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The life cycle of *Anisakis simplex* in the Norwegian Deep (northern North Sea)

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Abstract Copepoda (*Calanus finmarchicus* $n = 1{,}722$, *Paraeuchaeta norvegica* $n = 1{,}955$), Hyperiidae ($n = 3{,}019$), Euphausiacea (*Meganyctiphanes norvegica* $n = 4{,}780$), and the fishes *Maurolicus muelleri* ($n = 500$) and *Pollachius virens* ($n = 33$) were collected in the Norwegian Deep (northern North Sea) during summer 2001 to examine the importance of pelagic invertebrates and vertebrates as hosts of *Anisakis simplex* and their roles in the transfer of this nematode to its final hosts (Cetaceans). Third stage larvae (L3) of *A. simplex* were found in *P. norvegica*, *M. muelleri* and *P. virens*. The prevalence of *A. simplex* in dissected *P. norvegica* was 0.26%, with an intensity of 1. Prevalences in *M. muelleri* and *P. virens* were 49.6% and 100.0%, with mean intensities of 1.1–2.6 (total fish length ≥6.0–7.2) and 193.6, respectively. All specimens of *C. finmarchicus* and *M. norvegica* examined were free of anisakid nematode species and no other parasites were detected. *P. norvegica*, which harboured the third stage larvae, is the obligatory first intermediate host of *A. simplex* in the investigated area. Though there was no apparent development of larvae in *M. muelleri*, this fish can be considered as the obligatory second intermediate host of *A. simplex* in the Norwegian Deep. However, it is unlikely that the larva from *P. norvegica* can be successfully transmitted into the cetacean or pinniped final hosts, where they reach the adult stage. An additional growth phase and a second intermediate host is the next phase in the life cycle. Larger predators such as *P. virens* serve as paratenic hosts, accumulating the already infective stage from *M. muelleri*. The oceanic life cycle of *A. simplex* in the Norwegian Deep is very different in terms of hosts and proposed life cycle patterns of *A. simplex* from other regions, involving only a few intermediate hosts. In contrast to earlier suggestions, euphausiids have no importance at all for the successful transmission of *A. simplex* in the Norwegian Deep. This demonstrates that this nematode is able to select definite host species depending on the locality, apparently having a very low level of host specificity. This could explain the wide range of different hosts that have been recorded for this species, and can be seen as the reason for the success of this parasite in reaching its marine mammal final hosts in an oceanic environment.

Introduction

The Norwegian Deep is a rather extensive shelf channel which extends from the Norwegian Sea into the north-eastern North Sea and Skagerrak, with depths ranging from about 150 to 700 m. The shelf channel influences the pattern of inflow of Atlantic water masses to the North Sea as well as the outflow from the area, and has a characteristic hydrographical structure which is more stable and less affected by seasonal variation than waters of the shallower areas (Furnes et al. 1986). The pelagic and demersal fish fauna of the Norwegian Deep differs from the fish fauna in adjacent shallow areas, resembling species assemblages which are found along the outer shelf of the northeast Atlantic (Bergstad 1990). The western and the southern slopes appear to be feeding and overwintering areas for some fish species from adjacent shallow waters, particularly populations of *Pollachius virens* (saithe) and *Trisopterus esmarki* (Norway pout) (Bergstad 1990).

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One of the most numerous mesopelagic fish species, and an integral part of the zooplankton community from Norwegian and North Atlantic waters, is *Maurolicus muelleri* (pearlside) (Gjøsæter 1981; Bergstad 1990). This cosmopolitan and short-lived sternoptychid fish is most abundant in deep waters near continental shelves but is rare in the open ocean (Boehlert et al. 1994; Ikeda 1996). The planktivorous *M. muelleri* occurs in shoals at depths of mainly between 100 and 400 m by day with a dusk migration into the upper 100 m (Badcock 1984). It feeds primarily on euphausiids and copepods (Gjøsæter 1981). Cladocerans were the dominant food item, followed by veliger larvae (bivalvia) and copepods, whereas the intake of large copepods increased with the size of the fish (Rasmussen and Giske 1994). *M. muelleri* appears to be the most abundant mesopelagic fish in the Norwegian Deep and is an important food item for larger fishes, such as *P. virens*, *Salmo salar* (salmon) and *Micromesistius poutassou* (blue whiting) (Gjøsæter 1981; Rasmussen and Giske 1994).

The carnivorous copepod *Paraeuchaeta norvegica* is a common zooplankton species in fjords and North Atlantic waters and plays an important role in the pelagic food chain (Park 1995; Skarra and Kaartvedt 2003). Typically, large copepods live relatively deep during the daytime and migrate into shallow waters at night, thus performing regular vertical migrations (Hays et al. 1994; Skarra and Kaartvedt 2003).

Parasitological studies of anisakid nematodes in *M. muelleri* from the Norwegian Deep are scarce compared to studies from other regions. Berland (1961) recorded larvae of *Hysterothylacium aduncum* from Norwegian waters. Kristoffersen and Salvanes (1998) reported high prevalences of larval nematodes found in *M. muelleri* from the Trondheim fjord (Norway). The most common metazoan parasite species in *M. muelleri* from Herdle fjord (Norway) was *H. aduncum* (Hamre and Karlsbakk 2002). Klimpel et al. (2003a) showed that *M. muelleri* specimens from the Norwegian Deep were heavily infested with a high number of larval *Anisakis simplex* and *H. aduncum*. Both anisakid nematodes use various invertebrates as first intermediate hosts, and larger crustaceans and fishes as second or paratenic hosts (Smith 1983; Køie 1993, 2001). Cetaceans and sometimes pinnipeds serve as final hosts of *A. simplex* (Kerstan 1992), whereas the final hosts of *H. aduncum* are bony fishes (Køie 1993). However, the general life cycle of *A. simplex* involves several marine fish species which act as intermediate or paratenic hosts (Køie 2001). Being an important prey of several larger piscivorous fishes (Bergstad 1991a, 1991b; Rasmussen and Giske 1994), *M. muelleri* seems to play an important role in the life cycle of *A. simplex*.

The present study was conducted in the Norwegian Deep (northern North Sea), which is connected with the Atlantic Ocean and the Baltic Sea (Skagerrak, Kategatt). This site was chosen for a number of important reasons: some aspects of the life cycle of *A. simplex* are still poorly understood and controversial, *A. simplex* is present in fish and whales, potential intermediate hosts (copepods, euphausiids) are found in great density, transport hosts (different fish species and cephalopods) are present, final hosts such as *Phocoena phocoena* (harbour porpoise) are present year round in the area, and other cetacean final hosts such as *Balaenoptera acutorostrata* (minke whale), *Globicephala melas* (long-finned pilot whale), *Lagenorhynchus albirostris* (white-beaked dolphin) and *Tursiops truncatus* (common bottlenose dolphin) visit the area during summer (Hays et al. 1998a, 1998b; Reid et al. 2003). Consequently, all potential hosts required to complete the life cycle of *A. simplex* are found in the area.

The aim of this study was to determine the life cycle of *A. simplex* in the Norwegian Deep. This might explain the occurrence of larval *A. simplex* in *M. muelleri*, and provide further information on the general life cycle strategy of this abundant and also economically important marine fish nematode in an open and deep water environment. Finally, the role of the different intermediate hosts in the life cycle of *A. simplex* in the Norwegian Deep is clarified.

Materials and methods

Samples were collected in the Norwegian Deep during the R.V. Heincke cruise 147 in May 2001. Stations were located south-east of Norway, covering an area between 57°42 N and 57°30 N, and 08°35 E and 06°53 E (Fig. 1).

M. muelleri was collected at a depth of between 175 and 215 m. The fishes were caught on 20 May 2001 using a benthopelagic net (Kombitrawl 10, 10 mm mesh size); the towing time was approximately 30 min. Additionally, a total of 33 *P. virens* were collected between 20 May and 28 May 2001 using the same procedure. All fish specimens were deep frozen at −20°C immediately after catching. Zooplankton samples were taken at the same station using an Isaac-Kidd mid-water trawl (IKMT 6, 300 μm mesh size). The IKMT 6 was applied at different depths from 200 to 10 m; towing time was approximately 60 min. Ship speed during sampling was kept at 3 knots. Zooplankton samples were initially preserved in a 4% formalin seawater solution which was buffered with borax.

Fish were stored at the laboratory and subsequently prepared for dissection. Specimens of *M. muelleri* were measured (total length = TL) and sorted into different size classes, which varied between 4.8 and 7.2 cm. Each length class (size range: 0.1 cm) contained 20 specimens. A total of 500 specimens were chosen for dissection. The body cavity, gastrointestinal tract, belly flaps and musculature were examined for larval *A. simplex* and other metazoan parasites under a stereomicroscope. Additionally, the stomach contents were removed for examination and food items were identified to the lowest possible taxonomic level. The frequency of occurrence (*F*) of prey items in non-empty stomachs was calculated

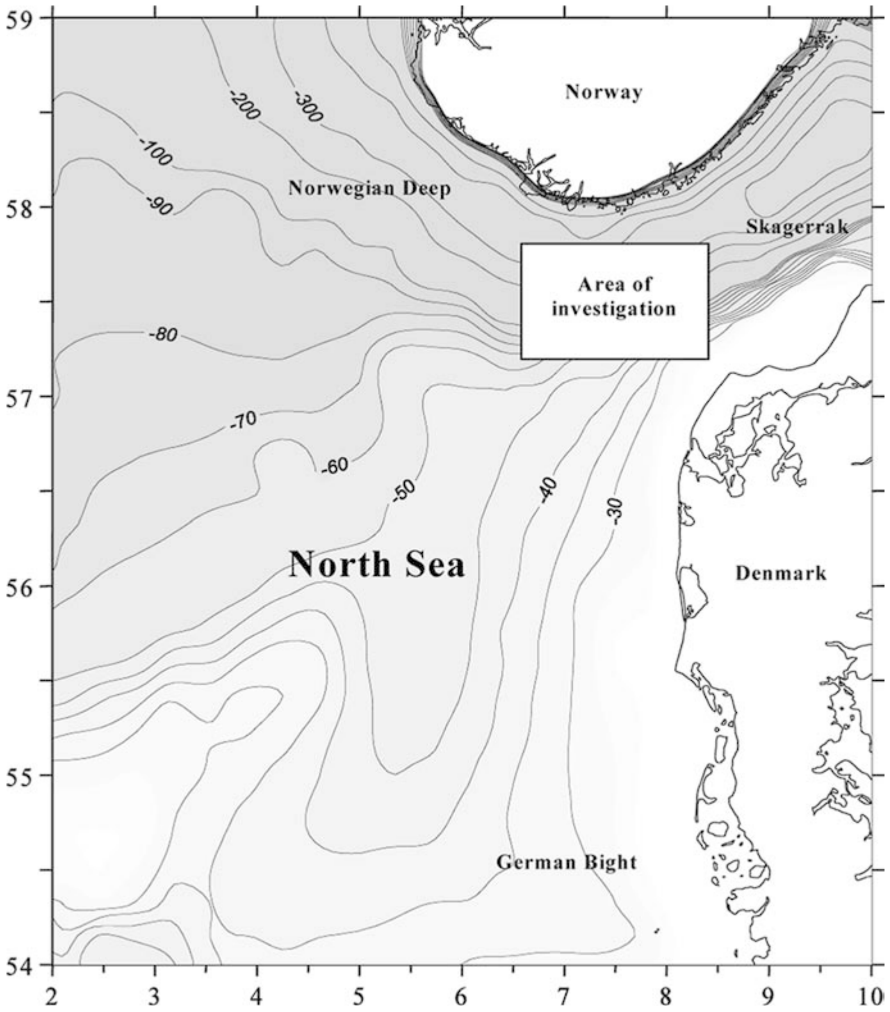


Fig. 1 Map of the area of investigation. Stations were located south-east of Norway, covering an area between 57°42 N to 57°30 N and 08°35 E to 06°53 E

(Hyslop 1980). In addition, specimens of *P. virens* were measured and the body cavity, gastrointestinal tract, belly flaps and musculature were examined for *A. simplex*. The stomach contents were analysed and the preyed upon species were recorded. Prey found in the mouth cavity of fish were excluded from the diet analysis, due to possible net feeding.

Hyperiidae, calanoid Copepoda (*Paraeuchaeta norvegica*, *Calanus finmarchicus*), and Euphausiacea (*Meganyctiphanes norvegica*) were sorted from the zooplankton samples and identified under a stereomicroscope. A total of 1,955 *P. norvegica*, 1,722 *C. finmarchicus*, 3,019 hyperiids and 4,780 *M. norvegica* were examined for parasite larval stages, especially for anisakid nematodes, under a stereomicroscope. Infested specimens were sorted quantitatively.

Anisakid nematodes were fixed in 4% borax buffered formalin and preserved in 70% ethanol/5% glycerine for later taxonomic work. For identification purposes, the nematodes were dehydrated in a graded ethanol series and transferred to 100% glycerine (Riemann 1988).

The ecological and parasitological terminology used (e.g. prevalence, mean intensity, etc.) follow the definitions of Bush et al. (1997). Correlation analysis used the Spearman's rank correlation.

Results

Food composition and larvae of *A. simplex* in *M. muelleri* and *P. virens*

A total of 500 *M. muelleri*, 20 per 0.1 cm size class, ranging from 4.8 to 7.2 cm TL, with total weights ranging from 0.758 to 3.526 g, were sampled to examine the feeding ecology. Two copepod species, *C. finmarchicus* and *P. norvegica*, were the most abundant prey organisms found in the stomach contents. *M. norvegica* and hyperiids were less abundant as prey species and were solely encountered in fish larger than 6.2 cm (Fig. 2, Table 1). For *M. muelleri* of all length classes, especially for individuals ranging from 4.8 to 5.3 cm, *C. finmarchicus* was the main prey organism. No significant correlation between the mean intensity of the copepods found in the stomach contents and total fish length was detected ($r_s^2 = 0.0851$, $P > 0.05$, Fig. 2). With an increasing total length of *M. muelleri*, there was a change in food

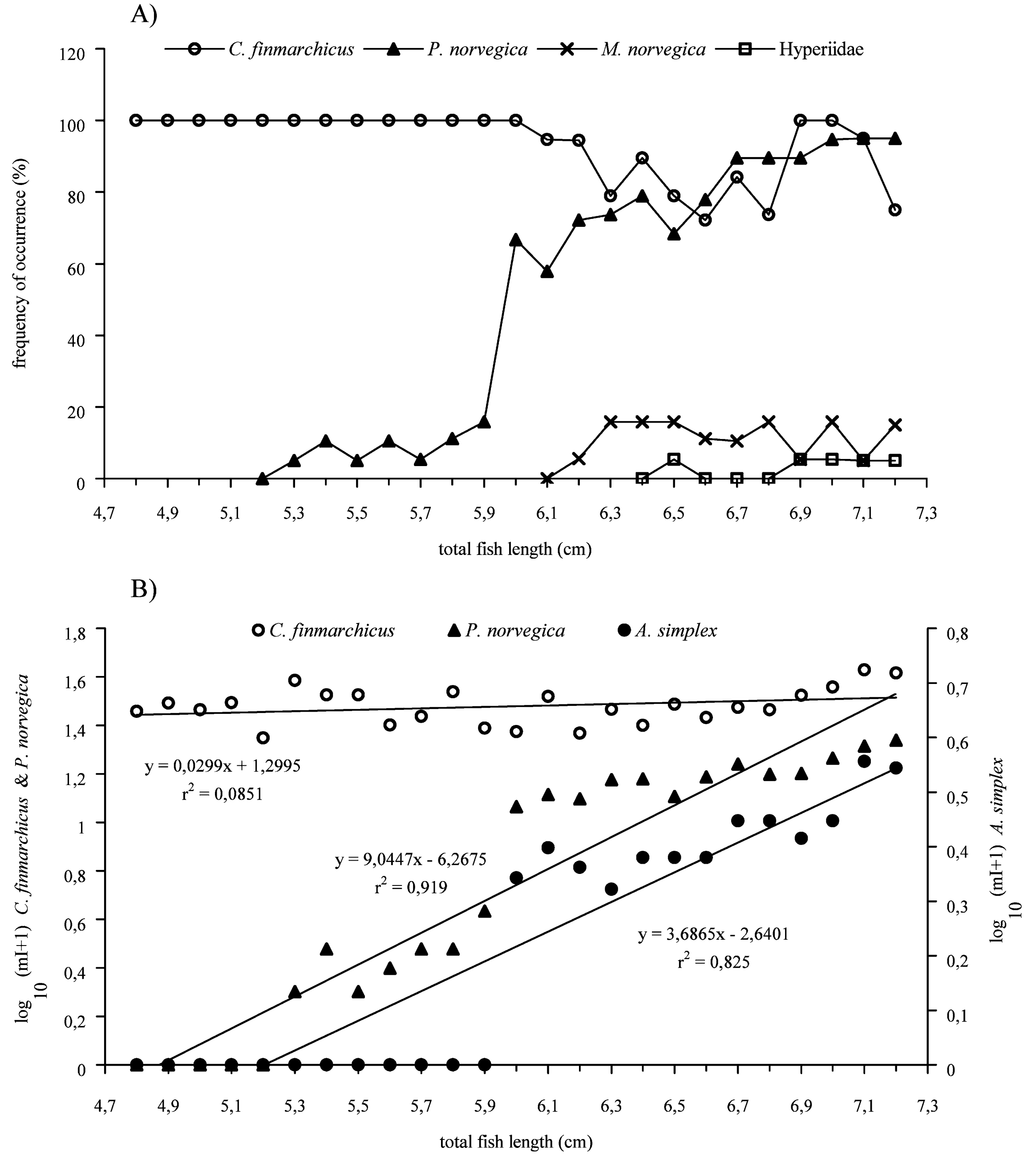


Fig. 2A, B Food composition and parasitation with *Anisakis simplex* of 500 *Maurolicus muelleri* (length classes between 4.8 and 7.2 cm) from the Norwegian Deep. **A** Frequency of occurrence (%) of the prey items identified in the stomach in relation to the size of *M. muelleri*. **B** Mean intensity of *A. simplex* and of the prey items *Calanus finmarchicus* and *Paraeuchaeta norvegica* in relation to the size of *M. muelleri*

composition from *C. finmarchicus* to *P. norvegica*. *M. muelleri* larger than 5.3 cm fed more often on *P. norvegica* than smaller individuals. In this case, we found a positive correlation between the mean intensity of the ingested copepods and the total length of *M. muelleri* ($r_s^2 = 0.919$, $P < 0.01$, Fig. 2).

Eight metazoan parasite species were isolated from *M. muelleri* during this study: three adult Digenea (*Brachyphallus crenatus*, *Derogenes varicus*, *Lecithaster confusus*), three larval Cestoda (*Scolex pleuronectis*, *Phyllobothrium* sp., Pseudophyllidea indet.) and two larval Nematoda (*A. simplex*, *H. aduncum*). Only the anisakid nematode *A. simplex* was abundant in the examined hosts. *A. simplex* were found as third stage larvae (L3) in the body cavities of *M. muelleri* with total lengths of ≥6.0 cm. The total prevalence for all examined *M. muelleri* was 25.8%, while the prevalence for individuals from 6.0 cm total length on was 49.6% and therefore significantly higher. The mean intensity of *A. simplex* was between 1.1 and 2.6 (total fish length≥6.0–7.2 cm), being positively correlated with the total length of *M. muelleri* ($r_s^2 = 0.825$, $P < 0.01$, Fig. 2, Table 1).

Table 1 Stomach contents and parasitation by *Anisakis simplex* in relation to the total fish length of *Maurolicus muelleri*. *TL* Total fish length (cm), *F* frequency of occurrence (%), *I* intensity, *mI* mean intensity, *P* prevalence (%)

Prey group	TL	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9	7.0	7.1	7.2
Calanus finmarchicus	F	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	94.7	94.4	78.9	89.5	78.9	72.2	84.2	73.7	100.0	100.0	95.0	75.0
	I	3–71	8–58	11–58	10–95	3–53	1–84	4–89	3–67	2–66	5–54	2–84	2–67	2–63	4–111	1–61	3–87	1–52	2–102	4–78	3–61	3–67	2–63	1–87	11–131	5–119
	mI	27.7	30.0	28.1	30.1	21.3	37.5	32.6	32.6	24.2	26.4	33.6	23.5	22.7	32.1	22.3	28.3	24.1	29.7	26.1	28.8	28.1	32.4	35.2	41.5	40.3
Paraeuchaeta norvegica	F						5.0	10.5	5.0	10.5	5.3	11.1	15.8	66.7	57.9	72.2	73.7	78.9	68.4	77.7	89.5	89.5	89.5	94.7	95.0	95.0
	I						1	1–3	1	1–2	2	1–3	1–5	1–27	2–21	3–24	2–22	3–28	1–27	2–27	1–32	1–35	2–29	2–35	2–56	3–47
	mI						1.0	2.0	1.0	1.5	2.0	2.0	3.3	10.6	12.0	11.5	14.0	14.1	11.8	14.4	16.4	14.8	14.9	17.4	19.6	20.8
Meganyctiphanes norvegica	F															5.6	15.8	15.8	15.8	11.1	10.5	15.8	5.3	15.8	5.0	15.0
	I															2	1–4	1–5	1–2	1–2	1–2	2–3	1	1–6	1	1–2
	mI															2.0	2.3	2.3	1.3	1.5	1.5	2.3	1.0	3.0	1.0	1.7
Hyperiidae	F																		5.3				5.3	5.3	5.0	5.0
	I																		1				1	1	1	1
	mI																		1.0				1.0	1.0	1.0	1.0
Number of stomachs	*n*	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
	with content	20	20	20	19	18	20	19	20	19	19	18	19	18	19	18	19	19	19	18	19	19	19	19	20	20
	empty	0	0	0	1	2	0	1	0	1	1	2	1	2	1	2	1	1	1	2	1	1	1	1	0	0
Parasite	TL	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9	7.0	7.1	7.2
Anisakis simplex	P (%)													30.0	40.0	40.0	35.0	25.0	35.0	40.0	60.0	60.0	45.0	50.0	85.0	100.0
	I													1–2	1–4	1–2	1–2	1–2	1–2	1–2	1–3	1–4	1–4	1–3	1–9	1–8
	mI													1.2	1.5	1.3	1.1	1.4	1.4	1.4	1.8	1.8	1.6	1.8	2.6	2.5
Number of fish examined	*n*	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20

A total of 33 *P. virens* (38.5–59.5 cm total length; 550.2–2203.1 g total weight) were examined for their feeding ecology and parasitation rates. The individuals of *P. virens* examined fed mainly on pelagic prey that consisted of *M. norvegica* and *M. muelleri*. Hyperiids, larval decapods and copepods were found in minor proportions. The predominant parasite species was *A. simplex* with a prevalence of 100.0% and a mean intensity of 193.6 (range 32–390). The third stage larvae (L3) were isolated from the musculature, stomach (free in the lumen), stomach wall, liver and the other organs of the body cavity.

Larvae of anisakid nematodes (especially *A. simplex*) in zooplankton

Only third stage larvae (L3) of *A. simplex* and *H. aduncum* occurred in *P. norvegica* and hyperiids, respectively. Five *P. norvegica* were detected carrying an *A. simplex* larva (L3) (prevalence 0.26%, intensity 1,

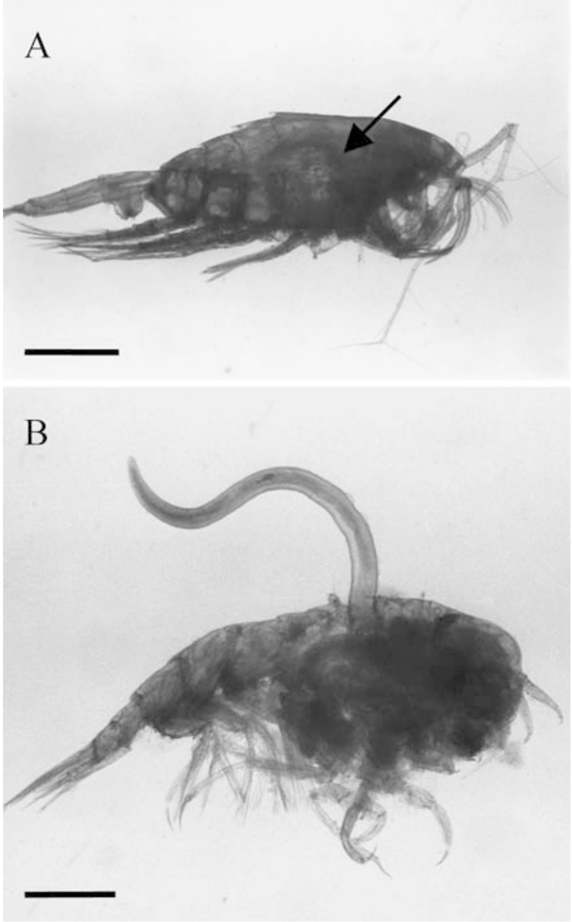


Fig. 3A, B Third stage larva (L3) of *Anisakis simplex* and *Hysterothylacium aduncum* from invertebrate hosts from the zooplankton samples collected in the Norwegian Deep. **A** *Paraeuchaeta norvegica* with third stage larva of *A. simplex* coiled in the haemocoel (*bar* = 0.15 mm). **B** *H. aduncum* third stage larva in the haemocoel of a hyperiid (*bar* = 0.22 mm)

Fig. 3) and 59 hyperiids were found that contained one larva of *H. aduncum* each (prevalence 1.95%, intensity 1, Fig. 3). No other parasites were detected in either species. All of the specimens of *C. finmarchicus* and *M. norvegica* examined were free of anisakid nematode species and no other parasites were detected.

The life cycle of *A. simplex* in the Norwegian Deep

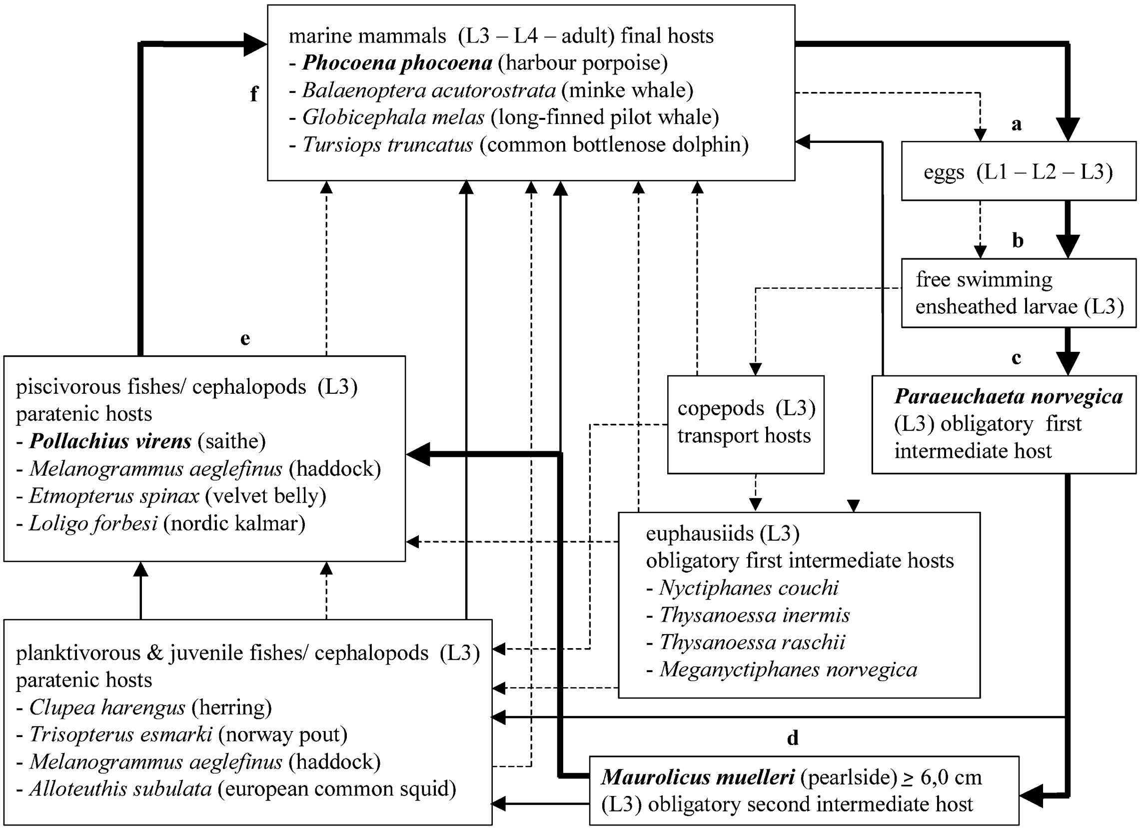
Figure 4 presents a diagrammatic representation of the life cycle of *A. simplex*. (a) Eggs in which two moults are believed to take place (L1–L2–L3) lead to (b) free swimming ensheathed third stage larvae (L3). These are eaten by the obligatory first intermediate host *P. norvegica* which leads to exsheathed third stage larva (L3) (c). *P. norvegica* is in turn eaten by the obligatory second intermediate host *M. muelleri* (d), with third stage larvae (L3) infective to the final hosts. Paratenic hosts (e) (especially *P. virens*) with third stage larvae (L3) which are infective to the final hosts (f) (mainly *Phocoena phocoena*, also migrating cetaceans) in which two moults take place (L3–L4–adult).

Discussion

The present study is the first investigation of larval *A. simplex* in different host species from the Norwegian Deep. In its larval stages, the whaleworm *A. simplex* is mainly a parasite of marine pelagic fishes and cephalopods, while adults are mostly found in cetaceans and sometimes pinnipeds (Strømnes and Andersen 2000; Abollo et al. 2001). These marine mammals serve as final hosts, with *P. phocoena* as local and *B. acutorostrata*, *G. melas*, *L. albirostris* and *T. truncatus* as migratory species (Reid et al. 2003). The whaleworm has been reported as a parasite from approximately 200 fish species, 25 cephalopod species and 53 mammal species worldwide (Lick 1991; Abollo et al. 2001; Ugland et al. 2004). Palm et al. (1999) noted that in German costal waters (including the North and Baltic Seas), 17 species of marine fish harbour larval stages of *A. simplex*. In Canadian Atlantic waters, the larvae of *A. simplex* have been found in 41 different fish species (McDonald and Margolis 1995).

Studies of *A. simplex* in fishes from the Atlantic Ocean and the North Sea have focused mainly on commercial species, such as *Clupea harengus* (herring), *P. virens*, *Gadus morhua* (cod) and *Sebastes marinus* (redfish) (e.g. Banning and Becker 1978; Højgaard 1999; Strømnes and Andersen 1998, 2000). Additionally, studies such as those of Mattiucci et al. (1997, 1998, 2002) and Kijewska et al. (2000, 2002) have presented new methods for the identification of *A. simplex* by comparing genetic and biochemical traits. Hays et al.

Fig. 4 Modified life cycle of *A. simplex* in the Norwegian Deep (*bold lines* main life cycle, *fine lines* secondary life cycle) and the general life cycle in oceanic areas (*dashed lines*)



(1998a, 1998b) investigated the life cycle of this parasite in the St. Lawrence estuary (northwest Atlantic) and Køie (2001) experimentally with hosts from the Baltic Sea. Little is known concerning the life cycle dynamics of *A. simplex* from the Norwegian Deep.

A. simplex is considered to follow a pelagic life cycle and undergo four moults before it reaches the adult stage. Cetaceans acquire the nematodes by preying on intermediate hosts (crustaceans, fish, cephalopods) and serve as final hosts, harbouring third stage and fourth stage larvae and adults, including sexually mature individuals. The nematode eggs are excreted with the faeces of cetaceans and embryonate in the seawater (Køie 2001). Køie et al. (1995) found larvae surrounded by two cuticles prior to hatching. They were able to swim and used mainly pelagic crustacean hosts, such as copepods and euphausiids, and were surrounded by sheaths with lateral extensions, which may be an adaptation to pelagic conditions (Køie et al. 1995). When the larvae is ingested by crustaceans, *A. simplex* is probably released from the second stage cuticle by the action of the mouthparts of the host. This allows the third stage larvae to penetrate the host gut prior to establishing themselves in the haemocoel (Køie et al. 1995).

Larger invertebrates (mainly euphausiids) are thought to be important second intermediate hosts and various fish species and cephalopods serve as paratenic hosts, acquiring *A. simplex* through the food chain. If small fishes are preyed on by larger piscivorous fishes, the larvae are capable of reinfecting the latter without moulting. Piscivorous fishes may thus accumulate enormous numbers of larvae (Lile 1998), which is also demonstrated in the present study.

Individual *P. virens* examined in this study were highly infested with *A. simplex*. Supposedly, infestation rates of marine fishes, such as *P. virens*, are mainly a function of the ingested food (e.g. Lile 1998; Klimpel et al. 2003b). Thus, we conclude that the infestation rates of marine fishes mirror local hydrographic conditions, local aggregations of potential intermediate hosts and the extent to which they are integrated into the parasite life cycle. In the area investigated, the prey of *P. virens* consists solely of pelagic organisms, feeding predominantly on the most abundant species, i.e. *M. muelleri* and *M. norvegica*. These findings suggest that the life cycle of *A. simplex* in this area takes place by utilizing only a limited number of host species.

M. muelleri is one of the most common species in the Norwegian Deep and an important food source of piscivorous fish (Gjøsæter 1981; Bergstad 1990; Rasmussen and Giske 1994). Vertical migrations are known: in the northern North Sea *M. muelleri* occurs in depths between 150 and 200 m during the day and between 10 and 40 m at night (Kaartvedt et al. 1998). Examination of stomach contents in this study showed that the food spectrum of *M. muelleri* was small during the sampling period. Their food consisted mainly of the copepod species *C. finmarchicus* and *P. norvegica*, while *M. norvegica* and hyperiids were of minor importance. *C. finmarchicus* was the most important prey item of smaller *M. muelleri*, while larger individuals fed predominantly on *P. norvegica*. This relates to a spatial correspondence in the distribution of small and large individuals of *M. muelleri* and their respective prey organisms. Smaller individuals stay in the upper water layers where ambient temperatures are highest (Giske et al. 1990), while larger *M. muelleri* are encountered in deeper water. *P. norvegica*, like its predator, undergoes diurnal vertical migrations. Typically, large copepods stay in deeper water during the daytime and migrate into shallow layers at night (Skarra and Kaartvedt 2003). Therefore, smaller *M. muelleri* can prey more easily on *C. finmarchicus*, 2.4–5.0 mm in size, that are abundant in shallower water, than on the larger individuals of *P. norvegica* that occur in deeper waters (Skarra and Kaartvedt 2003). Only *M. muelleri* larger than 5.3 cm, and especially those larger than 6.0 cm, can successfully prey on *P. norvegica*, 6.0–8.5 mm in size (Park 1995).

M. norvegica also undergoes vertical migrations and feeds on copepods. Euphausiids are regarded as the most important intermediate hosts of *A. simplex* in marine environment, and they are therefore proposed as the main vector of this nematode for ichthyoid hosts (e.g. Højgaard 1999). The absence of L3 in 4,780 specimens of *M. norvegica* in the present study, and the low prevalences found in other studies contradict this. Smith (1971) found only one larva in 3,178 *M. norvegica* and Hays et al. (1998a) identified only one larva in 9,681 *M. norvegica*. Klimpel et al. (2003a) found no *A. simplex* in 3,650 euphausiids. None of the 4,780 specimens of *M. norvegica* examined in the present study were infested with larvae of *A. simplex*. We conclude that *M. norvegica* is of minor or no real importance as an intermediate host for the anisakid nematode *A. simplex* in the Norwegian Deep. Klimpel et al. (2003a) suggested *M. muelleri* as the main transport host of *A. simplex* to juvenile *Etmopterus spinax* (velvet belly). These authors demonstrated that juvenile *E. spinax* that fed exclusively on euphausiids (*M. norvegica*) were not infested with *A. simplex*, whereas specimens preying on euphausiids and *M. muelleri*, or on *M. muelleri* alone, were infested. Thus *E. spinax* becomes infested by the uptake of *M. muelleri* and not *M. norvegica*.

Summarizing the life cycle of *A. simplex* in the Norwegian Deep, *P. norvegica* is included as the obligatory first intermediate host, *M. muelleri* as the obligatory second intermediate host (as direct infestation from *P. norvegica* to the final hosts is unlikely) and *P. virens* as the main paratenic host. *M. muelleri* accumulates the L3 by preying on infested *P. norvegica*, since the L3 of *A. simplex* were only found in specimens larger than 6.0 cm total length that were able to feed on this prey item. *C. finmarchicus* and *M. norvegica* are of no importance for the completion of the *A. simplex* life cycle in the Norwegian Deep. Finally *P. phocoena* serves as the local final host, because the harbour porpoise can show high infestation rates with *A. simplex* (Herreras et al. 1997). Previous studies have shown that harbour porpoises feed primarily on small schooling prey species. In the North Atlantic, the diet is usually dominated by clupeid and gadoid fishes (e.g. Rae 1965; Recchia and Read 1989; Fontaine et al. 1994). In northern areas, such as the Norwegian Deep and Skagerrak (Börjesson et al. 2003) and in the northern Gulf of St. Lawrence (Fontaine et al. 1994), clupeids are replaced by *M. muelleri* or *Mallotus villosus* (capelin). Cetaceans such as *B. acutorostrata*, *G. melas*, *L. albirostris* and *T. truncatus* constitute the migratory final hosts, occurring in Norwegian waters especially during the summer. They play an important role in the transport of the Norwegian Deep population of *A. simplex* into other regions of the North Atlantic.

In conclusion, the present study shows that the Norwegian Deep is enzootic for *A. simplex*. It also demonstrates that this nematode is able to utilize definite host species, depending on the specific locality, apparently having a very low level of host specificity. A combination of different factors, namely the geographical region with the local community together with the feeding ecology and habitat preferences of the intermediate and final hosts, can be seen as the main reasons for the observed infestation and life cycle patterns. This could explain the wide range of different hosts that have been reported for this species, and can be seen as the reason for the success of this parasite in reaching its marine mammal final hosts in an oceanic environment.

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