between the two sites: 22.8 mm at Langøya (n = 5; SD = 1.5) and 19.4 mm at Torbjørnskjær (n = 26; SD = 3.0; Figure 3.3). This difference was statistically significant (T-test, df = 12, P = 0.002).

The average length of *H. aduncum* was not significantly different between the two sites (T-test, df = 42, P = 0.82): 35.2 mm at Langøya (n = 153; SD = 13.2) and 34.6 mm at Torbjørnskjær (n = 32; SD = 15.2; Figure 3.3).

The average length of *C. osculatum* was not significantly different between the two sites (T-test, df = 93, P = 0.27): 14.7 mm at Langøya (n = 73; SD = 5.4) and 15.7 mm at Torbjørnskjær (n = 38; SD = 4.2; Figure 3.3).

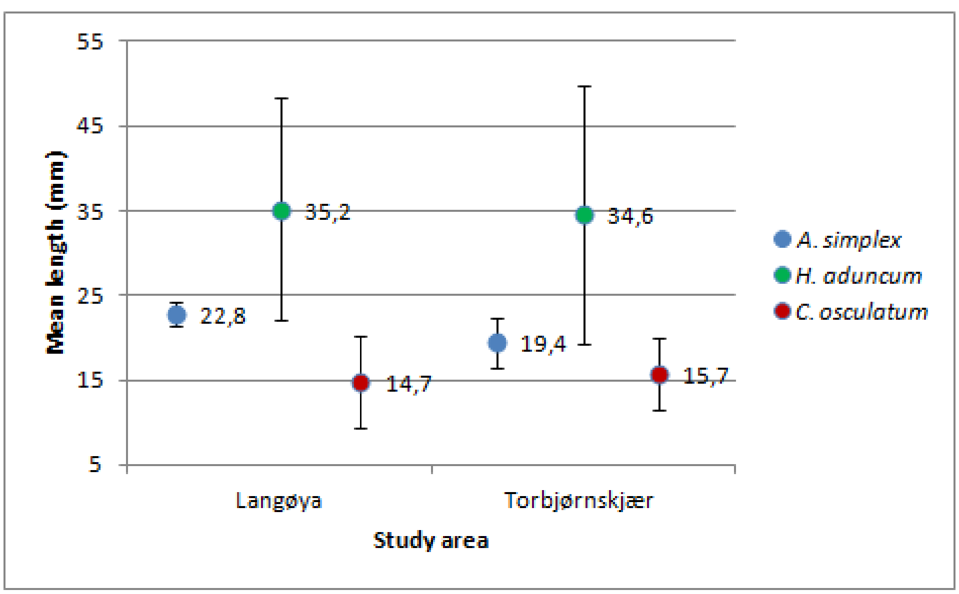

Figure 3.3. The mean lengths of the three nematodes *A. simplex*, *C. osculatum* and *H. aduncum* in all fish species at Langøya and at Torbjørnskjær. SD is given on the bars.

In American plaice, the average length of *H. aduncum* was not significantly different between the two sites (T-test, df = 9, P = 0.195): 35.2 mm at Langøya (n = 132; SD = 12.8) and 29.3 mm at Torbjørnskjær (n = 9; SD = 12.0; Figure 3.4). For witch flounder and common dab the t-test was not possible to apply since none of the fish at Torbjørnskjær were infected with *H. aduncum*. At Langøya the mean nematode length in witch flounder was 37.2 mm (n = 18; SD = 15.6) and in common dab it was 22.7 mm (n = 3; SD = 8.1).

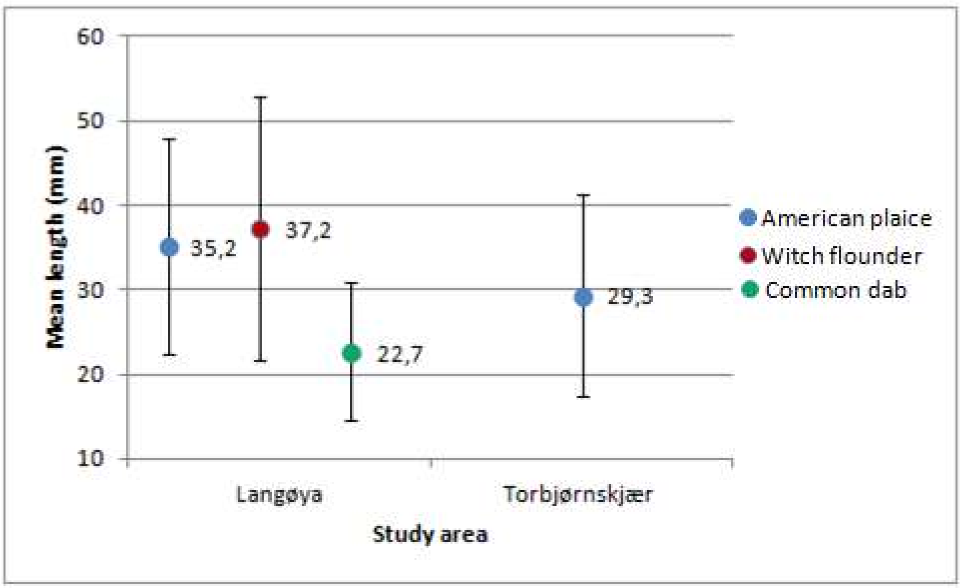

Figure 3.4. The mean length of *H. aduncum* in American plaice, witch flounder and common dab at Langøya and at Torbjørnskjær; SD is given on the bars.

In American plaice the mean length of *C. osculatum* was not significantly different between the two sites (T-test, df = 22, P = 0.236): 16.9 mm at Langøya (n = 49; SD = 4.3) and 15.5 mm at Torbjørnskjær (n = 13; SD = 3.6; Figure 3.5). For witch flounder and common dab the T-test was not possible to apply since none of the fish at Torbjørnskjær were infected with *C. osculatum*. At Langøya the mean nematode length in witch flounder was 12.7 mm (n = 3; SD = 4.9) while no common dab were infected with *C. osculatum*.

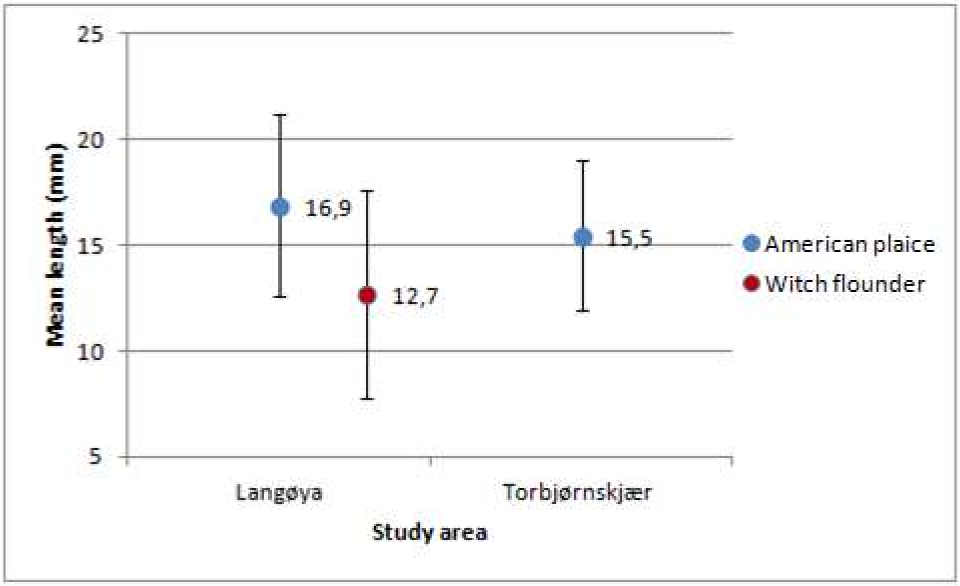

Figure 3.5. The mean length of *C. osculatum* in American plaice and witch flounder at Langøya and at Torbjørnskjær; SD is given on the bars.

In common dab the mean length of *A. simplex* was not significantly different between the two sites (T-test, df = 6, P = 0.053): 23.0 mm at Langøya (n = 3; SD = 2.0) and 19.2 mm at Torbjørnskjær (n = 10; SD = 3.4; Figure 3.6). For American plaice and witch flounder the T-test was not possible to apply since none of the fish at Langøya were infected with *A. simplex*. At Torbjørnskjær the mean nematode length in American plaice was 17.3 mm (n = 4; SD = 2.2) while no witch flounder were infected with *A. simplex*.

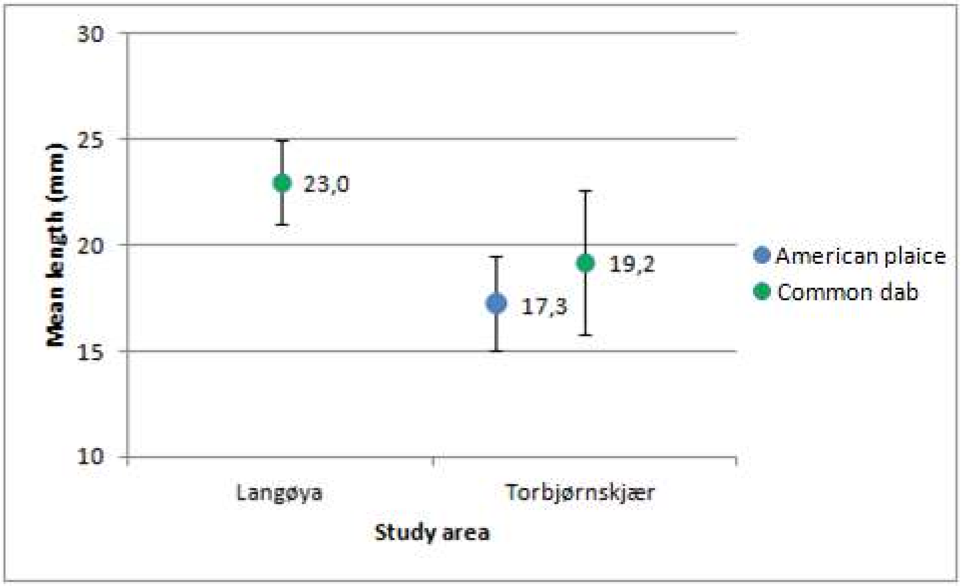

Figure 3.6. The mean length of *A. simplex* in American plaice and common dab at Langøya and at Torbjørnskjær; SD is given on the bars.

One *P. decipiens* that was found in an Atlantic cod sampled at Torbjørnskjær was 38 mm long. Among the three *C. heterochrous* that were sampled from American plaice at Langøya only one was measured for length and this individual was 12 mm.

3.3 Distribution of number of nematodes per fish

While the total nematode infection was over-dispersed in American plaice, it was random (Poisson) in witch flounder and common dab.

By pooling counts from all nematode species as well as sampling sites it was possible to produce smooth histograms (Figures 3.7 – 3.9). While the infection in American plaice was highly over-dispersed, it was not different from a random distribution (the Poisson distribution) in witch flounder and common dab. One individual of American plaice had 12 nematodes. For common dab and witch flounder the maximum numbers of nematodes per fish were respectively 3 and 4.

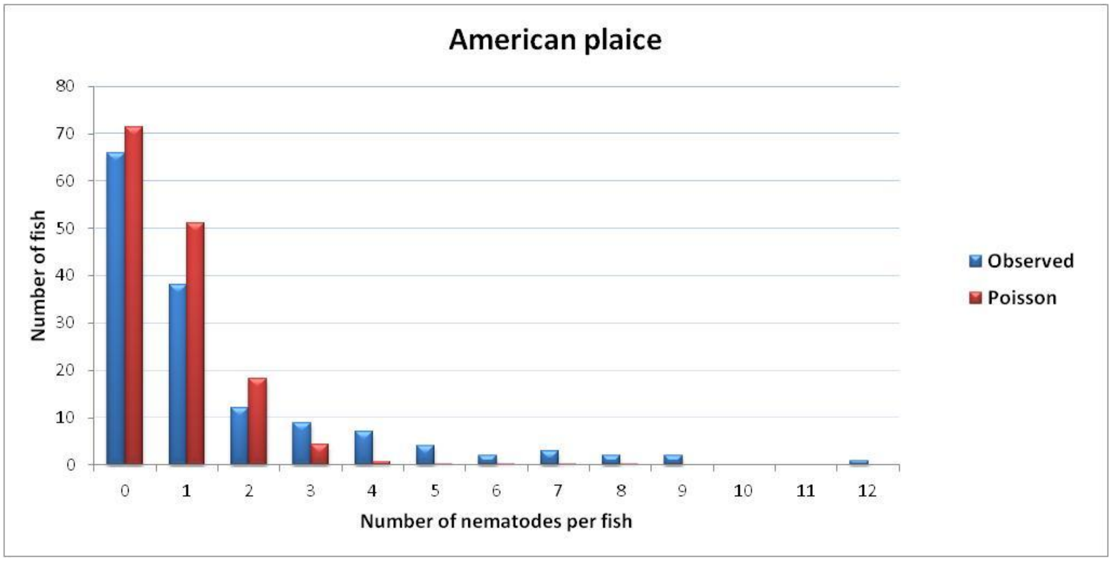

Figure 3.7. Approximation of the observed frequencies of the number of nematodes per American plaice from both study areas with the Poisson distribution (intensity parameter λ = 0.72). The fitted Poisson distribution is significantly different from the observed histogram (Chi-Square test, df = 3, P < 0.001).

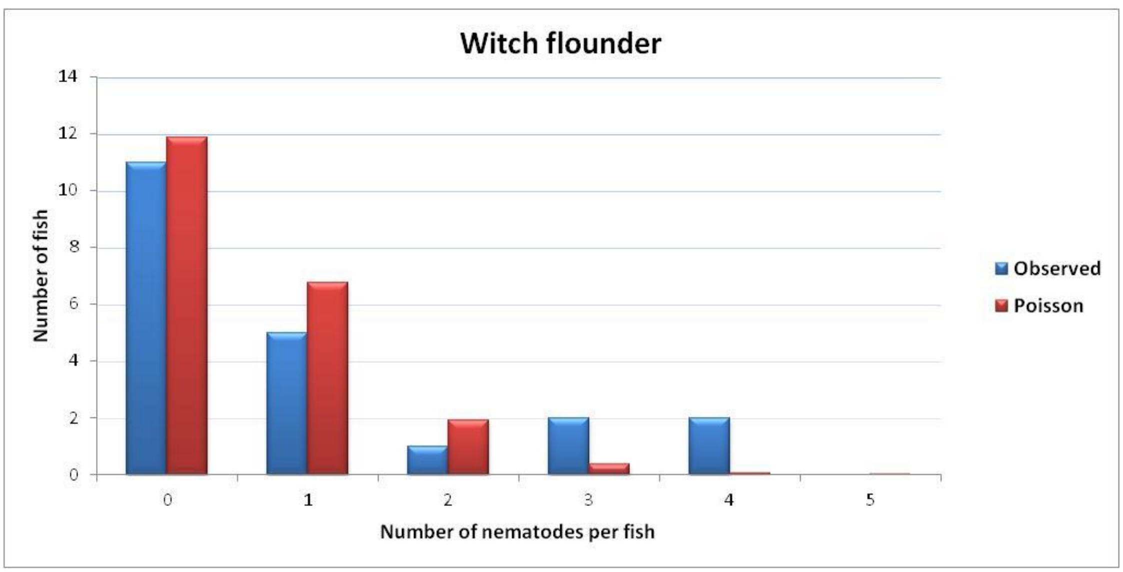

Figure 3.8. Approximation of the observed frequencies of the number of nematodes per witch flounder from both study areas with the Poisson distribution (intensity parameter λ = 0.57). Because of the small sample size, the predicted number of individuals with 3 or more parasites is less than 5 so it is not possible to perform a significance test.

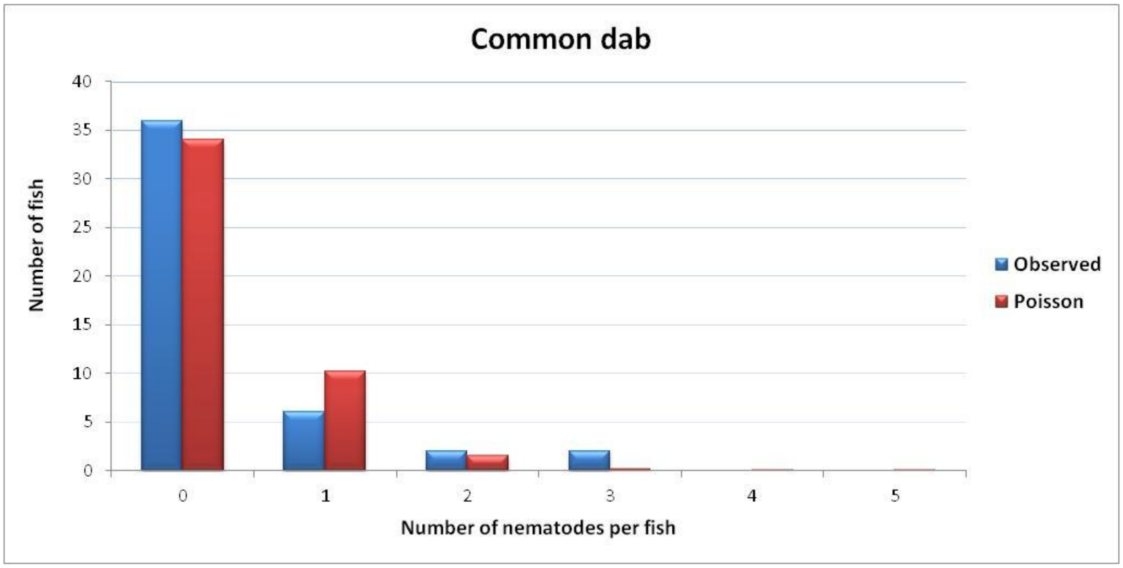

Figure 3.9. Approximation of the observed frequencies of the number of nematodes per common dab from both study areas with the Poisson distribution (intensity parameter $\lambda = 0.30$). Because of the small sample size, the predicted number of individuals with 3 or more parasites is less than 5 so it is not possible to perform a significance test.

Since the nematode species were pooled, it is of interest to identify their specific contribution to the infestation patterns (Table 3.4; more detailed tables are given in Appendix VI). 50 % of American plaice and 80 % of witch flounder were infected with only *H. aduncum*. In contrast, 80 % of common dab was infected with only *A. simplex*. In the over-dispersed infection pattern in American plaice there is also another noticeable structure: 26 % of the fish were only infected with *C. osculatum* and 17 % with both *H. aduncum* and *C. osculatum*.

Table 3.4. Number of fish infected with one or two different nematode species in the outer Oslofjord.

	American plaice	Witch flounder	Common dab
H. aduncum	41 (50 %)	8 (80 %)	2 (20 %)
C. osculatum	21 (26 %)	1 (10 %)	
A. simplex	2 (2 %)		8 (80 %)
C. heterochrous	2 (2 %)		
H. aduncum + C. osculatum	14 (17 %)	1 (10 %)	
H. aduncum + A. simplex	1 (1 %)		
H. aduncum + C. heterochrous	1 (1 %)		
TOTAL	**82 (100 %)**	**10 (100 %)**	**10 (100 %)**

3.4 Biological information of fish

There was a large covariation between the length and age in all fish species, but there was no relationship between the nematode burden and condition factor of the fish.

3.4.1 Length versus age

The age (based on the otoliths) and length of the fish (cm) had a large covariation (Figure 3.10). R^2 varied between 76 and 87 % for seven species (European hake, Atlantic cod, witch flounder, European plaice, common dab, shorthorn sculpin and American plaice). For whiting the age only explained 51 % of the variability in length, but this result is influenced by the low number of year classes in the regression analysis (whiting was only represented by age groups two and three).

Due to the small sample size, the relationship between age and length was not studied for haddock, Norway pout or European flounder (three, four and one individuals respectively). Since goldsinny-wrasse, rabbit fish, starry ray and grey gurnard do not have otoliths the age was not estimated for these four species.

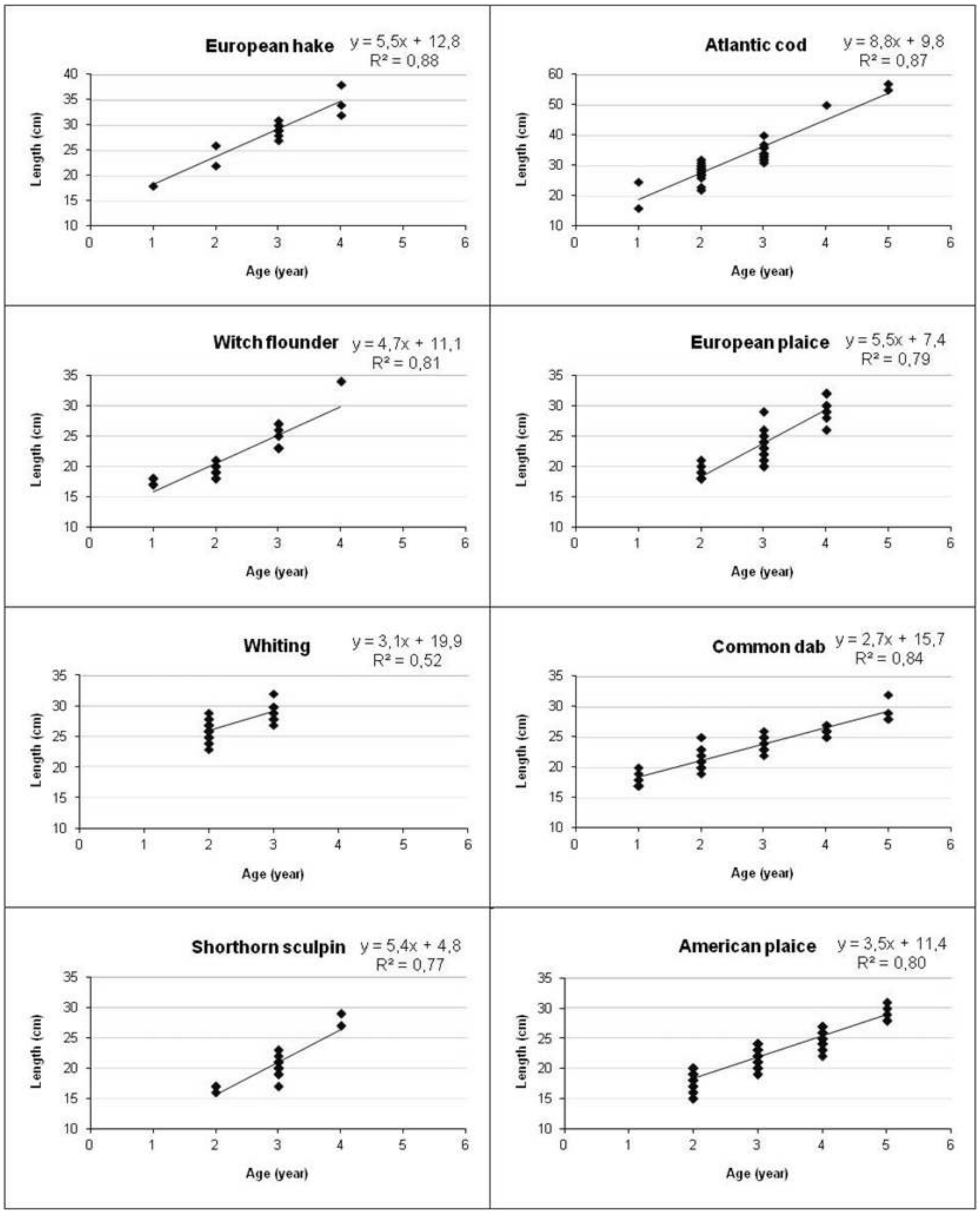

Figure 3.10. Age plotted against length for eight fish species sampled in the outer Oslofjord.

3.4.2 Condition factor

Figure 3.11 shows the relationship between the condition factor and the number of nematodes in the fish. The figure clearly shows that there was no relationship between these two factors. The same applies when all the fish are taken together and also for the three flatfish species separately.

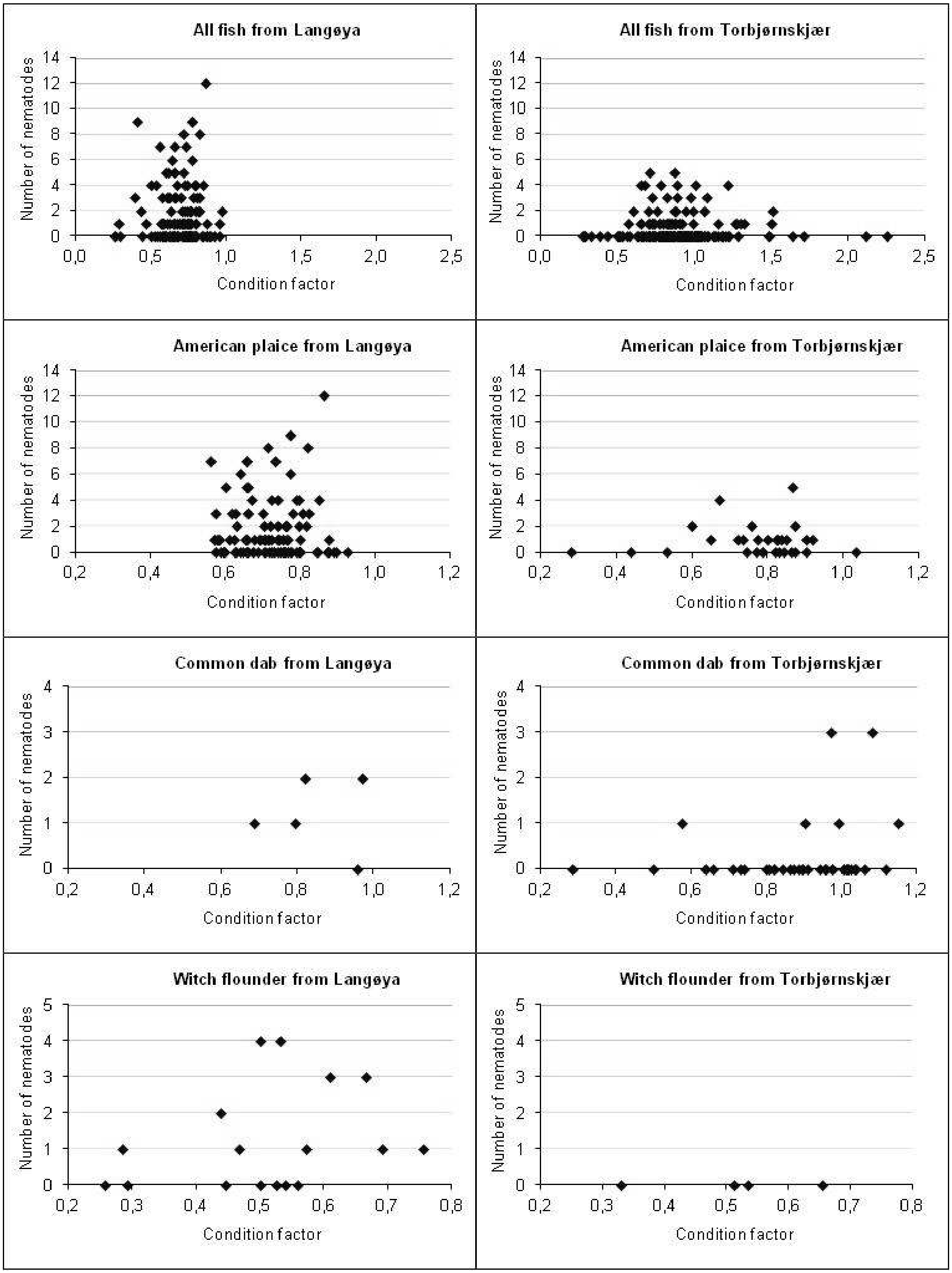

Figure 3.11. The number of nematodes plotted against the condition factor in fish at Langøya and at Torbjørnskjær. The relationship is shown for the three flatfishes separately and all fish combined.

4 Discussion

During this investigation in the outer Oslofjord 361 fish from 15 different species were collected via trawling at depths of between 80 and 100 m at the two locations, Langøya and Torbjørnskjær. There was considerable variation in species composition at the two sites (Figure 3.1; Appendix III). On the western side (151 fish from 8 species) the catches were dominated by American plaice and witch flounder and had low frequencies of common dab, Norway pout, European flounder, European hake, starry ray and rabbit fish. On the eastern side (210 fish from 11 species) the catches were dominated by common dab, European plaice, whiting, American plaice and Atlantic cod as well as having very low numbers of witch flounder, shorthorn sculpin, European hake, haddock, goldsinny-wrasse and grey gurnard.

Previous studies have mainly focused on nematodes reproducing in marine mammals (*P. decipiens* and *A. simplex*) and so there are few reports on the fish parasites *H. aduncum* and *C. heterochrous*. Several authors (Aspholm 1991; Hansen & Malmstrøm 2006; Damsgaard Jensen 2009) have remarked that the abundance of *A. simplex* seems to have been declining since the mid 1980's. Hansen & Malmstrøm (2006) found some evidence that *H. aduncum* has also been declining in the Oslofjord. According to my results the decline in *A. simplex* is still an ongoing process, but the abundances of *C. osculatum* and *H. aduncum* are significantly higher than recorded in previous years. In addition I made the first recording of *C. heterochrous* at Langøya area. Previously it has been only found from the inner Oslofjord (Hansen & Malmstrøm 2006).

4.1 Methods

When analyzing the results, some considerations should be taken into account. Fish were caught by different fishermen at Langøya and at Torbjørnskjær. Fish from the western side were bought from the fishermen after they were delivered to Oslo for sale. On the eastern side I had the possibility to sample fish before they were sorted for sale. Thus the samples from the eastern side were more random than the delivery from the western side.

The hydrographical conditions were similar at the two locations where the fish were caught, but there was a small difference in trawling depths (80 – 90 m at Langøya and 90 – 100 m at Torbjørnskjær). Water layers at these depths are homogeneous in the outer Oslofjord (Gade 1968, 1970; Andersen *et al*. 1970; Pederstad *et al*. 1993; Lekve *et al*. 1999; Baalsrud & Magnusson 2002), so the difference of 10 meters probably had no impact on the results.

When studying nematodes in fish, it is important to dissect the fish as soon as possible after death (Möller & Anders 1986). Therefore most of the fish were dissected the same day they were caught. Nematodes are known to survive for a long time after the host is dead, however the chance of detection declines after the host's death as *H. aduncum*, for example, has the tendency to migrate out of the fish through the anus, mouth or gills (Berland 1989, 2006; Figure 2.5). When I was working in the laboratory, live nematodes were found on the table shortly after the samples were brought in. These nematodes were excluded from the analyses since it was impossible to identify where they came from.

4.2 Infestation rate

In all the samples from both localities 136 of 361 fish were infected with nematodes (Appendix II). Approximately 0.9 nematodes were found per sampled fish and 2.5 nematodes per infected fish. *H. aduncum* was the most widespread nematode (found in 82 fish), followed by *C. osculatum* (56 fish) and *A. simplex* (22 fish). *H. aduncum* had also the highest abundance (0.5), followed by *C. osculatum* (0.3) and *A. simplex* (0.1).

This infestation pattern is consistent with previous studies in North-Atlantic (Andersen 1993; Køie 1993; Balbuena *et al*. 1998) which all report that *H. aduncum* is the most common nematode in fish. Berland (1989) concluded that *C. osculatum* sporadically occurs in fish along the Norwegian coast. However, previous theses conducted in the Oslofjord have reported large abundances of this nematode in fish and seals (Aspholm

1991; Damsgaar Jensen 2009; see harbour seal data in Appendix VII). They all concluded that *C. osculatum* has become more common in the Oslofjord. Furthermore, the low incidence of *A. simplex* supports the hypothesis of an ongoing negative trend in this nematode infection within the Oslofjord (Aspholm 1991; Hansen & Malmstrøm 2006; Damsgaard Jensen 2009).

H. aduncum seems to have a stable and very abundant population in the Oslofjord. One reason for this might be that it has a full life-cycle in the area. Although this worm is found in a large variety of different hosts (Berland 1961, 2006; Möller & Anders 1986; Andersen 1993; Balbuena *et al*. 1998), the pelagic amphipod *Themisto abyssorum* is documented as the most important intermediate host of *H. aduncum* in the Oslofjord (Svendsen 1990). This crustacean is a common component of plankton communities at temperate and high latitudes. In addition, it plays a significant role in the diet of many fish (Vinogradov 1999). By using *T. abyssorum* as a first intermediate host *H. aduncum* has a large potential for spreading and becoming the dominant nematode in fish.

A declining population of *A. simplex* in the Oslofjord may be induced by the fluctuation in host population. Both transport (e.g. Atlantic herring) and final hosts (e.g. harbour porpoises, *Phocoena phocoena*) have a variable occurrence in fjords. There have been incidences of reproducing *A. simplex* in harbour seal stomachs from the Oslofjord (Damsgaard Jensen 2009). However, the significance of pinnipeds as a true definitive host to *A. simplex* has been questioned (Berland 2006). Since I did not find any mature specimens in our harbour seals (Appendix VII) it is still an open question of how important these seals are for the reproduction of *A. simplex* in the outer Oslofjord. There are two reasons why ordinary considerations from population biology lead to the prediction that the abundance of *A. simplex* will go through cyclic trends in the Oslofjord. First, the harbour porpoises, which are final hosts for *A. simplex*, have a rather irregular occurrence in the area (Morten Bronndal and local fishermen *pers. comm.*). And secondly, the harbour seals, where a small number of *A. simplex* occasionally reproduce, have a fluctuating abundance due to virus outbreaks.

According to Køie & Fagerholm (1995), *C. osculatum* differs from other anisakid species found in the area. The newly hatched third-stage larvae of *C. osculatum* are directly infective to small fish individuals. In contrast, the larvae from the other species have to grow to obtain a certain size before they are capable of surviving in a fish intermediate host (Køie 1993). These differences may explain why *C. osculatum* is becoming so widespread in the Oslofjord. If the life cycle is simple, involving few transport hosts, there is a higher probability of reaching the final host faster. Consequently this allows *C. osculatum* to have more generations in the same time span compared to other anisakid species.

The percentage of infected fish with all nematode species pooled was significantly higher at Langøya than at Torbjørnskjær (55 % and 25 % respectively; Appendix II). The same directional difference was also observed to be significant in abundances (1.6 and 0.5 respectively) and intensities (2.9 and 1.8 respectively). Lähdekorpi (2011) also found a significant difference in the *P. decipiens* infection pattern at two close areas: Koster and Hvaler. She concluded that the much higher nematode burden at Koster is due to (1) a higher abundance of harbour seals, (2) the fish were caught closer to the seal skerries and (3) at Hvaler the seals only sporadically visit the area. These factors show that the nematode population is strictly dependent on the presence of the final host. Thus it is reasonable to assume that egg supply of *H. aduncum* and *C. osculatum* is higher at Langøya than at Torbjørnskjær due to the better chances of larvae reaching their final hosts and reproducing. On the other hand, *A. simplex* seems to have higher egg supply on the eastern side. However, since the three nematode species have different life-cycles and final hosts, it is preferable to study the infection patterns for *H. aduncum*, *C. osculatum* and *A. simplex* separately.

Considered separately, there were significant differences in the infection patterns for each of the parasites between the two study areas. On the western side *H. aduncum* was the main nematode species, infecting 41 % of the fish, while *A. simplex* was found to be infecting only 3% (Appendix II). On the eastern side the two species exhibited similar infection levels of 10 and 9 % respectively. The number of *H. aduncum* found at Langøya was five times higher than that found at Torbjørnskjær (162 and 32 respectively; Figure 3.2). However, the number of *A. simplex* found at Langøya was five times lower than that found at Torbjørnskjær (5 and 26 respectively). Furthermore, the number of fish sampled at both study areas differed only 1.4 times (151 and 210 respectively; Figure 3.1).

Hansen & Malmstrøm (2006) stated that the abundance of *H. aduncum* had decreased by about 75 % during the last 20 years. They suggested that this might be explained by a decline of the abundance of Atlantic cod in the Oslofjord. My data do not support a decline in the abundance of this nematode. On the other hand, a decline of Atlantic cod (Svedäng & Bardon 2003) may explain the marked difference in *H. aduncum* infection between the two sites because only one cod-fish were sampled at Langøya while 80 were sampled at Torbjørnskjær (Figure 3.1; Appendix III). At the same time, nine *H. aduncum* specimens were found in flatfish and 23 in cod-fish on the eastern side (Figure 3.2; Appendix II). Thus a decline in cod-fish might have resulted in the flatfish becoming more infected at Langøya.

Hansen & Malmstrøm (2006) also suggested that the lower number of *A. simplex* in flatfish should be an accepted phenomenon since this nematode follows a pelagic food chain. This hypothesis is not supported by my results. The number of *A. simplex* found in three flatfish species at both sites (3 at Langøya and 14 at Torbjørnskjær; Figure 3.2) are in accordance with what was found in other fish species (2 at Langøya and 12 at Torbjørnskjær). This indicates that the infection rate of *A. simplex* varies between the locations and may simply be due to the fact that the final hosts of *A. simplex* occur more often at Torbjørnskjær than at Langøya. *H. aduncum* on the other hand matures in various species of fish and are not so highly dependent on the distribution of a few hosts.

Three specimens of the flatfish nematode *C. heterochrous* were collected from American plaice at Langøya. This parasite has previously been found widespread in European waters, including the coast of Denmark (Køie 2000a). It was not known in the Oslofjord until Hansen & Malmstrøm (2006) made the first observation. They found it in American plaice and European plaice in the inner part of the Oslofjord. This might indicate that *C. heterochrous* is spreading in the Oslofjord with very low abundances. On the other hand, Køie (1993) showed that at the Faeroes, American plaice caught at 45 m were infected with this nematode whereas those caught at 342 m were not. She proposed that this might be influenced by the vertical distribution of the most important intermediate host, polychaeta *Nereis diversicolor* (down to 40 m; Køie 2000a). The trawling depths in my investigation were 80 – 100 m and in Hansen & Malmstrøm's (2006) study the depths were the same in the Inner Oslofjord and even deeper at Langøya area (120 – 150 m).

4.2.1 American plaice

The percentage of infected American plaice did not differ significantly between Langøya and Torbjørnskjær (55 and 53 % respectively; Table 3.1) and neither did the number of nematodes per fish. However, when only infected fish are considered, (i.e. intensity), the number of worms was significantly higher at Langøya than at Torbjørnskjær (2.9 and 1.6 respectively; Table 3.3).

The infection pattern in American plaice was completely different compared to the years 2004/2005. Hansen & Malmstrøm (2006) examined 20 American plaice, but only 2 individuals (10 %) were infected with nematodes; one in the inner Oslofjord and one at Torbjørnskjær. They found no infected American plaice at Langøya. These results indicate a much lower overall prevalence six years ago (10 % and 55 %; Hansen & Malmstrøm 2006; Table 3.1). However, these large differences must be viewed with precaution due to the small sample sizes.

Compared to Hansen & Malmstrøm (2006) the average abundance in American plaice at Torbjørnskjær has tripled from 0.3 to 0.9 nematodes per sampled fish. This is caused by the high infection rate of *C. osculatum* in my samples. Furthermore, my results showed that *C. osculatum* had higher, although not significantly, prevalence at Torbjørnskjær than at Langøya (30 % and 22 % respectively; Table 3.1). This result is rather interesting because, according to Berland (1989), this species is believed to be scarce in Norwegian waters. The previous theses have not reported any *C. osculatum* in American plaice (Aspholm 1991; Hansen & Malmstrøm 2006). My data shows that this is a rather frequent nematode in this flatfish (24 %), and indicates that the number of infected American plaice has been increasing during the last years in the outer Oslofjord. This positive trend is hard to explain since there are so few studies on *C. osculatum* in the Oslofjord. Køie & Fagerholm (1995) showed that the life-cycle of this parasite is different from other anisakid parasites due to the newly hatched third-stage larvae of *C. osculatum* that are directly infective to small specimens of fish. Hence it is possible that some unknown factors have had a positive influence on this nematode especially and thus induced a population increase in the Oslofjord (Balbuena *et al*. 1998).

My data also shows that *H. aduncum* has become a common parasite in American plaice at Langøya (44 %; Table 3.1). Hansen & Malmstrøm (2006) found one specimen in one fish at Torbjørnskjær, but no previous investigation has reported that *H. aduncum* is also infecting American plaice on the western side of the Oslofjord. Aspholm (1991) did not find any *H. aduncum* in American plaice at Torbjørnskjær, so my data indicates that the infestation burden of *H. aduncum* is increasing in the outer Oslofjord. A possible explanation is the declining Atlantic cod abundance as discussed by Hansen & Malmstrøm (2006).

Finally, Aspholm (1991) observed that at Torbjørnskjær 4 of 29 American plaice were infected with *A. simplex* with an abundance of 0.3. In addition, the intensity for *A. simplex* has decreased from 2.5 to 1.3 during last two decades (Table 3.3). This supports the hypothesis of a fluctuating abundance of *A. simplex* in the outer Oslofjord (Jensen & Idås 1992; Hansen & Malmstrøm 2006; Damsgaard Jensen 2009). As underlined in the previous sections, our present knowledge does not permit any conclusions to be drawn on the various hypotheses concerning which factors are influencing this variability of the number of *A. simplex*.

4.2.2 Witch flounder

While the percentage on infected witch flounder was high at Langøya (59 %; Table 3.1), no infected individual was found at Torbjørnskjær. However, this result might be skewed due to a small sample size (n = 4) on the eastern side. This result differs substantially to Hansen & Malmstrøm (2006). They found that witch flounder was only infected at the eastern site with the prevalence of 33 %. However, it should be noted that their sample size was also rather small: only 10 fish of which 3 were caught in that area. This indicates a similar fluctuation as was observed in American plaice. Flatfish at the western site are getting more infected with nematodes than at Torbjørnskjær.

4.2.3 Common dab

There was a significant difference in the numbers of infected common dabs between Langøya and Torbjørnskjær (80 % and 15 %; Table 3.1). Also the number of nematodes per sampled fish varied significantly between the two sites. The abundance was 6 times higher on the western side than on the eastern side (1.2 and 0.2; Table 3.2). On the other hand, the number of nematodes per infected fish was more even on the two sides (1.5 and 1.7; Table 3.3). As mentioned previously, these results might be skewed due to a very small sample size from Langøya (n = 5).

Aspholm (1991) sampled 17 common dabs at Torbjørnskjær but none were infected by nematodes. Although the sample sizes are rather small, these results are similar to those reported for American plaice and witch flounder and together these suggest that flatfish seem to be becoming more infected with nematodes.

At Langøya, *A. simplex* and *H. aduncum* had exactly the same infection patterns in common dab (Tables 3.1 – 3.3). At Torbjørnskjær only *A. simplex* was found in this flatfish. However, the percentage of fish infected with *A. simplex* was remarkably lower than at Langøya (15 % and 40 % respectively). In addition, among the three flatfishes only common dab is infected with *A. simplex* at Langøya. This result may be influenced by the fact that compared to other two flatfishes common dab has the shallowest distribution (down to 150 m). However, the sample size at Langøya (n = 5) is too low to draw any conclusions.

4.3 Variation in the length of nematodes

Since the length of a nematode reflects the species-specific adaptation to the hosts, we may use the average length as a measure of the breeding potential in the final host because the number of eggs (fecundity) is proportional to length (Ugland *et al*. 2004). Unfortunately the total length reacts differently to the various fluids used for fixation and colouring (Berland 1984), so it is difficult to compare length measurements reported from different investigations.

4.3.1 *Hysterothylacium aduncum*

In the outer Oslofjord the average length of *H. aduncum* (all fish from both sides pooled) was 35.0 mm. At Langøya the average length was 37.2 mm in witch flounder and 35.2 mm in American plaice (Figure 3.4). At Torbjørnskjær, the average length in American plaice was almost 8 mm lower (29.3 mm). However in common dab at Langøya the mean length was down to 22.7 mm. This indicates that American plaice and witch flounder are more suitable hosts for *H. aduncum* in these areas. This might suggest that there are some physiological or biological differences between American plaice, witch flounder and common dab that result in the two former species being more conducive to enhanced growth of *H. aduncum* (Möller & Anders 1986).

Tolonen & Karlsbakk (2003) studied *H. aduncum* in Atlantic herring from the Osterfjord and found that the third stage larvae varied from 2.6 to 9.5 mm. However, since the abundance of Atlantic herring was so low, they concluded that the role of this fish as a transport host was of little importance. In sharp contrast, the third stage of *H. aduncum* obtained an average length of 16.0 mm in American plaice and witch flounder in my investigation (Appendix V). Since the larvae enter the fish at 2 – 3 mm (Køie 1993), the growth is considerably better in the two flatfishes and strongly indicates that this group of fish should be considered as the true second intermediate hosts in the Oslofjord.

Gadoids are generally believed to be the main final host for *H. aduncum* (Berland 1961). Andersen (1993) studied the length of *H. aduncum* in Atlantic cod in the Oslofjord. Her observations of nematode lengths in the third stage (3 – 25 mm) and fourth stage (11 – 63 mm) correspond with my observations (10 – 23 mm and 11 – 61 mm respectively; Appendix V). On the other hand, the maximum length she recorded in adult worms was larger than in my specimens (85 and 66 mm respectively). This indicates that American plaice and witch flounder are probably not as good final hosts as Atlantic cod, but of the three flatfish species these two appear more suitable than common dab.

4.3.2 *Anisakis simplex*

In the outer Oslofjord the third stage of *A. simplex* had an average length of 20.0 mm with the largest sizes obtained in common dab at Langøya (23.0 mm; Figure 3.6, Appendix V). In North-East Atlantic and northern North Sea Smith (1983) reported the range 4.2 to 23.6 mm in euphausiids and 18.0 to 21.9 mm in blue whiting (*Micromesistius poutassou*). On the west coast of Norway Strømnes & Andersen (2003) found that saithe is a more suitable transport host for *A. simplex* larvae (mean length 25 mm) than Atlantic cod and redfish (*Sebastes marinus*; average length was 24 mm in both hosts). They also proposed the hypothesis that the growth of *A. simplex* third stage larvae is heavily influenced by the fat content of the tissue in which it is encapsulated. This is very plausible since their main intermediate host, the Atlantic herring, has a high fat content. A dependence of fatty tissue may also explain the lower mean length of *A. simplex* obtained in common dab in the outer Oslofjord.

4.3.3 *Contracaecum osculatum*

Compared to the other Anisakid parasites, *C. osculatum* larvae achieved the shortest length in the outer Oslofjord (average length 15.0 mm; Appendix V). This was the only species with a longer average length at Torbjørnskjær than at Langøya (15.7 and 14.7 mm respectively; Figure 3.3). In American plaice the mean lengths at Langøya and at Torbjørnskjær were approximately equal (16.9 and 15.5 mm respectively; Figure 3.5), but in witch flounder, which was only infected on the western side, the length was rather low (12.7 mm). These results indicate that American plaice is more suitable transport host for *C. osculatum* than witch flounder in the outer Oslofjord.

There are only few studies on the length of *C. osculatum* larvae in North-East Atlantic. Smith *et al*. (1990) reported a range of 8.5 – 26.3 mm in whiting in the northern North Sea, which is similar to what I observed in American plaice in the outer Oslofjord (9.0 – 26.0 mm; Appendix V). This might indicate that both whiting and American plaice are suitable transport hosts for this nematode. Damsgaard Jensen (2009) measured ten *C. osculatum* fourth stage larvae in harbour seals at Torbjørnskjær and recorded an 8 mm longer mean length than what was observed in the third stage larvae in my sampled fish in the same area. This is due to the marked growth and moulting to fourth stage undergone by these parasites within days of entering a seal (Køie & Fagerholm 1995). On the other hand, when studying grey seals in Bothnian Bay, Valtonen *et al*. (1988) found that *C. osculatum* achieved lengths of 2 – 24 mm in third stage and 5 – 24 mm in fourth stage. Thus *C. osculatum* third and fourth stage larvae were shorter in Bothnian Bay than what was recorded in northern North Sea (Smith *et al*. 1990) and in the Oslofjord (Damsgaard Jensen 2009; Appendix V). Therefore the conditions in the Bothnian Bay are not optimal for *C. osculatum*. However, we cannot exclude the possibility that there are different sibling species in the Oslofjord and Bothnian Bay (Mattiucci & Nascetti 2008).

4.4 Distribution of number of nematodes per fish

In American plaice (Figure 3.7) the distribution of the number of nematodes per fish had a heavy tail (some individuals were substantially more infected than the average level).

Since the deviation from the Poisson distribution was due to the heavy tail, the infestation was clearly over-dispersed. In witch flounder and common dab the sample size was too small to get the 5 or more predicted number of fish with 3 or more parasites required for testing for the significance of the Poisson approximation. However, the pooled data histograms suggest the presence of Poisson distribution since there is no heavy tail that indicates over-dispersion (Figures 3.8 – 3.9). This may be taken as evidence for a random infestation pattern in witch flounder and common dab.

Anderson & Gordon (1982) reviewed the processes influencing the frequencies of parasite numbers within the host populations, and divided the pattern of abundances into three distinct categories: (1) homogeneous (under-dispersed) infestation, where all hosts are infected with the same number of parasites, (2) random (regular) dispersed infestation following a Poisson distribution, and (3) heterogeneous or aggregated (over-dispersed) infestation where the majority of hosts have few or no parasites and a few hosts are heavily infected. These distributions are shaped by the stochastic processes in both the population dynamics (birth, death, immigration and emigration) and the environment (Scott & Dobson 1989). In general, stochastic factors of a demographic nature tend to generate a random pattern (Poisson distributions) and environmental variability tends to generate over-dispersion (Anderson & Gordon 1982; Luong *et al*. 2011).

A random distribution of nematodes can lead to a reduction in the reproduction success of the parasite, because a low density of conspecifics translates into a lower probability of the nematodes to reach the final host and mature (Luong *et al*. 2011). For example, harbour porpoise is considered to be the final host of *A. simplex* in the Oslofjord, but, since the abundance of this cetacean is low and fluctuating in this area, *A. simplex* have lower probability to reach the final host. This might be the reason why the abundance of this nematode has been reported to be in a decreasing trend in the Oslofjord (Aspholm 1991; Hansen & Malmstrøm 2006; Damsgaard Jensen 2009).

Most of the American plaice and witch flounder were infected with only *H. aduncum* (50 % and 80 % respectively; Table 3.4). In contrast, 80 % of common dab was infected with only *A. simplex*. In the over-dispersed infection pattern in American plaice there is also another noticeable structure: 26 % of the fish were only infected with *C. osculatum* and 17 % with both *H. aduncum* and *C. osculatum*. It is likely that a combination of different factors, especially the feeding ecology and habitat preferences of the fish can be the cause for the observed infestation patterns (Johnson 2004).

My results clearly indicate that in the outer Oslofjord American plaice and witch flounder harbour a more diverse parasite fauna, consisting primarily of *H. aduncum* and *C. osculatum* that have low host-specificity (Berland 1961, 1989). On the other hand, common dab harbours a relatively poor parasite fauna. However, it should be kept in mind that the sample sizes of witch flounder and common dab are too small to draw conclusions (only 10 individuals of each species).

With regard to interaction between the parasitic species, the average lengths of *C. osculatum* and *H. aduncum* in witch flounder were 7.0 and 37.7 mm (Appendix VI). When they occurred simultaneously the average lengths were respectively 15.5 and 33.5 mm. These results indicate that *C. osculatum* experiences longer and *H. aduncum* shorter average lengths when infecting witch flounder at the same time. In American plaice the difference was not so conspicuous. The average lengths of *C. osculatum* and *H. aduncum* were 16.4 and 34.2 mm when infecting alone and 16.9 and 33.5 mm when they occurred simultaneously. However, the average lengths of *A. simplex* and *H. aduncum* in American plaice were 17.7 and 34.2 mm when infecting alone. When they occurred simultaneously the average lengths were respectively 16.0 and 42.0 mm. These results indicate that *A. simplex* experiences shorter and *H. aduncum* longer average lengths when infecting American plaice at the same time.

Although these results might suggest that there could be an interaction between the species, we cannot make any conclusions for the following reasons: firstly, the patterns exploited here might be artificial since the sample sizes are quite small; secondly, the nematodes undergo remarkable growth in the fish host (Anderson 2000; Berland 2006), so the length is dependent on the time since the worm was taken up by the fish; thirdly, *A. simplex* and *C. osculatum* have fish as transport hosts so only third stage larvae can be found. In contrast, *H. aduncum* matures in fish, so the length of this species is more dependent on the developmental stage (Berland 1961, 1989, 1998; Anderson 2000). The indication of interspecific interaction on growth rates should therefore be taken as a preliminary hypothesis which is interesting to test in future research.

4.5 The number of nematodes in relation to the condition of fish

It is hypothesised that nematodes reduce the well-being of the fish (Wootton 1998). If this is true, then there should be a correlation between the number of nematodes and the condition of its host. According to my results the number of nematodes does not affect the condition of the fish (Figure 3.11). This result was quite clear when all the fish species were both pooled or considered separately at Langøya and at Torbjørnskjær.

Berland (2006) suggested that perhaps the nematode-fish relationship is more mutualism than parasitism. He argued that by boring into and moving through stomach contents, *H. aduncum* aids digestion by making way for the digestive fluids to penetrate deeper in food particles. On the other hand, *H. aduncum* has shown to cause mortality in cultured Atlantic herring larvae by causing damage to vital organs (Tolonen & Karlsbakk 2003). This indicates that various fish species react differently to *H. aduncum*.

4.6 Conclusions

H. aduncum was the most common nematode found in the flatfishes sampled in the outer Oslofjord. This result supports previous studies concluding that *H. aduncum* is the most common nematode in the North Atlantic (Andersen 1993; Køie 1993; Balbuena *et al*. 1998). A major factor for the widespread occurrence of this nematode is that it is not host-specific and the intermediate and final hosts are abundant in the area (Berland 1961, 2006; Möller & Anders 1986; Andersen 1993; Balbuena *et al*. 1998).

Berland (1989) reported that *C. osculatum* sporadically occurs in fish on the Norwegian coast. In addition to previous studies (Aspholm 1991; Damsgaar Jensen 2009; Døvle Johansen 2012), my data also support the conclusion that this parasite is becoming more abundant in the Oslofjord. This might be the result of a different life-cycle of this species (Køie 1993) or there might have been changes in the intermediate or final host's population that makes *C. osculatum* more widespread.

The observed abundance level of *A. simplex* in my investigation is also in accordance with previous studies conducted in the Oslofjord (Aspholm 1991; Hansen & Malmstrøm 2006; Damsgaard Jensen 2009). This nematode seems to be going through population decline and the most plausible explanations for this are that (1) harbour porpoises have a rather irregular occurrence in the outer Oslofjord, and (2) although reproducing females have been found in harbour seals, this seal is not a suitable final host.

Hansen & Malmstrøm (2006) reported the first occurrence of the flatfish parasite *C. heterochrous* in the Oslofjord. While they found this parasite in European and American plaice in the inner Oslofjord, I found it in American plaice at Langøya area. This result may indicate that *C. heterochrous* is more widespread in the Oslofjord than previously thought.

American plaice had equally high infection rates at both study sites. Only one *H. aduncum* specimen has been recorded in American plaice at Torbjørnskjær in previous studies (Hansen & Malmstrøm 2006). In contrast *H. aduncum* was the most common nematode infecting American plaice at Langøya. Therefore, these results indicate that flatfish are becoming more heavily infected with *H. aduncum* in the Oslofjord. In addition, the mean lengths of this nematode in American plaice and witch flounder show that these flatfish are suitable transport and final hosts for *H. aduncum*. At Torbjørnskjær the most common nematode infecting American plaice was *C. osculatum* and, based on the mean observed length, this flatfish must also be regarded as a suitable transport host for *C. osculatum*.

While the number of nematodes in witch flounder and common dab had a random (Poisson) distribution, it was overdispersed (some fish were far more infected than the average level) in American plaice. A diverse feeding behaviour combined with population fluctuation may explain the difference in the infestation pattern in the three flatfishes. In addition, the growth of the nematodes indicates that there is an interspecific relationship when more than one nematode species is infecting the fish simultaneously.

4.7 Future research

We were three master students who started the parasite project in the outer Oslofjord in 2010. Lähdekorpi (2011) investigated *P. decipiens* infection in shorthorn sculpins, Døvle Johansen (2012) investigated the parasites in harbour seals and the topic for my thesis was the infection in flatfish.

Lähdekorpi (2011) observed that compared to Hvaler, the shorthorn sculpins at Koster had a much higher burden of *P. decipiens*. She explained this difference by the consistent higher abundance of seals at Koster. Her data supported the hypothesis proposed by Aspholm *et al*. (1995): Since seals do not prey on shorthorn sculpins, and cod-fish have a low abundance of *P. decipiens* in the Oslofjord, heavily infected seals have eaten cod-fish which recently have consumed infected shorthorn sculpins. It is the existence of an important intermediate host (shorthorn sculpins) situated outside the main route in the food chain, which creates the extreme overdispersed distribution of the number of parasites per host. Thus some individuals of both fish and seals are infected by more than 10 times the average infection. These random (Poisson) and non-random (lognormal) distributions were documented in Lähdekorpi's thesis.

My data on the infection in flatfish also revealed these two types of infection pattern. While the parasite numbers followed a random distribution in witch flounder and common dab, it was highly overdispersed in American plaice. Future work should therefore try to reveal the ecological difference between these three flatfishes and search for potential important intermediate hosts outside the main route in the food chain.

Previous investigations in the outer Oslofjord have revealed a large temporal and spatial fluctuation of the Anisakid nematodes (Svendsen 1990; Aspholm 1991; Jensen & Idås 1992; Hansen & Malmstrøm 2006; Damsgaard Jensen 2009). This variability was also confirmed by Døvle Johansen (2012) for *P. decipiens*, *A. simplex* and *C. osculatum* in harbour seals. Based on these theses it seems that while the abundances of *H. aduncum* and *C. osculatum* are increasing in the Oslofjord, the abundance of *A. simplex* is declining. My data also indicate that *C. heterochrous* is spreading in the Oslofjord. These fluctuations in nematode abundance may be induced by many factors (e.g. environmental changes and variation in fish and marine mammal abundance). To obtain a better documentation of these trends, future research needs to obtain a larger collection of samples, covering a greater number of fish species, from more locations from throughout the Oslofjord.

Køie (1993) showed that the nematode burden of *C. heterochrous* is influenced by the depth of the trawling and explained it with the distribution of the intermediate host *Nereis diversicolor*. Furthermore, Klimpel & Rückert (2005) discovered that the stratification of the water column has a big influence for the *H. aduncum* infection level. The latter investigation focused on pelagic fish (haddock and whiting) and if we combine its analysis with Køie (1993) and my data on flatfish, we realize that there is a possibility that processes in the whole water column may influence the abundance of nematodes whether their larvae are predominately consumed by pelagic or benthic fish species. Future studies should therefore also focus on interactions between water depths which are affecting the nematode burden.

There are no previous studies addressing whether the nematodes infecting the same fish may influence the growth rate and/or survival of each other. My data shows that there might be interspecific interactions between the nematode species within the same fish. Thus, *H. aduncum* achieved shorter and *C. osculatum* longer average lengths when infecting flatfish at the same time. Further, *A. simplex* experienced shorter and *H. aduncum* longer average lengths when infecting American plaice simultaneously. This might indicate an interesting competing order among these three nematodes: *A. simplex* $<$ *H. aduncum* $<$ *C. osculatum*. Future research should therefore test this hypothesis of interspecific interaction by controlled experiments.

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APPENDIX

Appendix I

A complete list of all the fish dissected during 2010 and 2012.

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
1	Hake		18.08.2010	Torbjørnskjær	230	36										0
2	European plaice		18.08.2010	Torbjørnskjær	170	28										0
3	Shorthorn sculpin		18.08.2010	Torbjørnskjær	270	28										0
4	Shorthorn sculpin		18.08.2010	Torbjørnskjær	80	20										0
5	Atlantic cod		18.08.2010	Torbjørnskjær	80	24										0
6	Witch flounder		18.08.2010	Torbjørnskjær	220	35										0
1	Common dab		18.08.2010	Torbjørnskjær	50	26	3									0
2	Shorthorn sculpin		18.08.2010	Torbjørnskjær	45	20	3									0
3	Atlantic cod		18.08.2010	Torbjørnskjær	40	25	1									0
4	Witch flounder		18.08.2010	Torbjørnskjær	210	34	4									0
5	European plaice	Female	18.08.2010	Torbjørnskjær	70	29	3									0
6	Common dab	Female	18.08.2010	Torbjørnskjær	100	25	3									0
7	Common dab	Male	18.08.2010	Torbjørnskjær	80	23	2									0
8	Shorthorn sculpin	Female	18.08.2010	Torbjørnskjær	240	29	4									0
9	American plaice	Female	18.08.2010	Torbjørnskjær	130	29	5									0
10	Common dab	Female	18.08.2010	Torbjørnskjær	130	26	4									0
11	Hake	Male	18.08.2010	Torbjørnskjær	200	34	4									0
12	Common dab	Female	18.08.2010	Torbjørnskjær	200	29	5									0
13	Common dab	Female	18.08.2010	Torbjørnskjær	40	20	1									0
14	Witch flounder		18.08.2010	Torbjørnskjær	40	23	3									0
15	American plaice		18.08.2010	Torbjørnskjær	30	22	3									0
16	American plaice		18.08.2010	Torbjørnskjær	30	19	2									0

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
17	European plaice	Male	18.08.2010	Torbjørnskjær	180	29	4									0
1	Whiting	Male	22.09.2010	Torbjørnskjær	131	26	2									0
2	Haddock	Female	22.09.2010	Torbjørnskjær	121	24	2				2					2
3	Haddock	Female	22.09.2010	Torbjørnskjær	117	24	2									0
4	Haddock	Female	22.09.2010	Torbjørnskjær	101	22	2									0
5	Atlantic cod	Male	22.09.2010	Torbjørnskjær	242	29	2						1	1		2
6	Atlantic cod	Male	22.09.2010	Torbjørnskjær	219	29	2									0
7	Atlantic cod	Male	22.09.2010	Torbjørnskjær	124	23	2									0
8	Atlantic cod	Male	22.09.2010	Torbjørnskjær	187	27	2									0
9	Atlantic cod	Male	22.09.2010	Torbjørnskjær	186	28	2									0
10	Atlantic cod	Male	22.09.2010	Torbjørnskjær	192	27	2									0
11	Atlantic cod	Female	22.09.2010	Torbjørnskjær	176	26	2									0
12	Atlantic cod	Female	22.09.2010	Torbjørnskjær	100	22	2									0
13	Shorthorn sculpin	Female	22.09.2010	Torbjørnskjær	148	23	3									0
14	Shorthorn sculpin	Male	22.09.2010	Torbjørnskjær	323	27	4									0
15	European plaice	Male	22.09.2010	Torbjørnskjær	318	30	4									0
16	European plaice	Male	22.09.2010	Torbjørnskjær	370	32	4									0
17	European plaice	Female	22.09.2010	Torbjørnskjær	372	32	4									0
18	European plaice	Male	22.09.2010	Torbjørnskjær	203	26	4									0
19	European plaice	Female	22.09.2010	Torbjørnskjær	323	32	4									0
20	European plaice	Female	22.09.2010	Torbjørnskjær	150	24	3									0
21	European plaice	Female	22.09.2010	Torbjørnskjær	220	28	4									0
22	Witch flounder	Male	22.09.2010	Torbjørnskjær	115	26	3									0
23	Common dab	Female	22.09.2010	Torbjørnskjær	166	25	3									0
24	Common dab	Male	22.09.2010	Torbjørnskjær	175	25	4									0
25	Common dab	Male	22.09.2010	Torbjørnskjær	221	28	5									0

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
26	Common dab	Female	22.09.2010	Torbjørnskjær	155	25	3					1				1
27	Common dab	Female	22.09.2010	Torbjørnskjær	180	25	4					1				1
28	American plaice	Male	22.09.2010	Torbjørnskjær	182	30	5			1	2	1				4
29	Ballan wrasse	Female	28.09.2010	Sandøy	1022	43							2			2
30	Saithe	Male	29.09.2010	Sandøy	246	31	1									0
31	Pollack	Female	29.09.2010	Sandøy	1346	53	4	1	7	11	4	3				26
32	Pollack	Male	29.09.2010	Sandøy	1318	55	4					1				1
33	Starry skate	Female	29.09.2010	Sandøy	1830	90										0
34	Spurdog	Female	29.09.2010	Sandøy	2300	113										0
35	Atlantic cod	Female	30.09.2010	Sandøy	1280	50	4									0
36	Atlantic cod	Female	30.09.2010	Sandøy	1400	55	5		2		3					5
37	Atlantic cod	Female	30.09.2010	Sandøy	1540	57	5					1				1
38	Pollack	Male	30.09.2010	Sandøy	2000	56	5					13				13
39	Saithe	Female	30.09.2010	Sandøy	228	28	1									0
40	Lumpsucker		30.09.2010	Sandøy	738	31						2				2
41	Ballan wrasse	Male	30.09.2010	Sandøy	281	28										0
42	Spurdog	Male	30.09.2010	Sandøy	1160	87										0
43	Spurdog	Female	30.09.2010	Sandøy	1250	81										0
44	Hake		31.08.2011	Langøya	15	18	1									0
45	Norway pout		31.08.2011	Langøya	35	17	3					1		4		5
46	Norway pout		31.08.2011	Langøya	36	18	3					1		4		5
47	Norway pout		31.08.2011	Langøya	20	17	2							9		9
48	Norway pout		31.08.2011	Langøya	16	16	2							3		3
49	Rabbit fish		31.08.2011	Langøya	11	14(18)										0
50	American plaice	Female	31.08.2011	Langøya	20	15	2									0
51	American plaice		31.08.2011	Langøya	23	16	2	1	2	2	2					7

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
52	American plaice	Female	31.08.2011	Langøya	74	20	3									0
53	American plaice		31.08.2011	Langøya	120	25	4				1					1
54	Witch flounder		31.08.2011	Langøya	40	20	2	1			1			2		4
55	Witch flounder		31.08.2011	Langøya	14	17	1		1							1
56	Witch flounder		31.08.2011	Langøya	37	19	2									0
57	Witch flounder		31.08.2011	Langøya	84	23	3			1						1
58	Witch flounder		31.08.2011	Langøya	104	25	3			1	2					3
59	Witch flounder		31.08.2011	Langøya	15	18	1									0
60	Witch flounder		31.08.2011	Langøya	92	23	3			1						1
61	Witch flounder		31.08.2011	Langøya	36	19	2									0
62	Witch flounder		31.08.2011	Langøya	30	19	2		2							2
63	Witch flounder		31.08.2011	Langøya	23	17	1			1						1
64	Witch flounder		31.08.2011	Langøya	31	18	2	2	2							4
65	Witch flounder		31.08.2011	Langøya	17	18	1									0
66	Witch flounder		31.08.2011	Langøya	26	18	2									0
67	Starry ray		31.08.2011	Langøya	45	12; 20										0
68	Starry ray		31.08.2011	Langøya	22	10; 17										0
69	Starry ray		31.08.2011	Langøya	17	10; 18										0
70	Starry ray		31.08.2011	Langøya	32	12; 20										0
71	Starry ray		31.08.2011	Langøya	8	7; 14										0
72	Starry ray		31.08.2011	Langøya	17	9; 16										0
73	Shorthorn sculpin	Male	26.09.2011	Torbjørnskjær	58	17	2									0
74	Shorthorn sculpin	Female	26.09.2011	Torbjørnskjær	159	21	3									0
75	Shorthorn sculpin	Female	26.09.2011	Torbjørnskjær	119	21	3									0
76	Shorthorn sculpin	Female	26.09.2011	Torbjørnskjær	50	16	2							4		4
77	Shorthorn sculpin	Male	26.09.2011	Torbjørnskjær	120	20	3							1		1

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
78	Shorthorn sculpin	Male	26.09.2011	Torbjørnskjær	64	17	2							1		1
79	Shorthorn sculpin	Female	26.09.2011	Torbjørnskjær	119	20	3									0
80	Shorthorn sculpin	Female	26.09.2011	Torbjørnskjær	104	17	3									0
81	Atlantic cod		26.09.2011	Torbjørnskjær	417	36	3									0
82	Atlantic cod	Female	26.09.2011	Torbjørnskjær	537	40	3									0
83	Atlantic cod	Female	26.09.2011	Torbjørnskjær	373	33	3									0
84	Atlantic cod	Male	26.09.2011	Torbjørnskjær	237	30	2		1							1
85	Atlantic cod	Male	26.09.2011	Torbjørnskjær	277	31	3									0
86	Atlantic cod	Female	26.09.2011	Torbjørnskjær	349	32	3		2							2
87	Atlantic cod	Female	26.09.2011	Torbjørnskjær	370	34	3									0
88	Atlantic cod	Female	26.09.2011	Torbjørnskjær	172	27	2							1		1
89	Atlantic cod	Male	26.09.2011	Torbjørnskjær	447	36	3									0
90	Atlantic cod	Male	26.09.2011	Torbjørnskjær	252	30	2									0
91	Atlantic cod	Male	26.09.2011	Torbjørnskjær	175	28	2									0
92	Whiting	Female	26.09.2011	Torbjørnskjær	235	30	3									0
93	Whiting	Female	26.09.2011	Torbjørnskjær	167	29	2									0
94	Whiting	Female	26.09.2011	Torbjørnskjær	154	27	2									0
95	Atlantic cod	Male	26.09.2011	Torbjørnskjær	35	16	1									0
96	Ballan wrasse		26.09.2011	Torbjørnskjær	22	12								1		1
97	Grey gurnard	Female	26.09.2011	Torbjørnskjær	211	30						1		3		4
98	Grey gurnard	Female	26.09.2011	Torbjørnskjær	191	30								5		5
99	European plaice	Male	26.09.2011	Torbjørnskjær	280	30	4									0
100	European plaice	Male	26.09.2011	Torbjørnskjær	148	25	3									0
101	Common dab	Male	26.09.2011	Torbjørnskjær	179	27	4									0
102	Common dab	Female	26.09.2011	Torbjørnskjær	166	26	4									0
103	Common dab	Female	26.09.2011	Torbjørnskjær	171	26	4					3				3

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
104	Common dab		26.09.2011	Torbjørnskjær	107	22	3									0
105	Common dab	Male	25.10.2011	Torbjørnskjær	50	17	1									0
106	Common dab		25.10.2011	Torbjørnskjær	90	22	2									0
107	Common dab	Female	25.10.2011	Torbjørnskjær	100	23	3									0
108	Common dab	Female	25.10.2011	Torbjørnskjær	140	25	2									0
109	Common dab	Female	25.10.2011	Torbjørnskjær	57	18	1									0
110	Common dab	Male	25.10.2011	Torbjørnskjær	83	20	2									0
111	Common dab	Female	25.10.2011	Torbjørnskjær	190	26	4					3				3
112	Common dab	Female	25.10.2011	Torbjørnskjær	56	18	1									0
113	Common dab	Female	25.10.2011	Torbjørnskjær	82	21	2									0
114	Common dab	Female	25.10.2011	Torbjørnskjær	110	23	3					1				1
115	Common dab	Female	25.10.2011	Torbjørnskjær	320	32	5									0
116	Common dab	Female	25.10.2011	Torbjørnskjær	140	25	2									0
117	Common dab	Female	25.10.2011	Torbjørnskjær	140	27	4									0
118	Common dab	Female	25.10.2011	Torbjørnskjær	100	23	3									0
119	Common dab	Male	25.10.2011	Torbjørnskjær	95	21	2									0
120	Common dab	Male	25.10.2011	Torbjørnskjær	70	19	2									0
121	Common dab	Male	25.10.2011	Torbjørnskjær	70	23	2					1				1
122	Common dab	Male	25.10.2011	Torbjørnskjær	80	21	2									0
123	Common dab	Female	25.10.2011	Torbjørnskjær	70	20	2									0
124	Common dab	Male	25.10.2011	Torbjørnskjær	36	17	1									0
125	Common dab	Male	25.10.2011	Torbjørnskjær	47	17	1									0
126	Common dab	Female	25.10.2011	Torbjørnskjær	51	17	1									0
127	Common dab	Male	25.10.2011	Torbjørnskjær	55	19	1									0
128	Common dab	Male	25.10.2011	Torbjørnskjær	50	17	1									0
129	Common dab	Female	25.10.2011	Torbjørnskjær	81	20	2									0

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
130	Common dab	Male	25.10.2011	Torbjørnskjær	86	22	2									0
131	American plaice		25.10.2011	Torbjørnskjær	37	16	2			1						1
132	American plaice	Female	25.10.2011	Torbjørnskjær	66	20	2							1		1
133	American plaice	Female	25.10.2011	Torbjørnskjær	68	20	2		1							1
134	American plaice	Female	25.10.2011	Torbjørnskjær	68	21	3					1				1
135	American plaice		25.10.2011	Torbjørnskjær	35	18	2							2		2
136	American plaice	Female	25.10.2011	Torbjørnskjær	62	19	2									0
137	American plaice	Female	25.10.2011	Torbjørnskjær	52	20	2		1							1
138	American plaice	Female	25.10.2011	Torbjørnskjær	51	19	2									0
139	American plaice	Female	25.10.2011	Torbjørnskjær	38	17	2							1		1
140	American plaice	Female	25.10.2011	Torbjørnskjær	46	18	2									0
141	American plaice	Female	25.10.2011	Torbjørnskjær	46	18	2									0
142	American plaice	Female	25.10.2011	Torbjørnskjær	57	19	2									0
143	American plaice	Female	25.10.2011	Torbjørnskjær	60	19	2					2				2
144	American plaice	Female	25.10.2011	Torbjørnskjær	60	19	2									0
145	American plaice		25.10.2011	Torbjørnskjær	26	15	2									0
146	American plaice	Female	25.10.2011	Torbjørnskjær	78	21	3									0
147	American plaice	Female	25.10.2011	Torbjørnskjær	89	22	3							1		1
148	American plaice	Female	25.10.2011	Torbjørnskjær	69	20	3									0
149	American plaice	Female	25.10.2011	Torbjørnskjær	64	20	2			1						1
150	American plaice	Female	25.10.2011	Torbjørnskjær	52	19	3							2		2
151	American plaice	Female	25.10.2011	Torbjørnskjær	76	21	3									0
152	American plaice	Female	25.10.2011	Torbjørnskjær	85	21	3							1		1
153	American plaice	Female	25.10.2011	Torbjørnskjær	88	22	3							1		1
154	American plaice	Female	25.10.2011	Torbjørnskjær	110	22	4									0
155	American plaice	Female	25.10.2011	Torbjørnskjær	100	24	4							1		1

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
156	American plaice	Female	25.10.2011	Torbjørnskjær	120	24	4	2						3		5
157	European plaice		25.10.2011	Torbjørnskjær	69	18	2									0
158	European plaice		25.10.2011	Torbjørnskjær	75	19	2									0
159	European plaice		25.10.2011	Torbjørnskjær	110	23	3									0
160	European plaice		25.10.2011	Torbjørnskjær	95	21	3									0
161	European plaice	Male	25.10.2011	Torbjørnskjær	96	20	3									0
162	European plaice	Female	25.10.2011	Torbjørnskjær	170	26	3									0
163	European plaice	Male	25.10.2011	Torbjørnskjær	140	25	3									0
164	European plaice	Female	25.10.2011	Torbjørnskjær	110	22	3									0
165	European plaice	Male	25.10.2011	Torbjørnskjær	125	24	3									0
166	European plaice	Female	25.10.2011	Torbjørnskjær	260	29	4									0
167	European plaice	Male	25.10.2011	Torbjørnskjær	110	23	3									0
168	European plaice	Male	25.10.2011	Torbjørnskjær	61	18	2									0
169	European plaice	Male	25.10.2011	Torbjørnskjær	79	20	3									0
170	European plaice	Female	25.10.2011	Torbjørnskjær	59	18	2									0
171	European plaice		25.10.2011	Torbjørnskjær	55	18	2									0
172	European plaice	Female	25.10.2011	Torbjørnskjær	120	23	3									0
173	European plaice	Female	25.10.2011	Torbjørnskjær	86	21	3									0
174	European plaice	Female	25.10.2011	Torbjørnskjær	83	21	2									0
175	European plaice	Male	25.10.2011	Torbjørnskjær	59	19	2									0
176	European plaice	Male	25.10.2011	Torbjørnskjær	73	20	2									0
177	European plaice	Male	25.10.2011	Torbjørnskjær	105	22	3									0
178	European plaice	Female	25.10.2011	Torbjørnskjær	140	24	3									0
179	Shorthorn sculpin	Female	25.10.2011	Torbjørnskjær	91	19	3							1		1
180	Shorthorn sculpin	Female	25.10.2011	Torbjørnskjær	102	19	3									0
181	Shorthorn sculpin	Female	25.10.2011	Torbjørnskjær	140	21	3							2		2

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
182	Shorthorn sculpin	Female	25.10.2011	Torbjørnskjær	135	22	3					1				1
183	Whiting	Male	25.10.2011	Torbjørnskjær	200	28	3									0
184	Whiting	Female	25.10.2011	Torbjørnskjær	120	26	2									0
185	Whiting	Female	25.10.2011	Torbjørnskjær	200	30	3									0
186	Whiting	Female	25.10.2011	Torbjørnskjær	230	32	3									0
187	Whiting	Female	25.10.2011	Torbjørnskjær	115	26	2									0
188	Whiting	Female	25.10.2011	Torbjørnskjær	180	28	2									0
189	Whiting	Female	25.10.2011	Torbjørnskjær	140	26	2									0
190	Whiting	Female	25.10.2011	Torbjørnskjær	110	25	2							2		2
191	Whiting	Male	25.10.2011	Torbjørnskjær	90	23	2									0
192	Whiting	Female	25.10.2011	Torbjørnskjær	200	28	3									0
193	Whiting	Male	25.10.2011	Torbjørnskjær	140	27	2									0
194	Whiting	Male	25.10.2011	Torbjørnskjær	160	28	3		1			1		1		3
195	Whiting	Male	25.10.2011	Torbjørnskjær	140	27	2									0
196	Whiting	Female	25.10.2011	Torbjørnskjær	230	30	3		1							1
197	Whiting	Male	25.10.2011	Torbjørnskjær	210	29	3									0
198	Whiting	Male	25.10.2011	Torbjørnskjær	160	26	2									0
199	Whiting	Male	25.10.2011	Torbjørnskjær	145	26	2									0
200	Whiting	Male	25.10.2011	Torbjørnskjær	130	25	2					1				1
201	Whiting	Male	25.10.2011	Torbjørnskjær	140	26	2									0
202	Whiting	Female	25.10.2011	Torbjørnskjær	200	29	3									0
203	Whiting	Male	25.10.2011	Torbjørnskjær	130	26	2									0
204	Whiting		25.10.2011	Torbjørnskjær	140	27	2					1				1
205	Whiting	Male	25.10.2011	Torbjørnskjær	130	26	2									0
206	Whiting	Male	25.10.2011	Torbjørnskjær	120	25	2									0
207	Whiting	Male	25.10.2011	Torbjørnskjær	100	24	2									0

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
208	Whiting	Male	25.10.2011	Torbjørnskjær	170	28	2					1				1
209	Whiting	Male	25.10.2011	Torbjørnskjær	160	27	3									0
210	Atlantic cod	Male	25.10.2011	Torbjørnskjær	320	33	3					4				4
211	Atlantic cod	Male	25.10.2011	Torbjørnskjær	230	29	2			1	1					2
212	Atlantic cod	Female	25.10.2011	Torbjørnskjær	350	34	3				2			1		3
213	Atlantic cod	Male	25.10.2011	Torbjørnskjær	260	31	2	1								1
214	Atlantic cod	Female	25.10.2011	Torbjørnskjær	360	34	3									0
215	Atlantic cod	Male	25.10.2011	Torbjørnskjær	300	32	3									0
216	Atlantic cod	Male	25.10.2011	Torbjørnskjær	270	32	2		3							3
217	Atlantic cod	Male	25.10.2011	Torbjørnskjær	510	37	3		1	3						4
218	Hake	Male	25.10.2011	Torbjørnskjær	160	27	3									0
219	Hake	Female	25.10.2011	Torbjørnskjær	160	29	3				1					1
220	Hake	Female	25.10.2011	Torbjørnskjær	240	22	2									0
221	Hake	Male	25.10.2011	Torbjørnskjær	170	29	3									0
222	Hake	Male	25.10.2011	Torbjørnskjær	190	30	3									0
223	Hake	Male	25.10.2011	Torbjørnskjær	110	26	2									0
224	Hake	Male	25.10.2011	Torbjørnskjær	210	38	4									0
225	Hake	Male	25.10.2011	Torbjørnskjær	160	28	3				1					1
226	Hake	Male	25.10.2011	Torbjørnskjær	170	29	3					1				1
227	Hake	Female	25.10.2011	Torbjørnskjær	160	29	3				1	1		2		4
228	Hake	Male	25.10.2011	Torbjørnskjær	200	30	3			1						1
229	Hake	Female	25.10.2011	Torbjørnskjær	260	32	4									0
230	Hake	Male	25.10.2011	Torbjørnskjær	200	31	3									0
231	Whiting	Male	25.10.2011	Torbjørnskjær	100	24	2									0
232	Witch flounder		2.11.2011	Langøya	40	20	2									0
233	Witch flounder		2.11.2011	Langøya	53	21	2							1		1

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
234	Witch flounder	Female	2.11.2011	Langøya	110	27	3									0
235	Witch flounder	Male	2.11.2011	Langøya	120	27	3		1	1	1					3
236	American plaice	Female	2.11.2011	Langøya	76	21	3		2	1				5		8
237	American plaice	Female	2.11.2011	Langøya	76	22	3		1	1	6					8
238	American plaice	Female	2.11.2011	Langøya	105	23	4			5	4			3		12
239	American plaice	Female	2.11.2011	Langøya	44	17	2									0
240	American plaice	Female	2.11.2011	Langøya	60	19	3									0
241	American plaice	Female	2.11.2011	Langøya	34	17	2			1						1
242	American plaice	Male	2.11.2011	Langøya	45	19	2							1		1
243	American plaice	Female	2.11.2011	Langøya	42	18	2							2		2
244	American plaice	Female	2.11.2011	Langøya	45	18	2	3						3		6
245	American plaice	Male	2.11.2011	Langøya	43	19	2									0
246	American plaice	Male	2.11.2011	Langøya	44	18	2									0
247	American plaice	Male	2.11.2011	Langøya	67	22	3				1			1		2
248	American plaice	Female	2.11.2011	Langøya	130	26	4				4					4
249	American plaice	Female	2.11.2011	Langøya	100	23	3			3						3
250	American plaice	Female	2.11.2011	Langøya	61	19	2									0
251	American plaice	Female	2.11.2011	Langøya	70	20	3			1						1
252	American plaice	Female	2.11.2011	Langøya	68	20	3		2	2						4
253	American plaice	Male	2.11.2011	Langøya	64	20	3							1		1
254	American plaice	Female	2.11.2011	Langøya	72	22	3				1					1
255	American plaice	Female	2.11.2011	Langøya	85	22	3									0
256	American plaice	Male	2.11.2011	Langøya	93	23	3							2		2
257	American plaice	Male	2.11.2011	Langøya	80	23	3			3	4					7
258	American plaice	Female	2.11.2011	Langøya	107	24	4		1	4	4					9
259	American plaice	Female	2.11.2011	Langøya	110	24	4		1		1					2

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
260	American plaice	Female	19.01.2012	Langøya	125	28	5		1							1
261	American plaice	Female	19.01.2012	Langøya	92	23	3									0
262	American plaice	Female	19.01.2012	Langøya	120	25	4									0
263	American plaice	Female	19.01.2012	Langøya	105	26	4									0
264	American plaice	Female	19.01.2012	Langøya	82	23	3									0
265	American plaice	Female	19.01.2012	Langøya	84	22	3									0
266	American plaice	Female	19.01.2012	Langøya	80	23	3									0
267	American plaice	Female	19.01.2012	Langøya	91	24	3		2	1				2		5
268	American plaice	Female	19.01.2012	Langøya	101	24	3									0
269	American plaice	Female	19.01.2012	Langøya	103	26	4									0
270	American plaice	Female	19.01.2012	Langøya	104	24	4		1							1
271	American plaice	Female	19.01.2012	Langøya	80	24	3	1								1
272	American plaice	Female	19.01.2012	Langøya	90	23	3			1						1
273	American plaice	Female	19.01.2012	Langøya	93	22	3								1	0
274	American plaice	Female	19.01.2012	Langøya	85	23	3				2			1		3
275	American plaice	Female	19.01.2012	Langøya	114	27	4	1								1
276	American plaice	Female	19.01.2012	Langøya	104	24	3							1		1
277	American plaice	Male	19.01.2012	Langøya	105	26	4									0
278	American plaice	Female	19.01.2012	Langøya	110	26	4								1	0
279	American plaice	Female	19.01.2012	Langøya	110	25	4			1						1
280	American plaice	Female	19.01.2012	Langøya	130	27	4			2	2			1		5
281	American plaice	Female	19.01.2012	Langøya	110	25	4							1		1
282	American plaice	Female	19.01.2012	Langøya	110	24	4			2	2					4
283	American plaice	Female	19.01.2012	Langøya	130	26	4		1					1		2
284	American plaice	Female	19.01.2012	Langøya	130	26	4	1								1
285	Common dab	Male	26.01.2012	Langøya	90	21	2					2				2

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
286	Common dab	Male	26.01.2012	Langøya	110	24	3					1				1
287	American plaice	Female	26.01.2012	Langøya	76	22	3				1					1
288	American plaice	Female	26.01.2012	Langøya	88	23	3									0
289	American plaice	Female	26.01.2012	Langøya	105	24	4				1			1		2
290	American plaice	Female	26.01.2012	Langøya	78	21	3									0
291	American plaice		26.01.2012	Langøya	57	21	3			2				1		3
292	American plaice	Female	26.01.2012	Langøya	67	21	3	1								1
293	American plaice	Female	26.01.2012	Langøya	64	21	3							1		1
294	American plaice	Female	26.01.2012	Langøya	79	22	3		1							1
295	American plaice	Female	26.01.2012	Langøya	78	22	3		1	3	3					7
296	American plaice	Female	26.01.2012	Langøya	61	21	3									0
297	American plaice	Male	26.01.2012	Langøya	61	20	3		1					1		2
298	American plaice	Female	26.01.2012	Langøya	110	26	4							3		3
299	American plaice	Female	26.01.2012	Langøya	65	22	3							1		1
300	American plaice	Female	26.01.2012	Langøya	72	21	3									0
301	American plaice	Male	26.01.2012	Langøya	87	22	3	1		1						2
302	American plaice	Female	26.01.2012	Langøya	89	23	3									0
303	American plaice	Female	26.01.2012	Langøya	75	22	3			2						2
304	American plaice	Female	26.01.2012	Langøya	99	24	3			1						1
305	American plaice	Female	26.01.2012	Langøya	99	24	4									0
306	American plaice	Female	26.01.2012	Langøya	105	24	3									0
307	American plaice	Female	26.01.2012	Langøya	73	22	3									0
308	American plaice	Female	26.01.2012	Langøya	80	23	3			1						1
309	American plaice		26.01.2012	Langøya	70	23	3				2			1		3
310	American plaice	Female	26.01.2012	Langøya	93	23	3							1		1
311	American plaice	Female	26.01.2012	Langøya	83	22	3				3					3

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
312	American plaice	Female	26.01.2012	Langøya	106	23	4									0
313	American plaice	Female	26.01.2012	Langøya	107	24	4							9		9
314	American plaice	Female	26.01.2012	Langøya	120	25	4									0
315	American plaice	Female	26.01.2012	Langøya	110	24	4									0
316	American plaice	Female	26.01.2012	Langøya	115	27	4	1								1
317	American plaice	Female	26.01.2012	Langøya	130	27	4			1	2					3
318	American plaice	Female	26.01.2012	Langøya	130	27	4		1	2						3
319	American plaice	Male	26.01.2012	Langøya	200	31	5		2		1			1		4
320	European flounder	Male	2.02.2012	Langøya	210	28	4							1		1
321	American plaice	Female	2.02.2012	Langøya	80	23	3									0
322	American plaice	Female	2.02.2012	Langøya	76	23	3							1		1
323	American plaice	Female	2.02.2012	Langøya	88	23	3		4							4
324	American plaice	Female	2.02.2012	Langøya	78	23	3			5	1				1	6
325	American plaice	Female	2.02.2012	Langøya	74	21	3									0
326	American plaice	Female	2.02.2012	Langøya	84	22	3		2	1	1					4
327	American plaice	Female	2.02.2012	Langøya	89	23	3									0
328	American plaice	Female	2.02.2012	Langøya	86	22	3							3		3
329	American plaice	Female	2.02.2012	Langøya	102	25	4			1						1
330	American plaice	Female	2.02.2012	Langøya	91	23	3									0
331	American plaice	Male	2.02.2012	Langøya	97	23	3									0
332	American plaice	Female	2.02.2012	Langøya	90	23	3									0
333	American plaice	Male	2.02.2012	Langøya	110	26	4									0
334	American plaice	Female	2.02.2012	Langøya	110	26	4									0
335	American plaice	Female	2.02.2012	Langøya	110	26	4									0
336	American plaice	Female	2.02.2012	Langøya	110	25	4									0
337	American plaice	Female	2.02.2012	Langøya	170	28	5									0

Nr	Fish	Gender	Date	Area	Weight (g)	Length (cm)	Age (years)	H.a. L3	H.a. L4	H.a. ♂	H.a. ♀	A.s. L3	P.d. L3	C.o. L3	C.h.	Nem total
338	American plaice	Female	2.02.2012	Drøbak	69	20	3									0
339	American plaice	Female	2.02.2012	Drøbak	54	21	3									0
340	American plaice	Female	2.02.2012	Drøbak	68	22	3									0
341	American plaice	Female	2.02.2012	Drøbak	63	22	3									0
342	American plaice	Female	2.02.2012	Drøbak	66	22	3									0
343	American plaice	Female	2.02.2012	Drøbak	73	22	3									0
344	American plaice	Female	2.02.2012	Drøbak	86	23	3									0
345	American plaice	Female	2.02.2012	Drøbak	93	22	3									0
346	Common dab	Male	8.03.2012	Langøya	95	24	3			1						1
347	Common dab	Male	8.03.2012	Langøya	100	23	3	2								2
348	Common dab		8.03.2012	Langøya	210	28	5									0
349	American plaice		8.03.2012	Langøya	110	26	4									0
350	American plaice	Female	8.03.2012	Langøya	69	21	3									0
351	American plaice	Female	8.03.2012	Langøya	82	23	3									0
352	American plaice	Female	8.03.2012	Langøya	86	23	3		1							1
353	American plaice	Female	8.03.2012	Langøya	97	23	3									0
354	American plaice	Male	8.03.2012	Langøya	70	21	3									0
355	American plaice	Female	8.03.2012	Langøya	86	23	3									0
356	American plaice	Female	8.03.2012	Langøya	90	22	3									0
357	American plaice	Male	8.03.2012	Langøya	60	21	3									0
358	American plaice	Female	8.03.2012	Langøya	73	23	3		5							5
359	American plaice	Female	8.03.2012	Langøya	70	23	3									0
360	American plaice	Female	8.03.2012	Langøya	100	24	4									0
361	American plaice	Female	8.03.2012	Langøya	78	23	3									0

Appendix II

Nematode infection parameters in all fish at the two study areas.

Study area	Specie	Nr of fish	Infected fish	Prevalence (%)	Nr of nem.	Abundance	Intensity
Langøya	American plaice	116	64	55,2	190	1,64	2,97
	Rabbit fish	1	0	0,0	0	0,00	0,00
	Starry ray	6	0	0,0	0	0,00	0,00
	European hake	1	0	0,0	0	0,00	0,00
	Norway pout	4	4	100,0	22	5,50	5,50
	Common dab	5	4	80,0	6	1,20	1,50
	European flounder	1	1	100,0	1	1,00	1,00
	Witch flounder	17	10	58,8	21	1,24	2,10
	TOTAL	**151**	**83**	**55,0**	**240**	**1,59**	**2,89**
Torbjørnskjær	Goldsinny-wrasse	1	1	100,0	1	1,00	1,00
	American plaice	30	16	53,3	26	0,87	1,63
	Whiting	32	6	18,8	9	0,28	1,50
	Haddock	3	1	33,3	2	0,67	2,00
	Grey gurnard	2	2	100,0	9	4,50	4,50
	European hake	15	5	33,3	8	0,53	1,60
	European plaice	34	0	0,0	0	0,00	0,00
	Common dab	41	6	14,6	10	0,24	1,67
	Witch flounder	4	0	0,0	0	0,00	0,00
	Atlantic cod	30	10	33,3	22	0,73	2,20
	Shorthorn sculpin	18	6	33,3	10	0,56	1,67
	TOTAL	**210**	**53**	**25,2**	**97**	**0,46**	**1,83**
Oslofjord	**TOTAL**	**361**	**136**	**37,67**	**337**	**0,93**	**2,48**

Hysterothylacium aduncum						
Study area	**Specie**	**Infected fish**	**Prevalence (%)**	**Nr of nematodes**	**Abundance**	**Intensity**
Langøya	American plaice	51	44,0	141	1,22	2,76
	Rabbit fish	0	0,0	0	0,00	0,00
	Starry ray	0	0,0	0	0,00	0,00
	European hake	0	0,0	0	0,00	0,00
	Norway pout	0	0,0	0	0,00	0,00
	Common dab	2	40,0	3	0,60	1,50
	European flounder	0	0,0	0	0,00	0,00
	Witch flounder	9	52,9	18	1,06	2,00
	TOTAL	**62**	**41,1**	**162**	**1,07**	**2,61**
Torbjørnskjær	Goldsinny-wrasse	0	0,0	0	0,00	0,00
	American plaice	6	20,0	9	0,30	1,50
	Whiting	2	6,3	2	0,06	1,00
	Haddock	1	33,3	2	0,67	2,00
	Grey gurnard	0	0,0	0	0,00	0,00
	European hake	4	26,7	4	0,27	1,00
	European plaice	0	0,0	0	0,00	0,00
	Common dab	0	0,0	0	0,00	0,00
	Witch flounder	0	0,0	0	0,00	0,00
	Atlantic cod	7	23,3	15	0,50	2,14
	Shorthorn sculpin	0	0,0	0	0,00	0,00
	TOTAL	**20**	**9,5**	**32**	**0,15**	**1,60**
Oslofjord	**TOTAL**	**82**	**22,7**	**194**	**0,54**	**2,37**

Anisakis simplex						
Study area	**Specie**	**Infected fish**	**Prevalence (%)**	**Nr of nematodes**	**Abundance**	**Intensity**
Langøya	American plaice	0	0,0	0	0,00	0,00
	Rabbit fish	0	0,0	0	0,00	0,00
	Starry ray	0	0,0	0	0,00	0,00
	European hake	0	0,0	0	0,00	0,00
	Norway pout	2	50,0	2	0,50	1,00
	Common dab	2	40,0	3	0,60	1,50
	European flounder	0	0,0	0	0,00	0,00
	Witch flounder	0	0,0	0	0,00	0,00
	TOTAL	**4**	**2,6**	**5**	**0,03**	**1,25**
Torbjørnskjær	Goldsinny-wrasse	0	0,0	0	0,00	0,00
	American plaice	3	10,0	4	0,13	1,33
	Whiting	4	12,5	4	0,13	1,00
	Haddock	0	0,0	0	0,00	0,00
	Grey gurnard	1	50,0	1	0,50	1,00
	European hake	2	13,3	2	0,13	1,00
	European plaice	0	0,0	0	0,00	0,00
	Common dab	6	14,6	10	0,24	1,67
	Witch flounder	0	0,0	0	0,00	0,00
	Atlantic cod	1	3,3	4	0,13	4,00
	Shorthorn sculpin	1	5,6	1	0,06	1,00
	TOTAL	**18**	**8,6**	**26**	**0,12**	**1,44**
Oslofjord	**TOTAL**	**22**	**6,1**	**31**	**0,09**	**1,41**

Contracaecum osculatum						
Study area	**Specie**	**Infected fish**	**Prevalence (%)**	**Nr of nematodes**	**Abundance**	**Intensity**
Langøya	American plaice	26	22,4	49	0,42	1,88
	Rabbit fish	0	0,0	0	0,00	0,00
	Starry ray	0	0,0	0	0,00	0,00
	European hake	0	0,0	0	0,00	0,00
	Norway pout	4	100,0	20	5,00	5,00
	Common dab	0	0,0	0	0,00	0,00
	European flounder	1	100,0	1	1,00	1,00
	Witch flounder	2	11,8	3	0,18	1,50
	TOTAL	**33**	**21,9**	**73**	**0,48**	**2,21**
Torbjørnskjær	Goldsinny-wrasse	1	100,0	1	1,00	1,00
	American plaice	9	30,0	13	0,43	1,44
	Whiting	2	6,3	3	0,09	1,50
	Haddock	0	0,0	0	0,00	0,00
	Grey gurnard	2	100,0	8	4,00	4,00
	European hake	1	6,7	2	0,13	2,00
	European plaice	0	0,0	0	0,00	0,00
	Common dab	0	0,0	0	0,00	0,00
	Witch flounder	0	0,0	0	0,00	0,00
	Atlantic cod	3	10,0	3	0,10	1,00
	Shorthorn sculpin	5	27,8	9	0,50	1,80
	TOTAL	**23**	**11,0**	**39**	**0,19**	**1,70**
Oslofjord	**TOTAL**	**56**	**15,5**	**112**	**0,31**	**2,00**

Appendix III

Norwegian, English and Latin names of the fish species sampled with the frequencies in the samples at the two study areas.

Norwegian	English	Latin	Torbjørnskjær	Langøya
Bergnebb	Goldsinny-wrasse	*Ctenolabrus rupestris*	1 (0 %)	
Gapeflyndre	American plaice	*Hippoglossoides platessoides*	30 (14 %)	116 (76 %)
Havmus	Rabbit fish	*Chimaera monstrosa*		1 (1 %)
Hvitting	Whiting	*Merlangius merlangus*	32 (15 %)	
Hyse	Haddock	*Melanogrammus aeglefinus*	3 (1 %)	
Kloskate	Starry ray	*Amblyraja radiata*		6 (4 %)
Knurr	Grey gurnard	*Eutrigla gurnardus*	2 (1 %)	
Lysing	European hake	*Merluccius merluccius*	15 (7 %)	1 (1 %)
Øyepål	Norway pout	*Trisopterus esmarkii*		4 (3 %)
Rødspette	European plaice	*Pleuronectes platessa*	34 (16 %)	
Sandflyndre	Common dab	*Limanda limanda*	41 (21 %)	5 (3 %)
Skrubbe	European flounder	*Platichthys flesus*		1 (1 %)
Smørflyndre	Witch flounder	*Glyptocephalus cynoglossus*	4 (2 %)	17 (11 %)
Torsk	Atlantic cod	*Gadus morhua*	30 (14 %)	
Ulke	Shorthorn sculpin	*Myoxocephalus scorpius*	18 (9 %)	
TOTAL			**210**	**151**

Appendix IV

Tables that were used for G-test/Likelihood Ratio analyzes in the Intensity section.

All fish; All nematodes					
Observed	1	2 - 3	4 - 5	6 +	**TOTAL**
Langøya	**35**	**24**	**13**	**11**	83
Torbjørnskjær	**32**	**13**	**8**	**0**	53
Total	67	37	21	11	136

Expected	1	2 - 3	4 - 5	6 +
Langøya	**40,89**	**22,58**	**12,82**	**6,71**
Torbjørnskjær	**26,11**	**14,42**	**8,18**	**4,29**

All fish; *H. aduncum*					
Observed	1	2	3 - 4	5 +	**TOTAL**
Langøya	**28**	**9**	**17**	**8**	62
Torbjørnskjær	**12**	**5**	**3**	**0**	20
Total	40	14	20	8	82

Expected	1	2	3 - 4	5 +
Langøya	**30,24**	**10,59**	**15,12**	**6,05**
Torbjørnskjær	**9,76**	**3,41**	**4,88**	**1,95**

All fish; *C. osculatum*					
Observed	1 - 2	3 - 4	5 - 6	7 +	**TOTAL**
Langøya	**23**	**7**	**1**	**2**	33
Torbjørnskjær	**19**	**3**	**1**	**0**	23
Total	42	10	2	2	56

Expected	1 - 2	3 - 4	5 - 6	7 +
Langøya	**24,75**	**5,89**	**1,18**	**1,18**
Torbjørnskjær	**17,25**	**4,11**	**0,82**	**0,82**

All fish; *A. simplex*				
Observed	1	2	3 +	**TOTAL**
Langøya	**3**	**1**	**0**	4
Torbjørnskjær	**14**	**1**	**3**	18
Total	17	2	3	22

Expected	1	2	3 +
Langøya	**3,09**	**0,36**	**0,55**
Torbjørnskjær	**13,91**	**1,64**	**2,45**

American plaice; All nematodes				
Observed	1 - 2	3 - 5	6 +	**TOTAL**
Langøya	**36**	**18**	**10**	64
Torbjørnskjær	**14**	**2**	**0**	16
Total	50	20	10	80

Expected	1 - 2	3 - 5	6 +
Langøya	**40,00**	**16,00**	**8,00**
Torbjørnskjær	**10,00**	**4,00**	**2,00**

American plaice; *H. aduncum*				
Observed	1	2 - 3	4 +	**TOTAL**
Langøya	**23**	**14**	**14**	51
Torbjørnskjær	**4**	**2**	**0**	6
Total	27	16	14	57

Expected	1	2 - 3	4 +
Langøya	**24,16**	**14,32**	**12,53**
Torbjørnskjær	**2,84**	**1,68**	**1,47**

American plaice; *C. osculatum*			
Observed	1 - 2	3 +	**TOTAL**
Langøya	**20**	**6**	26
Torbjørnskjær	**8**	**1**	9
Total	28	7	35

Expected	1 - 2	3 +
Langøya	**20,80**	**5,20**
Torbjørnskjær	**7,20**	**1,80**

Common dab; All nematodes			
Observed	1 ind	2 to 3	**TOTAL**
Langøya	**2**	**2**	4
Torbjørnskjær	**4**	**2**	6
Total	6	4	10

Expected	1 ind	2 to 3
Langøya	**2,40**	**1,60**
Torbjørnskjær	**3,60**	**2,40**

Common dab; *A. simplex*			
Observed	1	2 - 3	**TOTAL**
Langøya	**1**	**1**	2
Torbjørnskjær	**4**	**2**	6
Total	5	3	8

Expected	1	2 - 3
Langøya	**1,25**	**0,75**
Torbjørnskjær	**3,75**	**2,25**

Appendix V

Length measurements of all the nematodes sampled at Langøya and at Torbjørnskjær.

Fish	Study area	Nematode	Stage	Length (mm)
American plaice	Torbjørnskjær	*A. simplex*	L3	15
American plaice	Torbjørnskjær	*A. simplex*	L3	16
American plaice	Torbjørnskjær	*A. simplex*	L3	18
American plaice	Torbjørnskjær	*A. simplex*	L3	20
Atlantic cod	Torbjørnskjær	*A. simplex*	L3	17
Atlantic cod	Torbjørnskjær	*A. simplex*	L3	18
Atlantic cod	Torbjørnskjær	*A. simplex*	L3	19
Atlantic cod	Torbjørnskjær	*A. simplex*	L3	20
Common dab	Torbjørnskjær	*A. simplex*	L3	15
Common dab	Torbjørnskjær	*A. simplex*	L3	15
Common dab	Torbjørnskjær	*A. simplex*	L3	18
Common dab	Torbjørnskjær	*A. simplex*	L3	18
Common dab	Torbjørnskjær	*A. simplex*	L3	19
Common dab	Torbjørnskjær	*A. simplex*	L3	19
Common dab	Torbjørnskjær	*A. simplex*	L3	20
Common dab	Torbjørnskjær	*A. simplex*	L3	20
Common dab	Langøya	*A. simplex*	L3	21
Common dab	Torbjørnskjær	*A. simplex*	L3	21
Common dab	Langøya	*A. simplex*	L3	23
Common dab	Langøya	*A. simplex*	L3	25
Common dab	Torbjørnskjær	*A. simplex*	L3	27
European hake	Torbjørnskjær	*A. simplex*	L3	18
European hake	Torbjørnskjær	*A. simplex*	L3	22
Grey gurnard	Torbjørnskjær	*A. simplex*	L3	22
Norway pout	Langøya	*A. simplex*	L3	22
Norway pout	Langøya	*A. simplex*	L3	23
Shorthorn sculpin	Torbjørnskjær	*A. simplex*	L3	20
Whiting	Torbjørnskjær	*A. simplex*	L3	18
Whiting	Torbjørnskjær	*A. simplex*	L3	21
Whiting	Torbjørnskjær	*A. simplex*	L3	23
Whiting	Torbjørnskjær	*A. simplex*	L3	26
American plaice	Langøya	*C. heterochrous*		12
American plaice	Langøya	*C. osculatum*	L3	9
American plaice	Langøya	*C. osculatum*	L3	9
American plaice	Langøya	*C. osculatum*	L3	10
American plaice	Torbjørnskjær	*C. osculatum*	L3	10
American plaice	Torbjørnskjær	*C. osculatum*	L3	10
American plaice	Langøya	*C. osculatum*	L3	11
American plaice	Langøya	*C. osculatum*	L3	11
American plaice	Langøya	*C. osculatum*	L3	12
American plaice	Torbjørnskjær	*C. osculatum*	L3	12

Fish	Study area	Nematode	Stage	Length (mm)
American plaice	Langøya	*C. osculatum*	L3	13
American plaice	Langøya	*C. osculatum*	L3	13
American plaice	Langøya	*C. osculatum*	L3	13
American plaice	Torbjørnskjær	*C. osculatum*	L3	13
American plaice	Torbjørnskjær	*C. osculatum*	L3	13
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	14
American plaice	Torbjørnskjær	*C. osculatum*	L3	14
American plaice	Langøya	*C. osculatum*	L3	15
American plaice	Langøya	*C. osculatum*	L3	15
American plaice	Langøya	*C. osculatum*	L3	15
American plaice	Langøya	*C. osculatum*	L3	15
American plaice	Langøya	*C. osculatum*	L3	16
American plaice	Langøya	*C. osculatum*	L3	16
American plaice	Langøya	*C. osculatum*	L3	16
American plaice	Langøya	*C. osculatum*	L3	16
American plaice	Langøya	*C. osculatum*	L3	17
American plaice	Langøya	*C. osculatum*	L3	17
American plaice	Langøya	*C. osculatum*	L3	17
American plaice	Langøya	*C. osculatum*	L3	17
American plaice	Torbjørnskjær	*C. osculatum*	L3	17
American plaice	Langøya	*C. osculatum*	L3	18
American plaice	Langøya	*C. osculatum*	L3	18
American plaice	Langøya	*C. osculatum*	L3	18
American plaice	Langøya	*C. osculatum*	L3	18
American plaice	Langøya	*C. osculatum*	L3	18
American plaice	Langøya	*C. osculatum*	L3	18
American plaice	Torbjørnskjær	*C. osculatum*	L3	18
American plaice	Torbjørnskjær	*C. osculatum*	L3	18
American plaice	Langøya	*C. osculatum*	L3	19
American plaice	Torbjørnskjær	*C. osculatum*	L3	19
American plaice	Torbjørnskjær	*C. osculatum*	L3	19
American plaice	Torbjørnskjær	*C. osculatum*	L3	19
American plaice	Torbjørnskjær	*C. osculatum*	L3	19
American plaice	Langøya	*C. osculatum*	L3	20
American plaice	Langøya	*C. osculatum*	L3	20
American plaice	Langøya	*C. osculatum*	L3	20
American plaice	Langøya	*C. osculatum*	L3	21
American plaice	Langøya	*C. osculatum*	L3	22

Fish	Study area	Nematode	Stage	Length (mm)
American plaice	Langøya	*C. osculatum*	L3	22
American plaice	Langøya	*C. osculatum*	L3	22
American plaice	Langøya	*C. osculatum*	L3	23
American plaice	Langøya	*C. osculatum*	L3	24
American plaice	Langøya	*C. osculatum*	L3	25
American plaice	Langøya	*C. osculatum*	L3	25
American plaice	Langøya	*C. osculatum*	L3	25
American plaice	Langøya	*C. osculatum*	L3	26
Atlantic cod	Torbjørnskjær	*C. osculatum*	L3	9
Atlantic cod	Torbjørnskjær	*C. osculatum*	L3	21
European flounder	Langøya	*C. osculatum*	L3	23
European hake	Torbjørnskjær	*C. osculatum*	L3	17
European hake	Torbjørnskjær	*C. osculatum*	L3	19
Goldsinny-wrasse	Torbjørnskjær	*C. osculatum*	L3	21
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	8
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	10
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	11
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	14
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	14
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	18
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	19
Grey gurnard	Torbjørnskjær	*C. osculatum*	L3	21
Norway pout	Langøya	*C. osculatum*	L3	3
Norway pout	Langøya	*C. osculatum*	L3	4
Norway pout	Langøya	*C. osculatum*	L3	5
Norway pout	Langøya	*C. osculatum*	L3	5
Norway pout	Langøya	*C. osculatum*	L3	6
Norway pout	Langøya	*C. osculatum*	L3	7
Norway pout	Langøya	*C. osculatum*	L3	7
Norway pout	Langøya	*C. osculatum*	L3	8
Norway pout	Langøya	*C. osculatum*	L3	8
Norway pout	Langøya	*C. osculatum*	L3	8
Norway pout	Langøya	*C. osculatum*	L3	9
Norway pout	Langøya	*C. osculatum*	L3	11
Norway pout	Langøya	*C. osculatum*	L3	11
Norway pout	Langøya	*C. osculatum*	L3	11
Norway pout	Langøya	*C. osculatum*	L3	12
Norway pout	Langøya	*C. osculatum*	L3	12
Norway pout	Langøya	*C. osculatum*	L3	13
Norway pout	Langøya	*C. osculatum*	L3	13
Norway pout	Langøya	*C. osculatum*	L3	14
Norway pout	Langøya	*C. osculatum*	L3	16
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	11
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	11
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	12

Fish	Study area	Nematode	Stage	Length (mm)
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	13
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	13
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	15
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	16
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	18
Shorthorn sculpin	Torbjørnskjær	*C. osculatum*	L3	19
Whiting	Torbjørnskjær	*C. osculatum*	L3	19
Whiting	Torbjørnskjær	*C. osculatum*	L3	21
Whiting	Torbjørnskjær	*C. osculatum*	L3	26
Witch flounder	Langøya	*C. osculatum*	L3	7
Witch flounder	Langøya	*C. osculatum*	L3	15
Witch flounder	Langøya	*C. osculatum*	L3	16
American plaice	Torbjørnskjær	*H. aduncum*	L3	12
American plaice	Langøya	*H. aduncum*	L3	13
American plaice	Langøya	*H. aduncum*	L3	13
American plaice	Langøya	*H. aduncum*	L3	13
American plaice	Langøya	*H. aduncum*	L3	14
American plaice	Torbjørnskjær	*H. aduncum*	L3	15
American plaice	Langøya	*H. aduncum*	L3	17
American plaice	Langøya	*H. aduncum*	L3	17
American plaice	Langøya	*H. aduncum*	L3	19
American plaice	Langøya	*H. aduncum*	L3	21
American plaice	Langøya	*H. aduncum*	L3	23
Atlantic cod	Torbjørnskjær	*H. aduncum*	L3	11
Common dab	Langøya	*H. aduncum*	L3	17
Common dab	Langøya	*H. aduncum*	L3	19
Witch flounder	Langøya	*H. aduncum*	L3	10
Witch flounder	Langøya	*H. aduncum*	L3	15
Witch flounder	Langøya	*H. aduncum*	L3	17
American plaice	Langøya	*H. aduncum*	L4	11
American plaice	Langøya	*H. aduncum*	L4	14
American plaice	Langøya	*H. aduncum*	L4	15
American plaice	Langøya	*H. aduncum*	L4	16
American plaice	Langøya	*H. aduncum*	L4	16
American plaice	Langøya	*H. aduncum*	L4	16
American plaice	Langøya	*H. aduncum*	L4	17
American plaice	Langøya	*H. aduncum*	L4	17
American plaice	Langøya	*H. aduncum*	L4	17
American plaice	Langøya	*H. aduncum*	L4	18
American plaice	Langøya	*H. aduncum*	L4	20
American plaice	Langøya	*H. aduncum*	L4	20
American plaice	Langøya	*H. aduncum*	L4	21
American plaice	Langøya	*H. aduncum*	L4	23
American plaice	Langøya	*H. aduncum*	L4	23
American plaice	Langøya	*H. aduncum*	L4	24

Fish	Study area	Nematode	Stage	Length (mm)
American plaice	Langøya	*H. aduncum*	L4	24
American plaice	Langøya	*H. aduncum*	L4	24
American plaice	Langøya	*H. aduncum*	L4	25
American plaice	Torbjørnskjær	*H. aduncum*	L4	25
American plaice	Langøya	*H. aduncum*	L4	26
American plaice	Langøya	*H. aduncum*	L4	26
American plaice	Torbjørnskjær	*H. aduncum*	L4	26
American plaice	Langøya	*H. aduncum*	L4	30
American plaice	Langøya	*H. aduncum*	L4	30
American plaice	Langøya	*H. aduncum*	L4	32
American plaice	Langøya	*H. aduncum*	L4	32
American plaice	Langøya	*H. aduncum*	L4	33
American plaice	Langøya	*H. aduncum*	L4	41
American plaice	Langøya	*H. aduncum*	L4	42
American plaice	Langøya	*H. aduncum*	L4	43
American plaice	Langøya	*H. aduncum*	L4	46
American plaice	Langøya	*H. aduncum*	L4	52
Atlantic cod	Torbjørnskjær	*H. aduncum*	L4	10
Atlantic cod	Torbjørnskjær	*H. aduncum*	L4	19
Atlantic cod	Torbjørnskjær	*H. aduncum*	L4	23
Atlantic cod	Torbjørnskjær	*H. aduncum*	L4	28
Atlantic cod	Torbjørnskjær	*H. aduncum*	L4	31
Atlantic cod	Torbjørnskjær	*H. aduncum*	L4	32
Atlantic cod	Torbjørnskjær	*H. aduncum*	L4	44
Whiting	Torbjørnskjær	*H. aduncum*	L4	21
Whiting	Torbjørnskjær	*H. aduncum*	L4	31
Witch flounder	Langøya	*H. aduncum*	L4	27
Witch flounder	Langøya	*H. aduncum*	L4	29
Witch flounder	Langøya	*H. aduncum*	L4	30
Witch flounder	Langøya	*H. aduncum*	L4	38
Witch flounder	Langøya	*H. aduncum*	L4	46
Witch flounder	Langøya	*H. aduncum*	L4	61
American plaice	Langøya	*H. aduncum*	Male	17
American plaice	Langøya	*H. aduncum*	Male	22
American plaice	Langøya	*H. aduncum*	Male	22
American plaice	Langøya	*H. aduncum*	Male	23
American plaice	Langøya	*H. aduncum*	Male	23
American plaice	Langøya	*H. aduncum*	Male	26
American plaice	Langøya	*H. aduncum*	Male	26
American plaice	Langøya	*H. aduncum*	Male	26
American plaice	Langøya	*H. aduncum*	Male	27
American plaice	Langøya	*H. aduncum*	Male	27
American plaice	Langøya	*H. aduncum*	Male	28
American plaice	Langøya	*H. aduncum*	Male	28
American plaice	Torbjørnskjær	*H. aduncum*	Male	28

Fish	Study area	Nematode	Stage	Length (mm)
American plaice	Langøya	*H. aduncum*	Male	29
American plaice	Langøya	*H. aduncum*	Male	29
American plaice	Langøya	*H. aduncum*	Male	29
American plaice	Langøya	*H. aduncum*	Male	30
American plaice	Langøya	*H. aduncum*	Male	30
American plaice	Langøya	*H. aduncum*	Male	30
American plaice	Langøya	*H. aduncum*	Male	31
American plaice	Langøya	*H. aduncum*	Male	31
American plaice	Langøya	*H. aduncum*	Male	31
American plaice	Langøya	*H. aduncum*	Male	32
American plaice	Langøya	*H. aduncum*	Male	32
American plaice	Langøya	*H. aduncum*	Male	32
American plaice	Torbjørnskjær	*H. aduncum*	Male	32
American plaice	Langøya	*H. aduncum*	Male	33
American plaice	Langøya	*H. aduncum*	Male	33
American plaice	Torbjørnskjær	*H. aduncum*	Male	33
American plaice	Langøya	*H. aduncum*	Male	34
American plaice	Langøya	*H. aduncum*	Male	34
American plaice	Langøya	*H. aduncum*	Male	34
American plaice	Langøya	*H. aduncum*	Male	34
American plaice	Langøya	*H. aduncum*	Male	35
American plaice	Langøya	*H. aduncum*	Male	35
American plaice	Langøya	*H. aduncum*	Male	35
American plaice	Langøya	*H. aduncum*	Male	38
American plaice	Langøya	*H. aduncum*	Male	38
American plaice	Langøya	*H. aduncum*	Male	39
American plaice	Langøya	*H. aduncum*	Male	39
American plaice	Langøya	*H. aduncum*	Male	39
American plaice	Langøya	*H. aduncum*	Male	40
American plaice	Langøya	*H. aduncum*	Male	43
American plaice	Langøya	*H. aduncum*	Male	43
American plaice	Langøya	*H. aduncum*	Male	44
American plaice	Langøya	*H. aduncum*	Male	46
American plaice	Langøya	*H. aduncum*	Male	46
American plaice	Langøya	*H. aduncum*	Male	46
American plaice	Langøya	*H. aduncum*	Male	47
American plaice	Langøya	*H. aduncum*	Male	49
American plaice	Langøya	*H. aduncum*	Male	51
Atlantic cod	Torbjørnskjær	*H. aduncum*	Male	28
Atlantic cod	Torbjørnskjær	*H. aduncum*	Male	35
Atlantic cod	Torbjørnskjær	*H. aduncum*	Male	37
Atlantic cod	Torbjørnskjær	*H. aduncum*	Male	40
Common dab	Langøya	*H. aduncum*	Male	32
European hake	Torbjørnskjær	*H. aduncum*	Male	25
Witch flounder	Langøya	*H. aduncum*	Male	26

Fish	Study area	Nematode	Stage	Length (mm)
Witch flounder	Langøya	*H. aduncum*	Male	27
Witch flounder	Langøya	*H. aduncum*	Male	40
Witch flounder	Langøya	*H. aduncum*	Male	40
Witch flounder	Langøya	*H. aduncum*	Male	42
American plaice	Langøya	*H. aduncum*	Female	33
American plaice	Langøya	*H. aduncum*	Female	35
American plaice	Langøya	*H. aduncum*	Female	36
American plaice	Langøya	*H. aduncum*	Female	36
American plaice	Langøya	*H. aduncum*	Female	36
American plaice	Langøya	*H. aduncum*	Female	37
American plaice	Langøya	*H. aduncum*	Female	37
American plaice	Langøya	*H. aduncum*	Female	38
American plaice	Langøya	*H. aduncum*	Female	40
American plaice	Langøya	*H. aduncum*	Female	40
American plaice	Langøya	*H. aduncum*	Female	41
American plaice	Langøya	*H. aduncum*	Female	41
American plaice	Langøya	*H. aduncum*	Female	41
American plaice	Langøya	*H. aduncum*	Female	41
American plaice	Langøya	*H. aduncum*	Female	42
American plaice	Langøya	*H. aduncum*	Female	42
American plaice	Langøya	*H. aduncum*	Female	42
American plaice	Langøya	*H. aduncum*	Female	43
American plaice	Langøya	*H. aduncum*	Female	44
American plaice	Langøya	*H. aduncum*	Female	44
American plaice	Torbjørnskjær	*H. aduncum*	Female	45
American plaice	Langøya	*H. aduncum*	Female	47
American plaice	Langøya	*H. aduncum*	Female	47
American plaice	Torbjørnskjær	*H. aduncum*	Female	48
American plaice	Langøya	*H. aduncum*	Female	49
American plaice	Langøya	*H. aduncum*	Female	50
American plaice	Langøya	*H. aduncum*	Female	50
American plaice	Langøya	*H. aduncum*	Female	51
American plaice	Langøya	*H. aduncum*	Female	51
American plaice	Langøya	*H. aduncum*	Female	51
American plaice	Langøya	*H. aduncum*	Female	52
American plaice	Langøya	*H. aduncum*	Female	52
American plaice	Langøya	*H. aduncum*	Female	53
American plaice	Langøya	*H. aduncum*	Female	54
American plaice	Langøya	*H. aduncum*	Female	54
American plaice	Langøya	*H. aduncum*	Female	54
American plaice	Langøya	*H. aduncum*	Female	55
American plaice	Langøya	*H. aduncum*	Female	55
American plaice	Langøya	*H. aduncum*	Female	56
American plaice	Langøya	*H. aduncum*	Female	56
American plaice	Langøya	*H. aduncum*	Female	56

Fish	Study area	Nematode	Stage	Length (mm)
American plaice	Langøya	*H. aduncum*	Female	56
American plaice	Langøya	*H. aduncum*	Female	57
American plaice	Langøya	*H. aduncum*	Female	57
American plaice	Langøya	*H. aduncum*	Female	62
American plaice	Langøya	*H. aduncum*	Female	66
Atlantic cod	Torbjørnskjær	*H. aduncum*	Female	51
Atlantic cod	Torbjørnskjær	*H. aduncum*	Female	60
Atlantic cod	Torbjørnskjær	*H. aduncum*	Female	72
European hake	Torbjørnskjær	*H. aduncum*	Female	39
European hake	Torbjørnskjær	*H. aduncum*	Female	48
European hake	Torbjørnskjær	*H. aduncum*	Female	57
Haddock	Torbjørnskjær	*H. aduncum*	Female	40
Haddock	Torbjørnskjær	*H. aduncum*	Female	60
Witch flounder	Langøya	*H. aduncum*	Female	52
Witch flounder	Langøya	*H. aduncum*	Female	53
Witch flounder	Langøya	*H. aduncum*	Female	57
Witch flounder	Langøya	*H. aduncum*	Female	60
Atlantic cod	Torbjørnskjær	*P. decipiens*	L3	38

Appendix VI

Detailed table of the infestation pattern in the three flatfish species at both study areas.

American plaice	Langøya			Torbjørnskjær			Outer Oslofjord		
	Nr of fish	Nr of nematodes	Mean length	Nr of fish	Nr of nematodes	Mean length	Nr of fish	Nr of nematodes	Mean length
A. simplex	-	-	**-**	2	3	**17,7**	2	3	**17,7**
H. aduncum	37	100	**34,5**	4	4	**27,8**	41	104	**34,2**
C. osculatum	13	27	**16,6**	8	10	**15,7**	21	37	**16,4**
C. heterochrous	2	2	**-**	-	-	**-**	2	2	**-**
C. osculatum +	13	22	**16,5**	1	3	**14,7**	14	25	**16,9**
H. aduncum	13	35	**34,8**	1	2	**13,5**	14	37	**33,5**
A. simplex +	-	-	**-**	1	1	**16,0**	1	1	**16,0**
H. aduncum	-	-	**-**	1	3	**42,0**	1	3	**42,0**
H. aduncum +	1	5	**50,0**	-	-	**-**	1	5	**50,0**
C. heterochrous	1	1	**12,0**	-	-	**-**	1	1	**12,0**

Witch flounder	Langøya; Outer Oslofjord		
	Nr of fish	Nr of nematodes	Mean length
H. aduncum	8	16	**37,7**
C. osculatum	1	1	**7,0**
C. osculatum +	1	2	**15,5**
H. aduncum	1	2	**33,5**

Common dab	Langøya			Torbjørnskjær			Outer Oslofjord		
	Nr of fish	Nr of nematodes	Mean length	Nr of fish	Nr of nematodes	Mean length	Nr of fish	Nr of nematodes	Mean length
A. simplex	2	3	**23,0**	6	10	**19,2**	8	13	**20,1**
H. aduncum	2	3	**22,7**	-	-	**-**	2	3	**22,7**

Appendix VII

Biological information of seals.

Nr	Species	Date	Area	Chest blubber (mm)	Abdominal blubber (mm)	Sex	Age (years)	Weight (kg)	Circum-ference (cm)	Length (cm)
1	*P. vitulina*	2.06.2010	Sandøy	28	30	Female	2	39	89	123
2	*P. vitulina*	3.06.2010	Sandøy	26	32	Male	7-10	80	101	153
3	*P. vitulina*	5.06.2010	Sandøy	48	48	Female	10+	112	111	170
4	*P. vitulina*	18.08.2010	Hvaler	28	32	Male	7-8	80	102	145
5	*P. vitulina*	22.09.2010	Hvaler	30	25	Male	5-6	70	100	150
6	*P. vitulina*	28.09.2010	Sandøy	25	25	Male	3 months	21	62	100
7	*P. vitulina*	29.09.2010	Sandøy	27	29	Male	3 months	26	72	105

Nematodes identified from seals.

Nr	Seal	Date	Study area	A.s. L3	A.s. L4	P.d. L3	P.d. L4	P.d. ♀	P.d. ♂	C.o. L4	C.o. ♀	C.o. ♂
1	*P. vitulina*	2.06.2010	Sandøy				2	7	12			
2	*P. vitulina*	3.06.2010	Sandøy		7		3	12	9			
3	*P. vitulina*	5.06.2010	Sandøy	3	1		3	6	5			
6	*P. vitulina*	28.09.2010	Sandøy							1		
7	*P. vitulina*	29.09.2010	Sandøy	2			2					
4	*P. vitulina*	18.08.2010	Hvaler	18			4	1	2	6	3	2
5	*P. vitulina*	22.09.2010	Hvaler	20	3	1	2	2	4	5		3