Parasitol Res (2003) 89: 245–251
DOI 10.1007/s00436-002-0741-1

ORIGINAL PAPER

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Metazoan parasites and food composition of juvenile *Etmopterus spinax* (L., 1758) (Dalatiidae, Squaliformes) from the Norwegian Deep

Received: 8 August 2002 / Accepted: 2 September 2002 / Published online: 18 October 2002

Abstract A total of 37 juvenile *Etmopterus spinax* from the Norwegian Deep were examined for stomach contents and metazoan ecto- and endoparasites. These squaliform elasmobranchs were caught by benthopelagic net in May 2001 at a depth of 194–214 m. The euphausiid *Meganyctiphanes norvegica* and the teleost *Maurolicus muelleri* were the principal prey organisms. With increasing total length of *E. spinax*, the frequency of *Meganyctiphanes norvegica* prey decreased and that of *M. muelleri* increased. Seven different metazoan parasite species were found: adult Monogenea (2), larval and adult Cestoda (3), and larval Nematoda (2). The predominant parasites were an unidentified monocotylid monogenean and the cestode *Aporhynchus norvegicus*, with respective prevalences of infestation of 83.8% and 81.1%. The sites of infestation were the gills (*Squalonchocotyle spinacis*, Monogenea), nasal cavities (Monocotylidae indet.), body cavity (*Lacistorhynchus tenuis*, Cestoda), stomach wall and organs of the body cavity (*Anisakis simplex*, Nematoda), and stomach and spiral valve (*A. norvegicus* and Pseudophyllidea indet., Cestoda; *Hysterothylacium aduncum*, Nematoda). No other metazoan parasite taxa were found, and the musculature was free of parasites. Five new host and three new locality records were established. *M. muelleri* seems to be an important intermediate host for the endoparasitic nematodes which were found, with *E. spinax* serving as a paratenic host. *E. spinax* also serves as an intermediate host for the trypanorhynch cestode *L. tenuis*, and as the definitive host for the two monogeneans and the trypanorhynch *A. norvegicus*. The latter uses *Meganyctiphanes norvegica* as the second intermediate host in the Norwegian Deep. The relationship between the feeding ecology, habitat, and vagility of *E. spinax* and the resulting parasite fauna is discussed.

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Introduction

The genus *Etmopterus* Rafinesque, 1810 occurs in all oceans, with several species living near to the bottom along the continental shelves and upper slopes. *Etmopterus spinax* (L., 1758) is the only reported lantern shark from the Norwegian Deep (Bergstad 1990). Its distribution extends from Iceland to southern Africa and the Mediterranean Sea (Compagno 1984; McEachran and Branstetter 1984). This shark occurs in single or small shoals at depths of between 70 and 2,000 m, but primarily between 200 and 500 m (Compagno 1984).

According to Compagno (1984), *E. spinax* is known to feed on small fishes, cephalopods, and crustaceans. MacPherson (1980) studied the diet (stomach contents) of juvenile and adult *E. spinax* from the Mediterranean Sea, and found Euphausiacea [especially *Meganyctiphanes norvegica* (Sars, 1857)], Decapoda, unidentified fish and Cephalopoda to be the main prey items. Bello (1997) studied the diet of juvenile and adult *E. spinax* from the Adriatic Sea, and found crustaceans, bony fishes and cephalopods, especially specimens of the family Sepiolidae, to be the major components in the stomachs. To date, no information on the diet of juvenile *E. spinax* from the Norwegian Deep is available.

Parasitological studies can help to analyse the diets of fish species, because parasites can be used as biological indicators of prey species and their origin (Campbell et al. 1980; Palm et al. 1998). On the other hand, diet analyses can indicate the life cycle biology of the parasites detected, giving information on the ecology of the host and the parasite. So far, parasitological studies on fish species from the deep water off the north-eastern North Sea and Skagerrak, the Norwegian Deep, are scarce (Klimpel et al. 2001) compared to studies on commercially important fish from the neighbouring shallow coastal and shelf regions (Palm et al. 1999).

Williams (1959) studied the parasite fauna of various fish species from the coast of Great Britain. For *E. spinax*, the author recorded the cestode *Phyllobothrium squali* from the spiral valve. Beveridge (1990) described material of the cestode *Aporhynchus norvegicus*, which was obtained from this shark at several localities in the northern Atlantic. Mauchline and Gordon (1984) studied the parasite fauna in the stomach of 145 *E. spinax* (Rockall Trough, northeast Atlantic Ocean), and found a cestode and nematode prevalence of 3% and 1%, respectively. Brinkmann (1952) studied the monogenea fauna of 180 *E. spinax* from the Trondheimsfjord and Herdla (Norway). The only monogenean found was a single specimen of *Squalonchocotyle spinacis*. Klimpel et al. (2001) listed four parasite species from *E. spinax* at depths of below 200 m.

The aim of the present study was to analyse the diet and prey items of juvenile *E. spinax* in order to gain information on the feeding ecology of this shark species in the Norwegian Deep. For the first time, the parasite fauna of juvenile *E. spinax* as well as of its main prey items were studied to help determine the parasite life cycle biology at the studied locality. The relationship between the feeding ecology, habitat, and vagility of *E. spinax* from the Norwegian Deep and its parasite fauna is discussed.

Materials and methods

A total of 37 *Etmopterus spinax* were collected during a cruise of the German research vessel F.S. Heincke in the Norwegian Deep (57°30'–57°31'N 06°52'–07°03'E) at depths of between 194 and 214 m. The sharks were caught between 27 May and 28 May 2001 with a benthopelagic net. Additionally, a total of 200 specimens of *Maurolicus muelleri* Cocco, 1838 and 3,650 specimens of *Meganyctiphanes norvegica* from the same area were studied for parasites.

All *E. spinax* (total length 15.5–27.4 cm, total weight 13.2–88.9 g) were deep-frozen on board at –20°C directly after capture. The elasmobranchs were then stored in the laboratory and subsequently prepared for dissection. The presence of metazoan parasites within all organs was studied by using a stereomicroscope. Ectoparasite infestation was examined while the fish was still in a partly frozen state. Inspection included the skin, fins, eyes, nasal cavities, gills and the buccal and branchial cavity. Afterwards the body cavity and gastrointestinal tract were examined. Belly flaps and the musculature were examined for cestodes and nematodes over a light source. The stomach contents were identified to the species level.

Several parasites were isolated and fixed in 4% formalin buffered with borax solution and stored in 70% ethanol/5% glycerine for detailed identification. Nematodes were dehydrated in a gradated ethanol series and transferred to 100% glycerine (Riemann 1988). The transparency of the nematodes was increased by further treatment with a 1:1 glycerine/lactic acid solution. Monogenea and Cestoda were stained with acetic carmin, dehydrated, cleared with eugenol or creosote, and mounted in Canada balsam.

For parasite identification, original descriptions as well as those found in the pertinent literature were used: Brinkmann (1952), Kearn and Green (1983), Boeger and Kritsky (1989), and Kearn (1993) for Monogenea; Rees (1941), Dollfus (1942), Smith (1985), Beveridge (1990), and Bray et al. (1994) for Cestoda; Smith (1983b), Køie (1993), Moravec (1994), and Petter and Cabaret (1995) for Nematoda. The ecological and parasitological terminology used (e.g. prevalence, mean intensity, etc.) is in accordance with the definitions provided by Bush et al. (1997).

Results

Food composition of *Etmopterus spinax*

In the present study, the diet of 37 juvenile *E. spinax* from the Norwegian Deep consisted exclusively of euphausiids and fish. A total of 91.9% of the stomachs contained *Meganyctiphanes norvegica*, and 40.5% contained *Maurolicus muelleri*. No further food items were detected.

The relationship between the total shark length and their stomach contents is given in Fig. 1. With the increasing length of *E. spinax*, there was a change in food composition from euphausiids to fish. Euphausiids were the main prey item of small specimens up to 19.1 cm total length. These sharks usually had 2–12 *Meganyctiphanes norvegica* in their stomachs. *E. spinax* specimens with a total length of more than 19.4 cm fed on a mixture of *Meganyctiphanes norvegica* and *Maurolicus muelleri*, with an increasing preference for *Maurolicus muelleri* with larger size up to 27.4 cm. The frequency of uptake was 1–4 *Meganyctiphanes norvegica*, or 1–4 *Maurolicus muelleri*. A significant correlation ($r = 0.913$, $P < 0.001$) existed between the total length of the sharks and the number of ingested *Maurolicus muelleri* (Fig. 1). When the total length of *E. spinax* increased, the frequency of capture rate of *Meganyctiphanes norvegica* decreased as the capture rate of *Maurolicus muelleri* increased.

Parasites of *E. spinax*

A total of seven parasite species were identified. Two different Monogenea, three different Cestoda, and two different Nematoda were found. The predominant species were an unidentified species of the monogenean family Monocotylidae and the cestode *Aporhynchus norvegicus*. The prevalence, intensity and site of infestation of each parasite species is given in Table 1. Five new host and three new locality records were established.

Two different monogeneans were found on the sharks (Table 1). *Squalonchocotyle spinacis* had a prevalence of 13.5% and a mean intensity of 1.2 (1–2) on the gills. An unidentified monocotylid monogenean was most predominant, inhabiting the nasal cavities at a prevalence of 83.8% and a mean intensity of 2.6 (1–6). A comparison

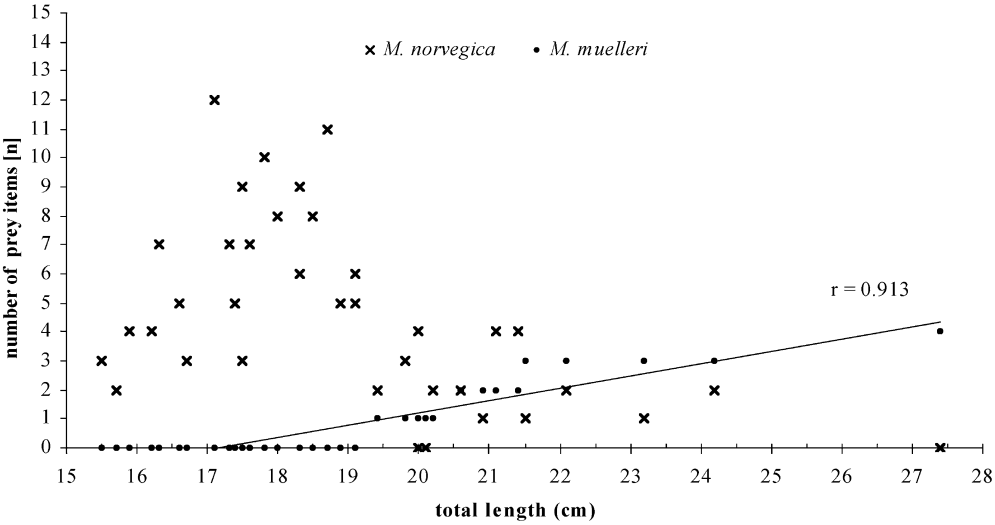

Fig. 1 Number of *Meganyctiphanes norvegica* and *Maurolicus muelleri* per stomach in relation to the size of *Etmopterus spinax* from the Norwegian Deep

Table 1 Prevalence (P) and mean intensity (mI) of infestation and site of parasites in *Etmopterus spinax* from the Norwegian Deep. An * indicates a new host record and a † a new locality record

Species of helminth	*n*	P (%)	mI (range)	Site
Monogenea				
Squalonchocotyle spinacis (Gotto, 1894) †	5	13.5	1.2 (1–2)	Gills
Monocotylidae indet.*, †	31	83.8	2.6 (1–6)	Nasal cavities
Cestoda				
Aporhynchus norvegicus (Olsson, 1868) †	30	81.1	3.5 (1–11)	Stomach, spiral valve
Lacistorhynchus tenuis (van Beneden, 1858) *	2	5.4	1.0 (1)	Body cavity
Pseudophyllidea indet. *	4	10.8	1.0 (1)	Spiral valve
Nematoda				
Anisakis simplex (Rudolphi, 1809) *	7	18.9	1.7 (1–5)	Stomach wall, body cavity
Hysterothylacium aduncum (Rudolphi, 1802) *	15	40.5	6.1 (2–20)	Stomach, spiral valve

of the opisthaptor with that of other monocotylids leads to the conclusion that they represent a hitherto undescribed species belonging to the genus *Squalotrema* or to *Triloculotrema*. Monocotylidae indet. is a new host and locality record, and the finding of *S. spinacis* represents a new locality record.

Cestoda was the most diverse taxon in the present study (Table 1). The only adult cestode found was *A. norvegicus*, infesting the spiral valve at a prevalence of 81.1% and a mean intensity of 3.5 (1–11). Plerocerci of *Lacistorhynchus tenuis* were isolated from the body cavity, with a prevalence of 5.4% and a mean intensity of 1.0. Larvae of an unidentified Pseudophyllidea were found in the spiral valve, with a prevalence of 10.8% and a mean intensity of 1.0. The present findings of *L. tenuis* and pseudophyllidean larvae represent new host records, and the finding of *A. norvegicus* represents a new locality record.

E. spinax specimens between 15.5 and 16.7 cm total length, which contained an average of 4 (2–7) *Meganyctiphanes norvegica* in their stomachs, were not infested with *A. norvegicus*. *E. spinax* between 17.1 and 19.1 cm total length had 7 (3–12 individuals) *Meganyctiphanes norvegica* within their stomachs, and *A. norvegicus* occurred with a prevalence and mean intensity of infestation of 100% and 2.3 (1–5), respectively. With a total length of 19.4 cm or more, *E. spinax* had taken 2 (1–4) *Meganyctiphanes norvegica*, with a prevalence of *A. norvegicus* of 100% and a mean intensity of 4.9 (1–11) (Fig. 2).

Two anisakid nematode species were identified, *Anisakis simplex* and *Hysterothylacium aduncum* (Table 1). The predominant nematode was *H. aduncum*, with a prevalence of 40.5% and a mean intensity of 6.1 (2–20). Third and fourth stage larvae (L3/L4) were found in the stomach and spiral valve. The L3 of *A. simplex* was isolated from the stomach wall and the organs of the body cavity, with a prevalence of 18.9% and a mean intensity of 1.7 (1–5). Infestation by both anisakid nematodes occurred together in *E. spinax*. The findings of *A. simplex* and *H. aduncum* in *E. spinax* represent new host records.

E. spinax that fed exclusively on *Meganyctiphanes norvegica* were not infested with either anisakid nematode, whereas specimens preying on *Meganyctiphanes norvegica* and *Maurolicus muelleri*, or on *Maurolicus muelleri* alone, were infested (Fig. 3). The number of anisakid nematodes increased with the number of ingested *Maurolicus muelleri* as well as with increasing total length of *E. spinax*. In sharks that had taken a single *Maurolicus muelleri*, the number of anisakid nematodes was 3–4, with two *Maurolicus muelleri* it was

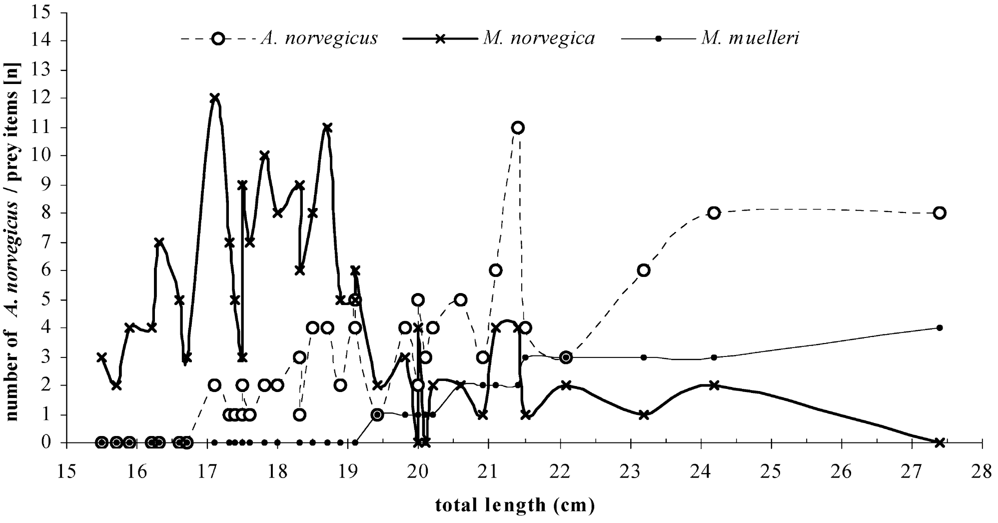

Fig. 2 Number of *Aporhynchus norvegicus* and number of preyed *Meganyctiphanes norvegica* and *Maurolicus muelleri* in relation to the size of *Etmopterus spinax* from the Norwegian Deep

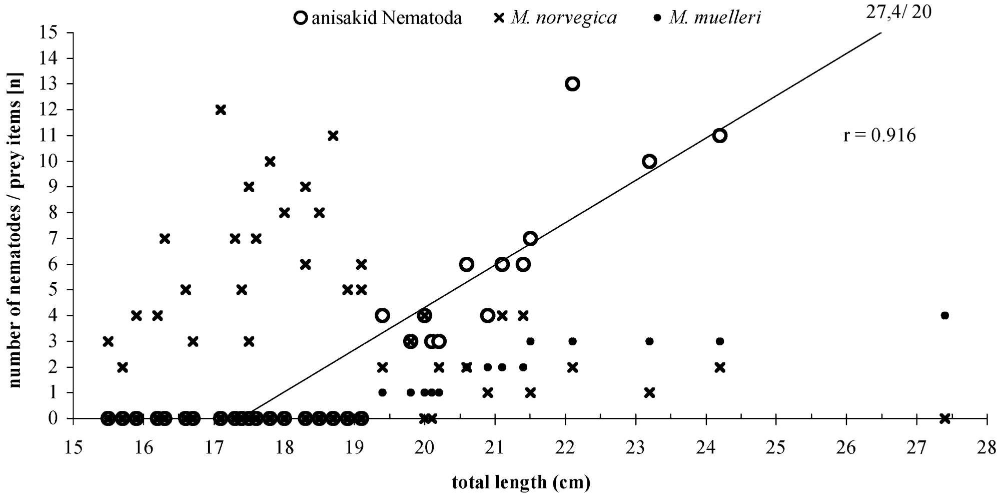

Fig. 3 Number of anisakid Nematoda and number of preyed *Meganyctiphanes norvegica* and *Maurolicus muelleri* in relation to the size of *Etmopterus spinax* from the Norwegian Deep

4–6, with three *Maurolicus muelleri* it was 7–13, and with four *Maurolicus muelleri* it was 20. There was a significant correlation ($r = 0.916$, $P < 0.001$) between fish length and the number of anisakid nematodes (Fig. 3).

Parasites of *Maurolicus muelleri* and *Meganyctiphanes norvegica*

A total of 200 *Maurolicus muelleri* were examined for metazoan parasites. Two larval anisakid nematode species were found located in or on organs of body cavity. Third stage larvae (L3) of *A. simplex* and third and fourth stage larvae (L3/L4) of *H. aduncum* were found at a prevalence of 41% and 100%, and a mean intensity of 2 (1–9) and 8 (1–24), respectively.

A total of 3,650 *Meganyctiphanes norvegica* specimens were studied for anisakid nematodes and other metazoan parasites. All of the specimens examined were free of nematode species and no other parasites were detected.

Discussion

The present study demonstrates the food composition and metazoan parasite fauna of juvenile *Etmopterus spinax* in the Norwegian Deep. The results clearly differ from previous stomach analyses of juvenile and adult *E. spinax* in other regions. MacPherson (1980) and Bello (1997) indicated a more diverse diet composition of *E. spinax* from the Mediterranean Sea, where among euphausiids, several species of decapods, fishes and cephalopods were present.

Euphausiids were the principal food of the smaller juvenile *E. spinax*, whereas the larger specimens mostly preyed upon fish (Fig. 1). This suggests a gradual shift from euphausiid to fish feeding with increasing body length. Smaller juvenile *E. spinax* easily preyed on *Meganyctiphanes norvegica* of the appropriate size, whereas *Maurolicus muelleri* was not consumed, due to an upper limit in prey size. Larger *E. spinax* are capable of preying on *Maurolicus muelleri* of any size. Both identified prey species are readily available throughout the region, as Båmstedt and Karlson (1998) and Gjøsæter (1981) recorded a large biomass and a widespread distribution of both *Meganyctiphanes norvegica* and *Maurolicus muelleri* within the area studied. It is striking that neither cephalopods nor decapods were found in the stomach contents, although they form a common prey of *E. spinax* in the Mediterranean Sea (MacPherson 1980; Bello 1997). Possible explanations for this are the general scarcity of cephalopods in the Norwegian Deep (U. Piatkowski pers. comm.) and the reduced mobility of juvenile *E. spinax*, preventing the successfully capture of the fast swimming and highly mobile cephalopods. Such prey items can only be taken by larger sharks, as shown by studies from the Mediterranean Sea (MacPherson 1980; Bello 1997).

A total of seven different parasite species occurred on or in the elasmobranchs examined. Monogenea of the orders Monopisthocotylea and Polyopisthocotylea were previously recorded from sharks (e.g. Caira (1990; Cheung 1993). The distribution of Monogenea of the family Hexabothriidae appears to be restricted to the chondrichthyans (Euzet and Maillard 1974; Boeger and Kritsky 1989; Cheung 1993). The only previous record of Hexabothriidae on the gills of *E. spinax* was by Brinkmann (1952), who found a single specimen of *Squalonchocotyle spinacis* in a sample of 180 *E. spinax*. Our finding of Monogenea from the nasal cavities is the first record of a monocotylidean from *E. spinax*. Until now, most monogenean parasites were isolated from the skin or gills of elasmobranchs. Recently, specimens of the family Monocotylidae were recorded from the nasal cavities of rays (Kearn and Green 1983; Kearn 1993; Chisholm and Whittington 1999).

Several cestodes (*Aporhynchus norvegicus*, *Lacistorhynchus tenuis* and Pseudophyllidea indet.) were recorded in *E. spinax*. *A. norvegicus* and *L. tenuis*, both belonging to the order Trypanorhyncha, were found in the spiral valve and the body cavity, respectively. Trypanorhynch cestodes are common parasites of marine elasmobranchs, where they mature in the stomach or the spiral valve (Campbell and Beveridge 1994; Palm 1999). Though elasmobranchs are usually considered to be the final hosts of tetraphyllideans and trypanorhynchs (Campbell 1983; Palm 1997b), the discovery of larval *L. tenuis* in *E. spinax* indicates that these sharks are not necessarily the endpoint in the parasite life cycle of this parasite, but may also function as intermediate hosts. It is likely that small sharks serve as a food resource for other larger, possibly migrating sharks and piscivorous fishes in the surrounding area. Dollfus (1930, 1942) and recently Palm and Schröder (2001) demonstrated that some elasmobranchs not only represent the definitive host of such shark parasites, as small elasmobranchs are often preyed upon by larger ones (Caira 1990). The rarity of pseudophyllidean larvae in *E. spinax* might be explained by the fact that they typically infest bony fishes, with *E. spinax* being an untypical host for these cestodes.

The typical trypanorhynch life cycle includes a crustacean, especially copepods, as first intermediate host, invertebrates or teleosts as second intermediate hosts, and elasmobranchs as final hosts (Stunkard 1977; Palm 1997a). *Meganyctiphanes norvegica* is the second intermediate host for *A. norvegicus* at the locality studied. While *E. spinax* specimens up to 16.7 cm total length where uninfested, all specimens 17.1 cm total length and longer were infested. Accumulation of *A. norvegicus* might be explained by the feeding behaviour of *E. spinax*. Between 17.1 and 19.1 cm total length, *E. spinax* feed exclusively on *Meganyctiphanes norvegica*, but with a total length of 19.4 cm or more, they change their feeding behaviour, becoming more piscivorous (Fig. 2). The increase in mean intensity of *A. norvegicus* with the total length of *E. spinax* is therefore probably a result of continual consumption of *Meganyctiphanes norvegica*. Species belonging to the trypanorhynch cestode genus *Aporhynchus* are common parasites of squaliform sharks living in deep water (Klimpel et al. 2001). The present result illustrates, for the first time, that the euphausiid *Meganyctiphanes norvegica* is the obligatory host in the life cycle of this trypanorhynch in the Norwegian Deep. Euphausiids are also intermediate hosts for other trypanorhynchs (Shimazu 1975a, 1975b) as well as for nematodes (see below). *Meganyctiphanes norvegica* preys almost exclusively (85–95%) on *Calanus finmarchicus* (Gunnerus, 1770) within the study area (Båmstedt and Karlson 1998). Thus, calanoids are likely to represent the first intermediate host for *A. norvegicus*.

Larvae of the nematodes *Anisakis simplex* and *Hysterothylacium aduncum* were found on the stomach wall and in the body cavity, and in the stomach and spiral valve of *E. spinax*, respectively. Larval anisakids are rare in elasmobranchs, and this is the first record of anisakid nematodes in this shark species. Palm and Schröder (2001) found the larvae of two *Anisakis* species in four shark species from the Great Meteor Bank. In the North Sea, *A. simplex* and *H. aduncum* have been recorded from *Squalus acanthias* (L., 1758) (Orlowska 1979). Both nematodes use various invertebrates as first intermediate hosts, and larger crustaceans and fishes as second or paratenic hosts (Smith 1983a; Køie 1993, 2001). The final hosts of *A. simplex* are usually cetaceans and sometimes pinnipeds (Kerstan 1992), the final hosts of *H. aduncum* are bony fishes (Køie 1993). Infestation by these anisakid nematodes takes place via the food chain and the vector may have been *Maurolicus muelleri*, since *E. spinax* that fed exclusively on *Meganyctiphanes norvegica* were uninfested, whereas those that preyed upon *Meganyctiphanes norvegica* and *Maurolicus muelleri*, or on *Maurolicus muelleri* alone, were infested (Fig. 3).

Maurolicus muelleri is one of the most common species in the study area (Gjøsæter 1981; Bergstad 1990) and a principal prey of piscivorous fishes (Rasmussen and Giske 1994). This species undertakes vertical migrations and feeds mostly on euphausiids and on calanoid and cyclopoid copepods (Gjøsæter 1981). The results of this study showed that specimens of *Maurolicus muelleri* were infested with a large number of larval *A. simplex* and *H. aduncum*. It is likely that the intermediate host *Maurolicus muelleri* may acquire the infection by feeding upon calanoid and cyclopoid copepods. The euphausiid *Meganyctiphanes norvegica* preys mainly on *C. finmarchicus* within the study area (Båmstedt and Karlson 1998). None of the specimens of *Meganyctiphanes norvegica* examined were infested with nematodes in the present study. These results correspond closely with the studies by Smith (1971) and Hays et al. (1998), who found only a single larval anisakid nematode in 3,178 (northern North Sea) and 9,681 (St. Lawrence estuary) specimens of *Meganyctiphanes norvegica*, respectively. Højgaard (1999) examined the food items and metazoan parasites of *Pollachius virens* (L., 1758) from the Faroe Islands, and found a frequent co-occurrence of *Meganyctiphanes norvegica* and larvae of *A. simplex* together in the stomachs. The author suggested that third stage larvae (L3) of *A. simplex* may have been transmitted by *Meganyctiphanes norvegica*. Because of the absence of larval anisakid nematodes in our *Meganyctiphanes norvegica*, the infestation of juvenile *E. spinax* by *A. simplex* and *H. aduncum* occurred via the paratenic host, *Maurolicus muelleri*.

The present study demonstrates that juvenile *E. spinax* from the Norwegian Deep are highly parasitized, both in terms of the numbers of individuals and species of larval and adult helminths. Furthermore, there is a clear connection between parasite prevalence and the availability of infected intermediate hosts in the diet. The occurrence of *Meganyctiphanes norvegica*, however, is convincingly linked with the occurrence of *A. norvegicus*, but not convincingly linked with the occurrence of nematodes. Apparently *E. spinax* is infected with anisakid nematodes by feeding on the paratenic host *Maurolicus muelleri*.

Acknowledgements We are grateful to Dr. D.C. Kritsky, Idaho State University, Idaho, for providing additional information on the monogenean species, Dr. U. Piatkowski and Dr. R. Froese, Institut für Meereskunde, Kiel, for revising an earlier draft of the manuscript. The present study was supported by the Commission of the European Community (Q5RS-2000–30183, LIFECO).

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