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Fish parasites in the Arctic deep-sea: Poor diversity in pelagic fish species vs. heavy parasite load in a demersal fish

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Abstract

A total of 219 deep-sea fishes belonging to five families were examined for the parasite fauna and stomach contents. The demersal fish *Macrourus berglax*, bathypelagic *Bathylagus euryops*, and mesopelagic *Argentina silus*, *Borostomias antarcticus*, *Chauliodus sloani*, and *Lampanyctus macdonaldi* were caught at 243–708 m trawling depth in the Greenland and the Irminger Sea in 2002. A total of 21 different parasite species, six Digenea, one Monogenea, two Cestoda, seven Nematoda, one Acanthocephala, and four Crustacea, were found. The parasite diversity in the meso- and bathypelagic environment was less diverse in comparison to the benthal. *Macrourus berglax* had the highest diversity (20 species), usually carrying 4–10 different parasite species (mean 7.1), whereas *Bathylagus euryops* harbored up to three and *Argentina silus*, *Borostomias antarcticus*, *Chauliodus sloani* and *Lampanyctus macdonaldi* each up to two species. Most Digenea, Cestoda, Nematoda, Acanthocephala, and Crustacea are known from a wide host range. Several of the encountered parasites occurred at a very low prevalence ($<10\%$), indicating that the studied deep-sea fishes are most probably not instrumental to complete the parasite life cycles in the area of investigation. It is suggested that the lack of nutrients in the meso- and bathypelagial limits the abundance of potential first intermediate hosts of nematodes and cestodes, resulting in low infestation rates even of widely distributed, non-specific species. In contrast, the higher biomass in the benthic deep-sea environment increases the availability of potential intermediate hosts, such as molluscs for the digeneans, resulting in increased parasite diversity. Because many deep-sea fish have a generalistic feeding behavior, the observed different parasite diversity reflects a different depth range of the fish and not necessarily a specific fish feeding ecology.
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1. Introduction

The ocean is the largest ecosystem on earth. More than two thirds of the world's surface is covered by the sea with an average depth of 3800 m (Angel, 1993). The deep-sea below 200 m depth is characterized by the absence of sunlight, low

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temperature, high pressure, reasonably good oxygenation and physical homogeneity (Noble, 1973; Tyler, 1995). The mesopelagial (200–1000 m) is illuminated by diffuse light, and nutrients are available but scarce. The bathypelagial (1000–4000 m) is completely dark and can be characterized by food shortage (Castro and Huber, 1997). Jointly, these layers represent the largest area of the deep-sea (Bray et al., 1999). The abyssopelagial (4000–6000 m) and hadalpelagial (>6000 m) are also characterized by the scarcity of food. Bioluminescence and glowing black smokers are the only sources of light in the deep sea.

In the early 19th century, it was assumed that life did not exist in the deep sea below 700 m (Andres, 1996). Only during the following decades did it gradually become clear that the diversity of the deep-sea, and the upper abyssal zone in particular, surpasses that of some shallow-water habitats. This understanding was one of the principal foundations for the "Time-Stability Hypothesis" by Sanders (1969), who assumed that environmental stability and prolonged lack of habitat disturbance result in high species diversity. The scarcity of food in the highly stable deep-sea environment enables the formation of small niches, with the apportionment of the available resources. However, the general scarcity of food in the deep sea seems to make any specialization disadvantageous, resulting in an apparently low structural complexity of the food web. Because of the absence of light and the constant environmental conditions, the principal factors determining the settlement of organisms are food availability and water movement.

The Arctic deep-sea in general has the same characteristics as other deep-sea regions. However, as a zone of thermohaline convection, this part of the ocean has very characteristic water conditions and movements. Within the Arctic, the Greenland Sea is one of the most heavily exploited parts of the Atlantic Ocean. It is a dynamic region that is influenced by winds and several important currents, such as the East Greenland Current and the Irminger Current. Amongst others, they are responsible for the deep-sea convection in the North Atlantic (Pickart et al., 2003). Because of the strong demand for fish, all of the most common fish stocks are over-exploited. Modern fisheries are in search of new fishing grounds, including the deep-sea. This necessitates a better understanding of the exploitable fish species, including their biology and ecology.

The global fish fauna comprises approximately 29,000 species (Froese and Pauly, 2005). Of these, perhaps 10–15% (3800–4200 species) live in the deep-sea. Such limited diversity is somewhat surprising, considering the size of this ecosystem. Consequently, deep-sea fish species are likely to be very widespread, and their populations are very large but dispersed. Fish parasites are highly adapted to their fish hosts and often follow the natural food web to complete their life cycles. A low specialization in terms of the feeding ecology of the potential deep-sea fish hosts would allow low host specificity of the parasites, enabling them to infest a wide range of different hosts. Consequently, deep-sea fish parasites might be represented also by less diverse but widely distributed species.

Deep-sea fish parasites have been often neglected, although they represent an integral part of the deep-sea environment and form an essential part of marine biodiversity. While the knowledge of parasites is sufficient for commercially important fish species, the great majority of deep-sea fish has never been investigated in this respect. The studies so far show conflicting evidence. Orias et al. (1978) studied 84 bathypelagic fishes from the eastern Atlantic and found a low prevalence of 5%. Noble and Orias (1975) recorded a higher infestation of bathypelagic Melanostigma pammelas in comparison to mesopelagic specimens in the eastern Pacific Ocean. In contrast, Campbell et al. (1980) recorded high parasite prevalence in 1712 benthic deep-sea fish. The authors concluded that benthic deep-sea fish have a diverse parasite fauna consisting of adult as well as larval forms, whereas pelagic deep-sea fish mainly harbor larval Cestoda and Nematoda. After Marcogliese (2002), the parasite diversity decreases with depth to increase again close to the sea floor. In total, 421 species, less than 10% of the known number of deep-sea fishes, have been studied for metazoan parasites so far. These hosts harbor 621 different parasite species, with 1.5 parasite species per fish species (Klimpel et al., 2001).

According to food availability and consequently feeding ecology, meso-, bathypelagic and demersal fish follow different habits. This must be reflected also in their parasite fauna and diversity. The present study examined the parasite fauna of six different Arctic deep-sea fish species belonging to different oceanic environments between the east Greenland and the Irminger Sea, North Atlantic. The mesopelagial was represented by Argentina silus (Argentinidae), Borostomias antarcticus (Stomiidae),

Chauliodus sloani (Stomiidae), and *Lampanyctus macdonaldi* (Myctophidae), and the bathypelagial by *Bathylagus euryops* (Bathylagidae). *Macrourus berglax* (Macrouridae), the most frequent demersal species at the sampled locality, was studied for comparison. The parasite diversity, species composition and fish feeding ecology were studied in order to clarify possible differences or similarities in terms of parasite diversity, transfer mechanisms and life-cycles within the different habitats.

2. Materials and methods

2.1. Sample collection

Fish samples were collected in 2002 (between 23 October and 14 November) on board the German research vessel *Walther Herwig III* during international ICES and NAFO surveys within the east Greenland Sea and the Irminger Sea (Fig. 1). The deep-sea fish were caught with a Gloria net and a benthopelagic net at a trawling speed of approximately 4 knots. A total of 219 deep-sea fishes belonging to five families were examined for the parasite fauna and stomach contents. *Bathylagus euryops* Goode & Bean, 1896 (68 specimens), *Borostomias antarcticus* (Lönnberg, 1905) (10), *Chauliodus sloani* Bloch & Schneider, 1801 (21)

and *Lampanyctus macdonaldi* (Goode & Bean, 1896) (45) were caught at 700 m mean trawling depth (trawling depth range 680–708 m, Station 1, bottom depth range: 2900–3200 m), while *Argentina silus* (Ascanius, 1775) (40) was caught at 249 m mean trawling depth (trawling depth range 243–252 m, Station 1). The demersal fish *Macrourus berglax* Lacepède, 1801 (35) was caught at 334 m mean trawling depth (trawling depth range 278–387 m, Stations 2–9, bottom depth range 280–409 m). All fishes were deep frozen at $-40\,^{\circ}$C immediately after catch for subsequent examinations. Prior to examination, each fish specimen was defrosted to 0–$1\,^{\circ}$C. Morphometrical data such as standard length (SL) or, in the case of *Macrourus berglax*, the pre-anal length (PAL) and total weight (TW) were recorded to the nearest 0.1 cm and 0.1 g (Table 1).

2.2. Parasitological examination

The eyes, skin, fins, gills, nostrils, and mouth cavity of each fish specimen were studied for ectoparasites. The body cavity was opened to examine microscopically the liver, stomach, pyloric caeca, intestine, and gonads for endoparasites. The stomach weight was taken before and after the examination (to the nearest 0.001 g). The stomach content was removed and all food items were sorted
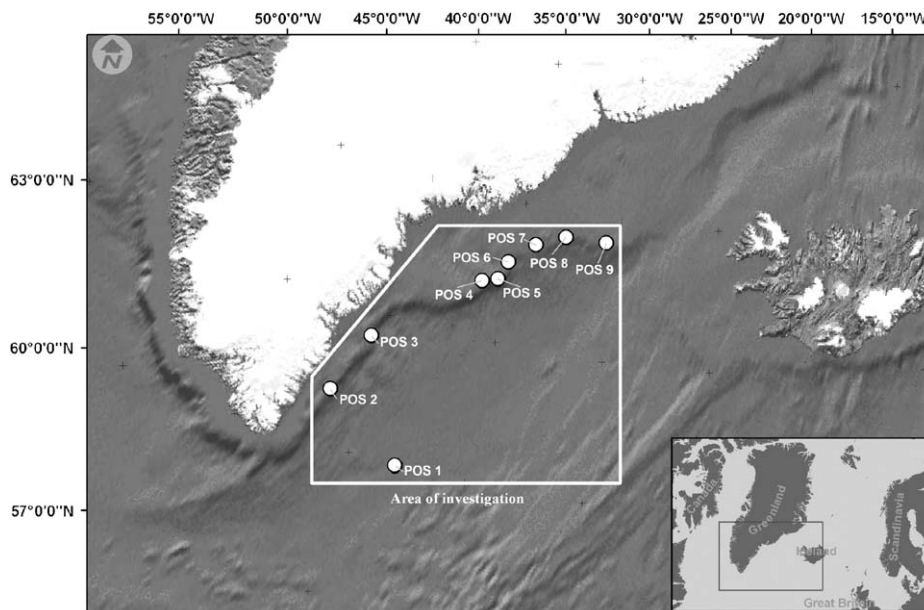

Fig. 1. Map of the area of investigation. POS, position.

Table 1
Number, mean length, and mean weight (range in parentheses) of the studied Arctic deep-sea fish

Fish species	n	PAL/SL (cm)	TW (g)
Macrourus berglax	35	6.1 (3.3–14.6)	391.7 (93.0–1150.4)
Bathylagus euryops	68	14.0 (9.8–18.0)	27.4 (6.7–58.4)
Argentina silus	40	13.4 (8.8–15.2)	22.5 (5.4–32.4)
Borostomias antarcticus	10	23.8 (17.3–30.8)	96.3 (19.2–229.5)
Chauliodus sloani	21	21.3 (12.8–28.1)	28.6 (3.6–73.4)
Lampanyctus macdonaldi	45	13.0 (11.0–14.9)	22.7 (13.2–31.4)

PAL, pre-anal length (*Macrourus berglax*); SL, standard length (all other fish species); TW, total weight.

and identified to the lowest possible taxonomic level, and grouped into taxonomic categories.

The isolated parasites were fixed in 4% borax-buffered formalin and preserved in 70% ethanol/ 5% glycerine. For identification purposes, nematodes were dehydrated in a graded ethanol series and transferred to 100% glycerine (Riemann, 1988). Digenea and Cestoda were stained with acetic carmine, dehydrated, cleared with Eugenol or Creosote, and mounted in Canada balsam. Parasite identification literature included original descriptions. The parasitological terminology used follows Bush et al. (1997): prevalence (*P*) is the number of infected fish with one or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined (expressed as a percentage); intensity (of infection, *I*) is the number of individuals of a particular parasite species in a single infected host (expressed as a numerical range); and mean intensity (of infection, *mI*) is the average intensity, in other words, it is the total number of parasites of a particular species found in a sample divided by the number of infected hosts. The term transport host is used for an intermediate host where no further larval development occurs. The diversity of the metazoan parasite fauna of each fish species was estimated by using the Shannon–Wiener diversity index (*H′*) and the evenness index (*E*) of Pielou (Magurran, 1988):

$$H' = H_s = -\sum_{i=1}^{s} p_i \ln p_i \quad E = H_s / \ln s,$$

where H_s is the diversity index, p_i the proportion of the individual (*i*th) species to the total, *s* is the total number of species in the community (species richness).

2.3. Analysis of the stomach contents

The numerical percentage of prey $N(\%)$, the weight percentage of prey $W(\%)$ and the frequency of occurrence $F(\%)$ were determined from the stomach contents (Hyslop, 1980). Using these three indices, an index of relative importance IRI (Pinkas et al., 1971) was calculated. The importance of a specific prey item increases with higher values for N, W, F and IRI:

Frequency of occurrence : $F(\%) = M_i / M \times 100,$

where M_i is the number of stomachs containing prey component i and M is the number of stomachs containing food.

Numerical percentage of prey i:

$N(\%) = N_i / N_\Sigma \times 100,$

where N_i is the number of prey specimen of prey group i and N_Σ is the total number of prey detected.

Weight percentage of prey i :

$W(\%) = W_i / W_\Sigma \times 100,$

where W_i is the weight (g) of prey group i and W_Σ is the TW (g) of prey detected.

Index of relative importance : $\text{IRI} = (N + W) \times F.$

3. Results

The analysis of 219 deep-sea fishes from different deep-sea environments in the Greenland and the Irminger Sea (Table 1) revealed high parasite diversity in the bottom-dwelling *Macrourus berglax* in comparison to the other pelagic deep-sea fish. A total of 20 different parasite species were found. The

Table 2
Numerical percentage of prey i (N%), weight percentage of prey i (W%), frequency of occurrence (F%), and the index of relative importance (IRI) of the food items identified from the stomach contents of the Arctic deep-sea fish

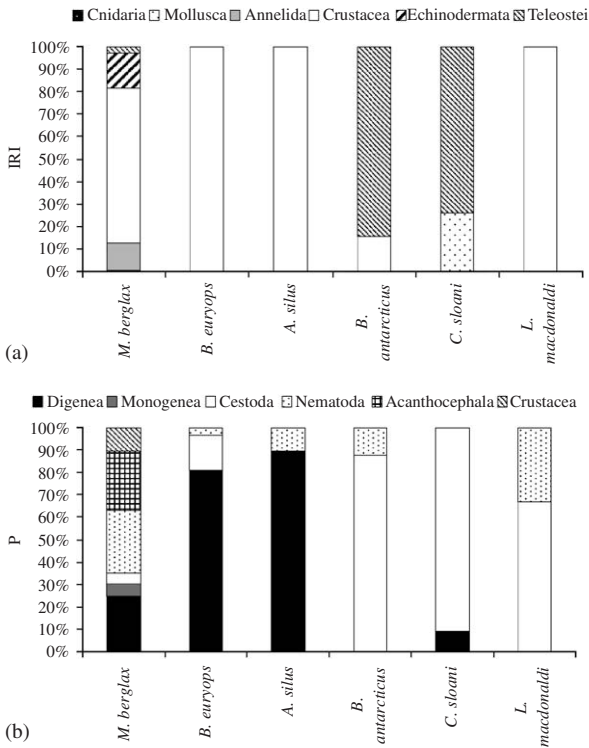| Prey category	Fish species																							
	Macrourus berglax				Bathylagus euryops				Argentina silus				Borostomias antarcticus				Chauliodus sloani				Lampanyctus macdonaldi			
	N%	W%	F%	IRI	N%	W%	F%	IRI	N%	W%	F%	IRI	N%	W%	F%	IRI	N%	W%	F%	IRI	N%	W%	F%	IRI
Cnidaria																								
Anthozoa	3.3	0.1	5.9	20																				
Mollusca																								
Bathypolypus arcticus	0.6	1.8	5.9	14																				
Cephalopoda																	25.0	78.4	25.0	2585				
Mollusca indet.	0.9	0.4	8.8	11																				
Annelida																								
Polychaeta	6.2	32.0	44.1	1685																				
Crustacea																								
Copepoda					18.2	2.7	19.0	397	33.3	1.1	30.8	1059									30.0	10.9	40.9	1673
Euphausiacea	11.3	10.1	44.1	944	18.2	18.9	19.0	705	26.7	63.4	30.8	2775									17.5	22.4	18.2	726
Pasiphaea multidentata																					2.5	22.6	4.5	113
Pandalus spp.	0.3	1.8	2.9	6																				
Decapoda									13.3	28.5	15.4	644	40.0	4.1	50.0	2205								
Themisto abyssorum																					5.0	3.6	9.1	78
Themisto gaudichaudi																					17.5	21.0	22.7	874
Themisto sp.																					2.5	2.8	4.5	24
Hyperiidae	24.9	4.8	47.1	1401																	20.0	16.4	27.3	994
Gammaridae	29.4	0.9	17.6	535																				
Amphipoda indet.	2.4	0.8	11.8	37																	2.5	0.2	4.5	12
Isopoda	16.3	20.0	35.3	1281																				
Ostracoda					4.5	0.5	4.8	24																
Crustacea indet.	8.6	4.0	41.2	517	59.1	77.9	61.9	8480	26.7	7.0	30.8	1038									2.5	0.2	4.5	12
Echinodermata																								
Ophiuroidea	19.0	13.4	67.6	2188																				
Teleostei																								
Hippoglossoides platessoides	0.6	0.7	5.9	7																				
Macrouridae	0.3	2.6	2.9	9																				
Fish indet.	2.4	6.7	20.6	188									60.0	95.9	75.0	11693	75.0	21.6	75.0	7245				

(a)

(b)

Fig. 2. (a) Food composition (IRI) of the six investigated fish species. (b) Composition of the parasite groups infecting the investigated fish species.

prevalence, intensity, and mean intensity for each parasite and fish species are given in Table 3. Six different groups of prey items were identified, belonging to the Cnidaria, Mollusca, Annelida, Crustacea, Echinodermata, and Teleostei. Table 2 provides a detailed information on the stomach contents of the examined fish. Fig. 2a illustrates the higher taxonomic groups of the identified prey items for each fish species.

3.1. Parasite diversity

Macrourus berglax usually carried 4–10 (mean 7.1) different parasite species, whereas Bathylagus euryops harbored up to three and Argentina silus, Borostomias antarcticus, Chauliodus sloani and Lampanyctus macdonaldi up to two species (mean below 1; Figs. 3 and 4a–f). The diversity was high in the demersal Macrourus berglax ($H' = 2.335$, $E = 0.779$) in comparison to the other bathy- and mesopelagic fishes. The diversity was clearly lower in Bathylagus euryops ($H' = 0.173$, $E = 0.649$), Argentina silus ($H' = 0.263$, $E = 0.379$), Borostomias antarcticus ($H' = 0.255$, $E = 0.368$), Chauliodus sloani ($H' = 0.255$, $E = 0.368$), and Lampanyctus macdonaldi ($H' = 0.682$, $E = 0.984$).
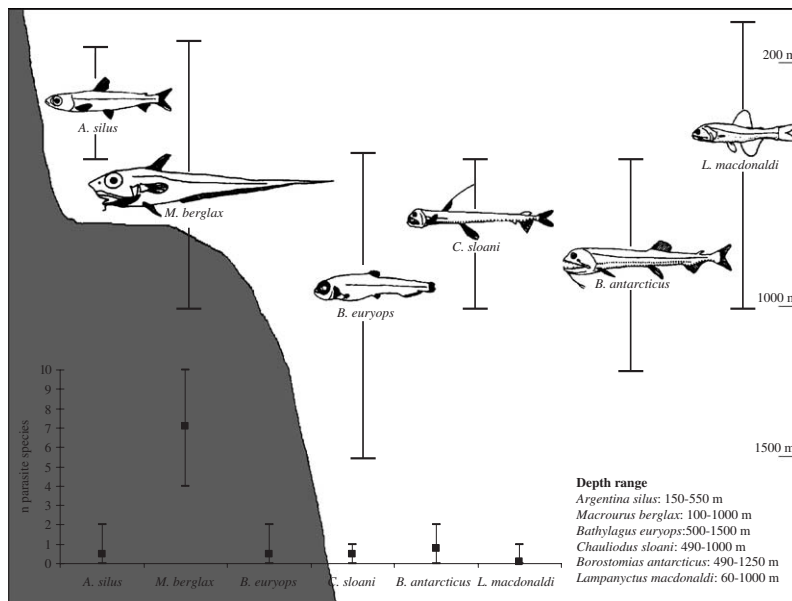
Fig. 3. Schematic representation of the depth range and the mean depth (represented by the mapped fishes) and the parasite diversity of the six analyzed Arctic deep-sea fish. Mean number of the different parasite species (■) and range (|) are given.
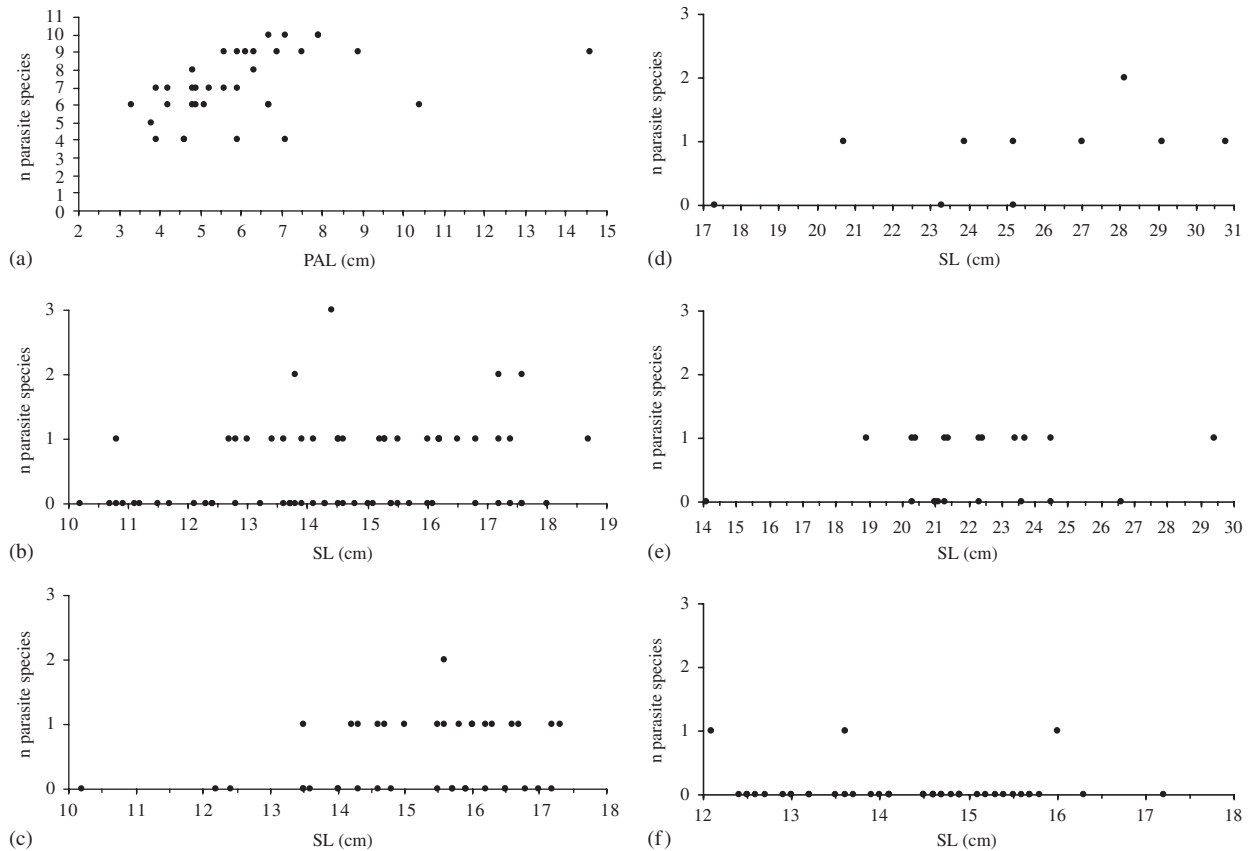
Fig. 4. Number of different parasite species in comparison to the fish length. (a) *Macrourus berglax*; (b) *Bathylagus euryops*; (c) *Argentina silus*; (d) *Borostomias antarcticus*; (e) *Chauliodus sloani*; (f) *Lampanyctus macdonaldi*. PAL, pre-anal length; SL, standard length.

3.2. Parasite composition and stomach contents

3.2.1. Macrourus berglax (a demersal nonmigrant) (Tables 2 and 3; Figs. 2a and b)

The parasite fauna of *Macrourus berglax* consisted of 20 different parasite species. The predominant parasites were the Digenea and Nematoda. The Digenea (*Derogenes varicus*, *Genolinea laticauda*, *Gibsonia borealis*, *Gonocerca phycidis*, and *Lepidapedon* sp.) were adult and located in the digestive tract. The highest infestation rates were calculated for *Genolinea laticauda*, *Gibsonia borealis* and *Gonocerca phycidis*. Only one adult Monogenea, *Macrouridophora macruri*, was found on the gills. Two larval (*Grillotia erinaceus*, Tetraphyllidea indet. (*Scolex pleuronectis*)) and one adult Cestoda (*Parabothriocephalus macruri*) were detected with low infestation rates. Seven Nematoda, *Anisakis simplex*, *Ascarophis* sp., *Capillaria gracilis*, *Hysterothylacium aduncum*, *Neoascarophis macrouri*, *Pseudoterranova decipiens*, and *Spinitectus oviflagellis*

were found. *Anisakis simplex*, *Hysterothylacium aduncum* and *Pseudoterranova decipiens* were isolated as larval stages, whereas the other nematodes as well as *Hysterothylacium aduncum* were in the adult stage. The adult Nematoda were located in the stomach (-wall), pyloric ceca and intestine, while the larvae were found exclusively in or on the organs of the body cavity. The adult stage of *Echinorhynchus gadi* (Acanthocephala) was located in the intestine. The adult Crustacea *Clavella adunca* and *Chondracanthodes radiatus* were located on the gills.

A total of 15 different food items (groups) belonging to the Crustacea, Echinodermata, Annelida, Cnidaria, Mollusca, and fish were identified. Of these, the diet of *Macrourus berglax* consisted predominantly of Crustacea, represented by Decapoda, Amphipoda, Isopoda, and Euphausiacea. Numerically, Gammaridae, Hyperiidae, Ophiuroidae, Isopoda, and Euphausiacea were dominant. In wet weight (*W*), the Polychaeta were followed by

Table 3
Prevalence (P), mean intensity (mI), and intensity (I) of infestation of the Arctic deep-sea fish

Parasite species	Fish species																							
	Macrourus berglax				Bathylagus euryops				Argentina silus				Borostomias antarcticus				Chauliodus sloani				Lampanyctus macdonaldi			
	adult/larva	P (%)	mI	I	adult/larva	P (%)	mI	I	adult/larva	P (%)	mI	I	adult/larva	P (%)	mI	I	adult/larva	P (%)	mI	I	adult/larva	P (%)	mI	I
Digenea																								
Derogenes varicus	a	20.0	3.4	1–10					a	42.5	1.5	1–4					a	4.8	1.0	1				
Genolinea laticauda	a	42.9	7.4	1–46																				
Gibsonia borealis	a	42.9	8.2	2–27																				
Gonocerca phycidis	a	62.9	2.1	1–10																				
Lecitophyllum botryophorum					a	38.2	1.2	1–2																
Lepidapedon sp.	a	2.9	5.0	5																				
Digenea indet.	a	5.7	1.0	1																				
Monogenea																								
Macrouridophora macruri	a	20.0	2.0	1–3																				
Cestoda																								
Grillotia erinaceus	l	2.9	1.0	1																				
Parabothriocephalus macruri	a	8.6	1.3	1–2																				
Bothriocephalidae indet.					pa	7.4	3.0	1–6																
Tetraphyllidea indet. (Scolex pleuronectis)	l	5.7	2.5	1–4									l	70.0	1.9	1–4	l	47.6	1.8	1–5		4.4	1.5	1–2
Nematoda																								
Anisakis simplex	l	42.9	3.1	1–12	l	1.5	1.0	1	l	5.0	1.0	1	l	10.0	1.0	1								
Ascarophis sp.	a	37.1	4.2	1–12																				
Capillaria gracilis	a	65.8	6.1	1–32																				
Hysterothylacium aduncum	a/l	28.6	2.2	1–7																				
Neoascarophis macrouri	a	71.4	13.6	1–37																				
Pseudoterranova decipiens	l	34.3	2.3	1–8																				
Spinitectus oviflagellis	a	40.0	8.6	1–49																				
Nematoda indet.	l	60.0	1.3	1–3																				
Acanthocephala																								
Echinorhynchus gadi	a	94.3	17.0	1–102																	l	2.2	4.0	4
Crustacea																								
Clavella adunca	a	37.1	1.8	1–4																				
Chondracanthodes radiatus	a	5.7	1.0	1																				

a, adult; l, larva; pa, pre-adult.

Isopoda, Ophiuroidea, Euphausiacea, and fish. The frequencies of occurrence (F) were highest for the Ophiuroidea, followed by Hyperiidae, Euphausiacea, Polychaeta, Isopoda, and fish. The Crustacea indet. (IRI 9632), especially Amphipoda, Euphausiacea and Isopoda, was the most important prey item for *Macrourus berglax*, followed by Echinodermata (2188), Annelida (1685), and fish (393). Prey species composition showed that the dominant identifiable food items were crustaceans.

3.2.2. Bathylagus euryops (a bathypelagic semi-migrant) (Tables 2 and 3; Fig. 2a and b)

Three different parasite species were isolated from *Bathylagus euryops*. The adult stage of the Digenea *Lecitophyllum botryophorum* was located in the stomach and intestine. An unidentified preadult of the Pseudophyllidea was collected from the stomach. The isolated parasites had two shallow bothria and an apical disk, similar to *Philobythos atlanticus* (Fig. 10.28 in Khalil et al., 1994). The identification, however, could not be confirmed with the lack of developed genitalia. A single third-stage larva of *Anisakis simplex* was encapsulated in the body cavity. *Bathylagus euryops* is the final (definitive) host for *Lecitophyllum botryophorum*, possibly the final host or the intermediate host for the preadult Cestoda and a transport host for *Anisakis simplex*.

Four groups of prey items were identified: Euphausiacea, Copepoda, Ostracoda, and Crustacea indet. Numerically, the Crustacea indet. was the most predominant, followed by Copepoda, Euphausiacea, and Ostracoda. In weight (W), Crustacea indet. and Euphausiacea exceeded the Copepoda and Ostracoda. The frequencies of occurrence (F) were highest for the Crustacea indet., followed by the Euphausiacea, Copepoda, and Ostracoda. The IRI was 8480 for Crustacea indet., 705 for Euphausiacea, 397 for Copepoda, and 24 for Ostracoda, indicating that the first was the main prey item.

3.2.3. Argentina silus (a mesopelagic non-migrant) (Tables 2 and 3; Fig. 2a and b)

Two different parasite species were found in *Argentina silus*: one Digenea and one Nematoda. The predominant parasite was *Derogenes varicus* (Digenea), and the adult stages were found in the stomach. The third-stage larvae of the anisakid Nematoda *Anisakis simplex* was encapsulated in the liver. *Argentina silus* is the final host for *D. varicus* and a transport host for *Anisakis simplex*.

All prey items belonged to the Crustacea, mainly Euphausiacea and Copepoda, with Decapoda having minor importance. Numerically, the Copepoda were dominant. In wet weight (W), the Euphausiacea were followed by the Decapoda, Crustacea indet., and Copepoda. The frequency of occurrence (F) was highest for the Euphausiacea, followed by Copepoda, Decapoda, and Crustacea indet. The IRI for Euphausiacea was 2775, followed by Copepoda (1059), Crustacea indet. (1038), and Decapoda (644), indicating that euphausiids were the main prey item of *Argentina silus*.

3.2.4. Borostomias antarcticus (a mesopelagic semi-migrant) (Tables 2 and 3; Fig. 2a and b)

Two different parasite species were recorded, one Cestoda and one Nematoda. The intestinal lumen of *Borostomias antarcticus* was infested with unidentified tetraphyllidean larvae (*Scolex pleuronectis*). These tetraphyllideans are distributed circumpolar and have been found in various fish species (e.g., Klimpel et al., 2001). However, further identification is not possible without strobila characters or knowledge of the life cycle. Third-stage larvae of the nematode *Anisakis simplex* were found in the body cavity encapsulated outside the intestine. *Borostomias antarcticus* serves as an intermediate host for *Scolex pleuronectis* and as a transport host for *Anisakis simplex*.

Borostomias antarcticus preyed almost exclusively on fish and Copepoda (IRI values were 11,693 for fish and 2205 for Copepoda).

3.2.5. Chauliodus sloani (a mesopelagic semi-migrant) (Tables 2 and 3; Fig. 2a and b)

Two different parasite species were found, one adult Digenea and one larval Cestoda. *Derogenes varicus* was located in the stomach and the larval tetraphyllidean cestode (*Scolex pleuronectis*) was found in the lumen of the stomach and intestine.

The prey group composition consists mostly of fishes. Numerically and according to the most frequent prey organism, fishes were followed by the Cephalopoda. By wet weight (W), Cephalopoda was the most important food item. The IRI indicates that *Chauliodus sloani* preyed mainly on fishes (7245) and Cephalopoda (2585).

3.2.6. Lampanyctus macdonaldi (a mesopelagic migrant) (Tables 2 and 3; Fig. 2a and b)

Only two parasite species, one Cestoda and one Nematoda, were found with very low infestation

rates. Tetraphyllidean larval stages (*Scolex pleuronectis*) were found in the pyloric ceca. The liver and intestine of one single *Lampanyctus macdonaldi* was infested by four so far unidentified Nematoda.

The diet consisted exclusively of crustaceans, belonging to the Copepoda, Euphausiacea, Amphipoda, and Decapoda. Specimens of *Lampanyctus macdonaldi* preyed mainly upon pelagic Amphipoda of the genus *Themisto*. Copepoda, Hyperiidae, and Euphausiacea had the highest numerical percentage of prey. By wet weight, the Decapoda *Pasiphaea multidentata* were followed by Euphausiacea, *Themisto gaudichaudi*, Hyperiidae, and Copepoda. The frequency of occurrence was highest for the Copepoda, followed by the Hyperiidae, *Themisto gaudichaudi*, and Euphausiacea. The IRI for Copepoda was 1673, followed by Hyperiidae (994), *Themisto gaudichaudi* (874), Euphausiacea (726), and *Pasiphaea multidentata* (113).

4. Discussion

This is the first parasitological study on six different Arctic deep-sea fish species in the East Greenland and the Irminger Sea. According to differences in their diet, migration habits, and habitat, the different fish show remarkable differences in the parasite species composition.

4.1. Macrourus berglax

The demersal *Macrourus berglax* is widely distributed in temperate and Arctic waters in the North Atlantic Ocean (Froese and Pauly, 2005). It belongs to the non-migratory, benthopelagic deep-sea fishes living at depths between 100 and 1000 m, but prefers a depth range of 300–500 m (Froese and Pauly, 2005) (Fig. 3). The parasite fauna as well as the food composition of *Macrourus berglax* is highly diverse (present study; Zubchenko, 1981; Klimpel et al., 2001). A total of 20 different parasite species occurred on or in the examined *Macrourus berglax*. Zubchenko (1981) similarly reported 20 parasite species from a sample of 30 fish specimens from the northwest Atlantic, with benthic organisms being the intermediate hosts for many of them.

Almost all helminth parasites encountered during the present study are known or believed to use planktonic and/or benthic invertebrates as first or second intermediate hosts. These include the species of the Digenea, Cestoda, Nematoda and Acanthocephala. The Digenea, such as *Derogenes varicus*, use demersal and planktonic Copepoda as the second intermediate hosts, and all three recorded that Cestoda use Copepoda as first intermediate hosts. The third-stage larvae of the nematode *Anisakis simplex* have been found primarily in larger deep-sea Copepoda and Euphausiacea (Klimpel et al., 2004), and *Hysterothylacium aduncum* also uses various planktonic and benthic invertebrates (crustaceans and non-crustaceans) as obligatory intermediate hosts (Køie, 1993; Klimpel and Rückert, 2005). Other nematodes, e.g., *Capillaria gracilis*, use oligochaete (and chironomid) as first intermediate hosts and fish as obligatory second intermediate hosts (Køie, 2001a), while *Echinorhynchus gadi*, *Ascarophis* sp., and *Pseudoterranova decipiens* use benthic Crustacea as obligatory intermediate hosts. Most of the above parasites (not all) may also be acquired and accumulated by *Macrourus berglax* as paratenic host through predation on infected macro-invertebrates and small fish, such as capelin (*Mallotus villosus*), pearlside (*Maurolicus muelleri*) and Myctophidae. According to the recorded parasite fauna, *Macrourus berglax* has the main function as final host for its deep-sea parasites, with only two Cestoda (unidentified Tetraphyllidea (*Scolex pleuronectis*), *Grillotia erinaceus*) and two Nematoda (*Anisakis simplex*, *Pseudoterranova decipiens*) infesting this fish as intermediate or paratenic host. Elasmobranchii serve as final hosts for the Cestoda species, where they mature in the stomach or spiral valve (Khalil et al., 1994; Klimpel et al., 2003; Palm, 2004). The life-cycle includes Crustacea as first and larger invertebrates or fish as second intermediate hosts (Khalil et al., 1994; Palm, 2004). *Macrourus berglax* acquires these parasites by feeding on the intermediate hosts and acts likewise as second intermediate or paratenic host. *Anisakis simplex* and *Pseudoterranova decipiens* use various invertebrates as first intermediate hosts and larger Crustacea and fishes as second intermediate or paratenic hosts. Final hosts for *Anisakis simplex* are mainly Cetacea, while pinnipeds are the final host for *Pseudoterranova decipiens* (Palm, 1999; Køie, 2001b; Klimpel et al., 2004). The final hosts are abundant inshore or during their seasonal migrations through the eastern Greenland Sea. The recorded ectoparasites, the monogenean *Macrouridophora macruri* and the two Crustacea (*Clavella adunca* and *Chondracanthodes radiatus*) were previously described from fishes of the family Macrouridae (Rubec and Dronen, 1994; Klimpel et al., 2001). Because the Monogenea have direct

life-cycles, they are considered host specific, and *Macrouridophora macruri* is a typical ectoparasite of *Macrourus berglax* and other macrourids.

The high parasite diversity of *Macrourus berglax* corresponds to a highly diverse diet. Crustacea were the predominant food items, followed by Ophiuroidea (Echinodermata), and Polychaeta (Annelida). Crustacea were also frequently recorded from other regions such as the northeast Atlantic, Mediterranean Sea, and Indian Ocean, the Barents and the Labrador Sea (Geistdoerfer, 1979) and Buffin Island (Konstantinov and Podrazhanskaya, 1972). The diet of *Macrourus berglax* changes with the size of the fish from smaller prey items to large fishes and squid, similar to other Macrouridae. Almost all identifiable prey items were deep-sea pelagic or hyperbenthic species, such as Hyperiidae, other Amphipoda, Euphausiacea, and pelagic fish larvae (e.g., *Hippoglossoides platessoides*). Many of these organisms do not carry out daily vertical migrations that could bring them in close proximity to the bottom. It can be concluded that in the East Greenland and the Irminger Sea, the demersal *Macrourus berglax* forages also within the water column and not only at the sea floor. The access to pelagic and benthopelagic intermediate hosts also explains the observed high parasite diversity and the important function of *Macrourus berglax* as a host for deep-sea parasites.

4.2. Bathylagus euryops

The bathypelagic *Bathylagus euryops* is distributed in the North Atlantic Ocean and occurs down to a depth of 1500 m (Froese and Pauly, 2005) (Fig. 3). The distribution in the Irminger Sea is relatively uniform, with a preferred depth below 500 m (Sigurðsson et al., 2002). The dominant parasite was the digenetic Trematoda *Lecithophyllum botryophorum*. Gajevskaja (1989) redescribed *Lecitophyllum botryophorum* in *Bathylagus euryops* from the northeast Atlantic, however, giving no infestation rates. *Lecitophyllum botryophorum* is a typical deep-sea parasite species. The deepest host record is noted for the deep-sea fish *Alepocephalus bairdii* at 1653 m (Bray, 2004), which corresponds to the depth distribution of *Bathylagus euryops*.

Less than 1% of the molluscs in shallow waters are Scaphopoda that are known to be first intermediate hosts for *Lecitophyllum botryophorum* (Køie et al., 2002). Their abundance increases with water depths (Gage and Tyler, 1991).

The preadult Cestoda in the stomach belonged to the Pseudophyllidea. Within that order of tapeworms, pelagic Crustacea harbor the procercoid and serve as first intermediate hosts. The plerocercoids develop in planktivorous fish (second intermediate hosts), while the adult Cestoda mature in piscivorous fishes as final hosts (Khalil et al., 1994). The preadult specimens resembled *Philobythos atlanticus*, a typical pseudophyllid (Philobythiidae) from deep-sea fishes and also from *Macrourus berglax*. In this case, *Bathylagus euryops* could serve as intermediate host, with *Macrourus berglax* being final host in the region. However, other pseudophyllids such as *Parabothriocephalus* spp. (Echinophallidae) and *Eubothrium* sp. (Triaenophoridae) have also been recorded from *Macrourus berglax* and other deep-sea fish. Thus, the bathypelagic *Bathylagus euryops* might also serve as an important intermediate host for these deep-sea pseudophyllids, or even represent a new final host.

Mauchline and Gordon (1983) analysed 175 *Bathylagus euryops* and found that the stomachs contained 61.5% of unidentified tissue, which is close to our results (69.1%). However, the food composition of *Bathylagus euryops* during the present study consisted exclusively of Crustacea, such as Euphausiacea and Copepoda. While scaphopods are intermediate hosts for *Lecitophyllum botryophorum*, copepods can be considered as first intermediate hosts for the pseudophyllid cestode, and Euphausiacea and Copepoda as first intermediate host for the Nematoda *Anisakis simplex*. In the latter case, this fish species might serve as second intermediate (Copepoda) or a transport host (Euphausiacea).

4.3. Argentina silus

The mesopelagic *Argentina silus* is distributed in the eastern and western Atlantic (Froese and Pauly, 2005) and occurs at depths between 140 and 1400 m (Johannessen and Monstad, 2003) (Fig. 3). The vertical distribution of *Argentina silus* varies during its lifetime. In Norwegian waters, juveniles occur at 200–300 m, and adults are common in deeper waters (Johannessen and Monstad, 2003).

Only two parasite species were detected, the Digenea *D. varicus* and the Nematoda *Anisakis simplex*. *D. varicus* is one of the most widespread (Køie, 1979) and least host-specific Digenea in fish (Køie, 2000). Mollusca (Gastropoda) act as first obligatory intermediate hosts. Køie (1979)

demonstrated that Copepoda (Calanoida) get infested with free-swimming cercariae and function as intermediate hosts. The life cycle of *Anisakis simplex* varies with habitat. Calanoid Copepoda or Euphausiacea are first intermediate hosts for *Anisakis simplex* third-stage larvae at different localities (Klimpel et al., 2003, 2004). Small pelagic fish species, such as pearlside (*Maurolicus muelleri*), and Cephalopoda act as obligatory (second) intermediate or transport hosts, while Cetacea and sometimes Pinnipedia are definitive hosts (e.g., Klimpel et al., 2003, 2004). Studies on *Argentina silus* along the Scotian Shelf and St. Pierre Bank revealed that young specimens are mid-water plankton feeders (Scott, 1969). Cohen (1958) found digested "shrimp-like crustaceans", which are supposed to be Euphausiacea in the stomach of western Atlantic specimens. The stomach contents also revealed fragments of salps and Ctenophora (Mauchline and Gordon, 1983). During the present study, only crustaceans were identified in the stomachs of *Argentina silus*. The predominant prey was Euphausiacea, followed by Copepoda. While the copepods can be considered as second intermediate hosts for *D. varicus*, both crustacean groups represent important first and second intermediate hosts for *Anisakis simplex* in the studied area.

4.4. Borostomias antarcticus

The mesopelagic *Borostomias antarcticus* is distributed in the eastern Atlantic and from Greenland south to the Bay of Biscay (Froese and Pauly, 2005) at a depth between 500 and 1200 m (Roberts, 1991) (Fig. 3). Sigurðsson et al., (2002) reported that they belong to a group of most common species with a relatively uniform distribution in the Irminger Sea.

Borostomias antarcticus preys mainly upon pelagic fishes and Crustacea (Froese and Pauly, 2005). Stomach analyses of *Borostomias antarcticus* from the Rockall Through contained semi-digested Mysidacea (Mauchline and Gordon, 1983), and Copepoda and fishes were the dominant prey items during the present study. While the Copepoda serve as intermediate hosts for the anisakid *Anisakis simplex* (see above), the predatory *Borostomias antarcticus* acquires and accumulates larval tetraphyllideans in high numbers by ingesting copepods or small pelagic fish species that are infested and serve as carriers. These cestodes are very common in all kinds of predatory oceanic fish and also in the deep-sea (e.g., Klimpel et al., 2001). Marine

Crustacea (Copepoda) are probably first intermediate hosts, different fish species act as second intermediate hosts, and Elasmobranchii serve as final hosts.

4.5. Chauliodus sloani

The mesopelagic *Chauliodus sloani* is distributed in the North Atlantic, the Mediterranean Sea and the Indian Ocean (Froese and Pauly, 2005) at a depth of 500 m (Sigorðsson et al., 2002) (Fig. 3). The predominant parasites were unidentified tetraphyllidean larvae (*Scolex pleuronectis*) from the intestine at a prevalence of 47.6%. Gartner and Zwerner (1989) already detected tetraphyllideans in the intestine of the same species. In addition, we isolated the Digenea *D. varicus* from the stomach at a prevalence of 4.8%. These data also correspond to the findings of Gartner and Zwerner (1989) in the western North Atlantic. The authors recorded one unidentified Digenea species in *Chauliodus sloani* at a prevalence of 2.8%.

Williams et al. (2001) examined the stomach of 57 *Chauliodus sloani* from the southern Tasmanian Sea and found Myctophiformes and Stomiiformes fish as main food items. During the present study, the stomachs of three specimens of *Chauliodus sloani* contained fragments of fish, and a further specimen fragments of Cephalopoda. Consequently, *Chauliodus sloani* seems to accumulate tetraphyllideans by ingesting infected juvenile fish or Cephalopoda. The small infestation rate with *D. varicus* can be explained by the separation of the mollusc first intermediate hosts from the mesopelagic environment (Køie, 1979).

4.6. Lampanyctus macdonaldi

The mesopelagic *Lampanyctus macdonaldi* is distributed in the North Atlantic Ocean, at the Antarctic polar front and between the subtropical convergence and Antarctic polar front (Hulley, 1984). In the Irminger Sea, this fish is a component of the deep-scattering layer at a depth range of 60–1000 m (Hulley, 1984; Magnússon, 1996; Sigurðsson et al., 2002) (Fig. 3).

The examined specimens of *Lampanyctus macdonaldi* revealed only two parasite species. One fish harbored three unidentified Nematoda within a cyst and one nematode in the intestine. Two further specimens were infested with larval stages of Tetraphyllidea indet. (*Scolex pleuronectis*). Gartner

and Zwerner (1989) examined 14 *Lampanyctus macdonaldi* from the Norfolk Submarine Canyon and detected only two *Ichthyophonus* and an unidentified cyst. The specimens had a mean SL of 10.1 cm and were smaller than our fish. The results of *Lampanyctus macdonaldi* contradict those from the other meso- and bathypelagic fishes. Although *Lampanyctus macdonaldi* had most stomachs filled with food (48.1%), this species showed the lowest parasite load. Stomach content analyses of *Lampanyctus macdonaldi* are quite rare and identified Mysidacea as the main food item (Mauchline, 1982). Our fish contained Copepoda, Euphausiacea, and Amphipoda instead. *Lampanyctus macdonaldi* is an extremely offshore (open-water) pelagic fish showing vertical migration at night (Hulley, 1984; Sigurðsson et al., 2002). At night, juvenile fish rise to the plankton-rich epipelagial nearly 60 m under the sea surface, while the adult fish stay at a depth of 250 m (Froese and Pauly, 2005). The low parasite infestation rate can be explained by the large distance of the typical habitat of *Lampanyctus macdonaldi* from both the sea floor and the continental shelf, limiting its access to infested fish parasite intermediate hosts.

5. Conclusion

Species diversity of marine fish parasites depends on the specific feeding behavior of the hosts, the availability of intermediate and final hosts, depth distribution, and host migration. Similarities in diet and habitat of potential host species result in a similar or even identical parasite fauna. In contrast, hosts with different food preferences may have large differences in their parasite fauna. Within the East Greenland and the Irminger Sea, a combination of different factors, especially the availability of the intermediate hosts and the habitat preferences of the fish, can be seen as the main reason for the observed infestation patterns.

The majority of parasites reported from the six different fish species show little host specificity, having been reported from a wide variety of hosts (e.g., Klimpel et al., 2001). These include most Digenea, most Cestoda, most Nematoda, Acanthocephala, and two Crustacea. Only *Gibsonia borealis* and *Neoascarophis macrouri* are specific to *Macrourus berglax*. *Parabothriocephalus macruri* and *Spinitectus oviflagellis* also infest other macrourids and gadiforms. Several of the encountered parasites occurred at a very low prevalence (< 10%). This might indicate that the studied deep-sea fishes are not instrumental for the completion of the parasite life-cycles within the area of investigation.

In general, the parasite fauna of the mesopelagic (*Argentina silus*, *Borostomias antarcticus*, *Chauliodus sloani*, *Lampanyctus macdonaldi*) and bathypelagic (*Bathylagus euryops*) deep-sea fishes are quite similar, while the parasite fauna of the demersal deep-sea fish (*Macrourus berglax*) is rather different. As suggested by Gartner and Zwerner (1989), the parasitism between benthic and meso- and bathypelagic fish is different. The observed differences are the result of ecological differences among the six species. The depth distributions of the meso- and bathypelagic species overlap considerably, and some of the fishes undergo diurnal migrations within the water column for feeding. However, both groups have only few and widely distributed non-specific parasites. This can be explained only by difficulties of the parasites to infest meso- or bathypelagic hosts due to low feeding (transmission) rates of the fish or by the general lack of parasites (low abundance) within the meso- and bathypelagic environment. In contrast, the demersal macrourid showed high parasite diversity, obviously being accessible by a wide range of different, and often also less host-specific, parasite species. The demersal as well as pelagic feeding behavior of *Macrourus berglax* results in an increased ingestion rate of potential intermediate hosts. In addition, the sea floor environment contains a higher biomass, resulting in the availability of more intermediate and final hosts.

The parasite composition of the six studied Arctic deep-sea fish in the East Greenland and the Irminger Sea supports the statement by Marcogliese (2002) that the parasite diversity decreases with depth to increase again close to the sea floor. It is suggested that the lack of nutrients in the meso- and bathypelagial limits the abundance of potential first intermediate hosts, resulting in low infestation rates even of widely distributed, non-specific parasites. In contrast, the higher biomass in the benthic deep-sea environment increases the availability of potential intermediate hosts, resulting in increased parasite diversity. Consequently, the deep-sea parasite diversity seems to be less dependent on a characteristic fish feeding ecology. It more likely reflects the specific depth range of the fish species, either being restricted to the meso- or bathypelagial or reaching into the benthic or epipelagic environment. Further studies are needed to verify this assumption with

further deep-sea fish species with different feeding ecologies and from other deep-sea environments.

Acknowledgements

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