

# Metazoan fish parasites of *Macrourus berglax* Lacepède, 1801 and other macrourids of the North Atlantic: Invasion of the deep sea from the continental shelf

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## Abstract

Between 2001 and 2003, a total of 105 *Macrourus berglax* Lacepède, 1801 were collected from Irminger Sea, at depths between 250 and 450 m, and were studied for parasites. Twenty-four different parasite species were identified. Nematodes (eight spp.) and digeneans (six spp.) were the most species rich, followed by crustaceans (four spp.), cestodes (three spp.), acanthocephalans (two spp.) and monogeneans (one sp.). Core species included the digenean *Gonocerca phycidis* (maximum 62.9% prevalence), the nematodes *Anisakis* sp. (62.9%), *Capillaria gracilis* (65.8%), *Hysterothylacium aduncum* (60.0%), *Neoascarophis macrouri* (88.6%), *Spinitectus oviflagellis* (82.9%), and the acanthocephalan *Echinorhynchus gadi* (97.1%). *M. berglax* was the final host for most of the parasites, and was infested with only a few larval forms. The species composition, diversity as well as the prevalence and intensity of infestation for most parasite species collected, were similar in the different years, indicating no distinct interannual variation at this deep-sea locality. Comparisons of the parasite fauna of *M. berglax* with macrourids belonging to the genera *Macrourus*, *Coryphaenoides*, *Coelorhynchus* and *Nezumia* revealed a similar infestation pattern amongst these deep-sea fish, consisting of the same or closely related species. This observation suggests that the parasite life-cycles in these benthopelagic deep-sea fishes follow similar pathways independent of geographical location. A similar habitat and food preference of macrourids results in a similar parasite fauna. The host specificity of some of the parasites is low, with most species (nine) infesting Teleostei, Gadiformes (six), Macrouridae (two), *Macrourus* spp. (one) and specifically *M. berglax* (five). Overlapping infestation patterns of *M. berglax* parasites with phylogenetically related gadiform fish from the continental shelf region suggest that the deep-sea parasite fauna in macrourids has evolved along with their hosts from parasite generalists that originated from the continental shelf. We propose that the parasite fauna of macrourids from the Mid-Atlantic Ridge harbours a similar parasite fauna and infestation pattern than that of macrourids from other parts of the world Oceans.

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## 1. Introduction

Fish parasites are a major component of aquatic biodiversity. The deep sea harbours a rich parasite fauna consisting of all major taxa. In total, 421 of the 3800–4200 known deep-sea fish species (<10%) have so far been studied for their metazoan parasites. These hosts harbour 621 different parasite species, with 1.5 parasite species per fish species (Klimpel et al., 2001). Though this figure is

lower than the approximately three to four metazoan species in each fish from the coastal and continental shelf region (Palm et al., 1999), some fish species show astonishing parasite richness.

According to food availability and consequently feeding ecology, mesopelagic, bathypelagic and benthopelagic fish follow different habits, and this is reflected in their parasite fauna and diversity. Klimpel et al. (2006a) demonstrated low parasite richness in five different meso- and bathypelagic fishes in comparison to a benthopelagic macrourid from the Arctic deep sea. The authors suggested that the low productivity in the meso- and bathypelagic zones limits

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the abundance of potential first intermediate hosts, resulting in low infestation rates of even widely distributed non-specific parasites. In contrast, the higher biomass and diversity of deep-sea benthos increases the availability of potential intermediate hosts, resulting in increased parasite diversity. Consequently, benthopelagic macrourids with a generalist feeding behaviour can be assumed to be amongst the most parasite-rich fish in the deep sea.

Due to their commercial exploitation by the fishing industry, macrourid fish are the best-studied deep-sea fish so far. Information on fish parasites is available for several species within the genera *Coryphaenoides*, *Coelorhynchus*, *Macrourus* and *Nezumia* (Klimpel et al., 2001). Fish parasitological studies revealed high parasite richness. Walter et al. (2002) recorded 22 of a total of 27 known parasite taxa in the Antarctic macrourid *Macrourus whitsoni* (Regan, 1913) from the southeastern Weddell Sea in 1996. According to Klimpel et al. (2006a), *Macrourus berglax* from the North Atlantic has high parasite diversity in comparison to mesopelagic fish (see also Zubchenko, 1981). Campbell et al. (1980) stated that macrourids, in general, show a greater similarity among themselves than with other teleosts and Walter et al. (2002) suggested a similar parasite diversity and species composition of Antarctic *M. whitsoni* to species from the sub-Antarctic, and also to that of *M. berglax* Lacepède, 1801 from the northern hemisphere. However, data on the interannual variability of deep-sea fish parasites are missing, and our knowledge on regional variations among macrourid fish parasites is lacking.

How fishes have invaded the deep sea is a widely discussed topic. Two possible strategies are known: (i) via Arctic and Antarctic fish species from the continental slope towards the deep sea or (ii) via originally pelagic fish species by means of extensive vertical migration (Klimpel et al., 2006a). Some fish parasites have been demonstrated to closely co-evolve with their teleost hosts (e.g., Jovelin and Justine, 2001), thus indicating their host's phylogeny. They also have been utilised as biological indicators for the host ecology (Palm and Schröder, 2001; Klimpel et al., 2008), including population structure (MacKenzie and Abaunza, 1998; Lester et al., 2001) and feeding biology (Palm et al., 1998; Palm, 1999). Consequently, fish parasites might be useful indicators for a better understanding of the evolution of deep-sea organisms and the invasion of the deep-sea habitat by their teleost hosts.

In general, fish parasite evolution follows that of their hosts. Palm (2004) and Palm and Klimpel (2007) stated that generalist parasites are the driving force for exploiting new host species and habitats, followed by specialisation and further species radiation. The present study was carried out in order to examine the parasite fauna of *M. berglax* from the Irminger Sea, north of the Mid-Atlantic Ridge (MAR). For the first time, specimens collected from 3 consecutive years were studied to understand the interannual variation in the parasite infestation of this deep-sea fish. The analysis of specific and non-

specific parasites together with a comparison of parasites from other macrourid fish was conducted in order to explain the origin of the observed parasite infestation pattern of *M. berglax*. The implications for the invasion of the MAR by deep-sea fish parasites are discussed.

## 2. Materials and methods

### 2.1. Sample collection

Fish samples were collected in 2001 (between 24 and 27 October), 2002 (between 23 October and 3 November) and 2003 (between 28 October and 10 November) on board the German research vessel *Walther Herwig III* during international ICES and NAFO surveys within the Irminger Sea. The deep-sea fishes were caught with a benthopelagic trawl at a trawling speed of approximately 3–4 knots. A total of 105 roughhead grenadiers, *M. berglax*, 35 specimens each year, were caught at a mean trawling depth of 361 m (range 329–405 m) in 2001, 334 m (range 278–387 m) in 2002 (see Klimpel et al., 2006a) and 377 m (range 340–413 m) in 2003. All fishes were deep frozen at  $-40^{\circ}\text{C}$  immediately after capture for later examination. Prior to examination, each fish specimen was defrosted to  $0-1^{\circ}\text{C}$ . Morphometric data including the total length (TL), pre-anal-length (PAL) and total weight (TW) were recorded to the nearest 0.1 cm and 0.1 g.

### 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 the liver, stomach, pyloric caeca, intestine and gonads microscopically for endoparasites.

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 graduated 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. The literature used to identify the parasites included original descriptions. Prevalence, intensity and mean intensity follow the recommendations of 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 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).

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

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

### 3. Results

The morphometric data were similar for the 3 years sampled. The mean TL of *M. berglax* were 39.5 cm (range 27.6–57.2 cm) in 2001, 38.6 cm (36.6–62.2 cm) in 2002 and 39.7 cm (17.0–53.5 cm) in 2003. The mean PAL were 5.9 cm (range 3.8–7.9 cm) in 2001, 6.2 cm (3.3–14.6 cm) in 2002 and 5.4 cm (2.0–9.5 cm) in 2003. The mean TW were 349.4 g (range 101.5–1042.0 g) in 2001, 391.7 g (93.0–1532.3 g) in 2002 and 418.5 g (19.7–967.4 g) in 2003.

The parasitological analysis of the 105 *M. berglax* from the Irminger Sea (Table 1) revealed a high parasite richness and diversity between 2001 and 2003. A total of 26 different parasite species (component community) were found, with 19, 23 and 24 species in the different years. The infracommunity (number of parasite species in the analysed population of *M. berglax* in each year) of the benthopelagic *M. berglax* consisted of three to nine parasite species (mean 5.9) in 2001, 5–11 parasite species (mean 7.8) in 2002, and 3–13 parasite species (mean 7.2) in 2003. The diversity was also high within the different years, ranging from  $H' = 1.619$ ,  $E = 0.095$  in 2001,  $H' = 2.170$ ,  $E = 0.103$  in 2002 and  $H' = 1.957$ ,  $E = 0.089$  in 2003.

The predominant group of parasites were the Digenea and Nematoda, most of them in the adult stage. The Digenea (*Derogenes varicus*, *Genolinea laticauda*, *Gibsonia borealis*, *Gonocerca phycidis*, *Lepidapedon* sp., *Steringotrema pagelli*) were adult and located in the digestive tract. The highest infestation rates were calculated for

Table 1  
Fish parasites in *Macrourus berglax* from 2001 to 2003

Parasite species (adult (a), larval (l))	2001			2002 <sup>a</sup>			2003		
	P (%)	mI	I	P (%)	mI	I	P (%)	mI	I
<b>Digenea</b>									
<i>Derogenes varicus</i> (a)	2.9	1.0	1	20.0	3.4	1–10	25.7	2.6	1–10
<i>Gibsonia borealis</i> (a)	5.7	8.0	1–12	42.9	8.2	2–27	34.3	8.9	1–36
<i>Gonocerca phycidis</i> (a)	42.9	1.3	1–2	62.9	2.1	1–10	45.7	2.7	1–7
<i>Genolinea laticauda</i> (a)	5.7	8.0	3–13	42.9	7.4	1–46	45.7	8.3	1–45
<i>Lepidapedon</i> sp. (a)	5.7	1.5	1–2	2.9	5.0	5	5.7	1.0	1
<i>Steringotrema pagelli</i> (a)	–	–	–	–	–	–	2.9	2.0	2
Digenea indet. (a)	5.7	1.0	1	5.7	1.0	1	11.4	1.5	1–2
<b>Monogenea</b>									
<i>Macrouridophora macruri</i> (a)	5.7	2.0	1–3	20.0	2.0	1–3	8.6	1.3	1–2
<b>Cestoda</b>									
<i>Grillotia erinaceus</i> (l)	–	–	–	2.9	1.0	1	5.7	1.0	1
<i>Parabothiocephalus macruri</i> (a)	2.9	1.0	1	8.6	1.3	1–2	8.6	3.3	2–5
Tetraphyllidea indet. (l) ( <i>Scolex pleuronectis</i> )	–	–	–	5.7	2.5	1–4	2.9	1.0	1
<b>Nematoda</b>									
<i>Anisakis</i> sp. (l)	62.9	2.6	1–10	42.9	3.1	1–12	54.3	3.6	1–31
<i>Ascarophis</i> sp. (a)	51.4	6.3	1–28	68.9	6.2	1–34	51.4	8.3	1–30
<i>Capillaria gracilis</i> (a)	42.9	2.6	1–10	65.8	6.1	1–32	45.7	2.1	1–7
<i>Hysterothylacium aduncum</i> (l, a)	48.6	1.5	1–4	28.6	2.2	1–7	60.0	4.2	1–9
<i>Ichthyofilaria bergensis</i> (a)	–	–	–	–	–	–	5.7	1.0	1
<i>Neoscarophis macrouri</i> (a)	88.6	19.8	1–88	71.4	13.6	1–37	60.0	36.9	1–411
<i>Pseudoterranova decipiens</i> (l)	22.9	1.3	1–2	34.3	2.3	1–8	40.0	2.5	1–7
<i>Spinitectus oviflagellis</i> (a)	82.9	26.2	1–599	40.0	8.6	1–49	57.1	22.4	1–144
Nematoda indet. (l)	5.7	1.0	1	60.0	1.3	1–3	22.9	1.3	1–2
<b>Acanthocephala</b>									
<i>Echinorhynchus gadi</i> (a)	97.1	21.4	1–100	94.3	17.0	1–102	91.4	25.5	1–104
<i>Corynosoma wegneri</i> (l)	–	–	–	–	–	–	5.7	2.0	1–3
<b>Crustacea</b>									
<i>Clavella adunca</i> (a)	31.4	2.3	1–7	37.1	1.8	1–4	25.7	2.8	1–7
<i>Chondracanthodes radiatus</i> (a)	2.9	1.0	1	5.7	1.0	1	2.9	1.0	1
<i>Nectobranchia producta</i> (a)	–	–	–	17.1	2.3	1–5	–	–	–
<i>Peniculus clavatus</i> (a)	–	–	–	2.9	1.0	1	–	–	–

P, prevalence; mI, mean intensity; I, intensity.

<sup>a</sup>See Klimpel et al. (2006a).

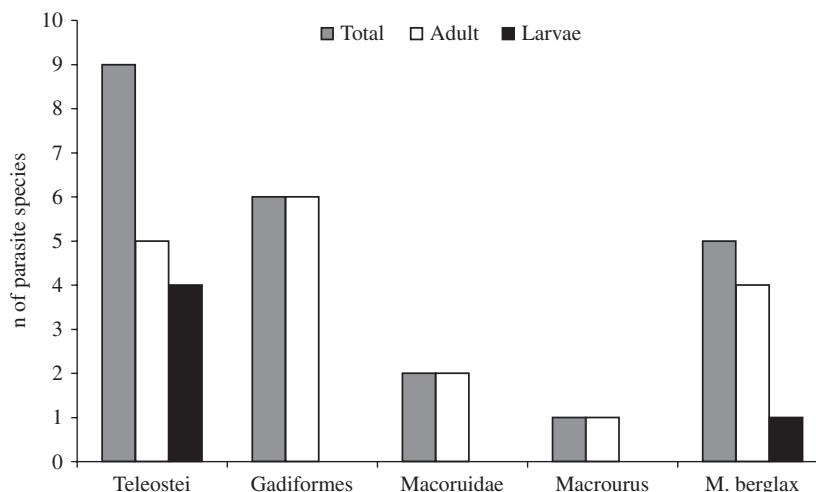


Fig. 1. Host range of *Macrourus berglax* parasites from the Irminger Sea.

*G. phycidis*, *G. laticauda* and *G. borealis* at total prevalences of 50.5%, 31.4% and 27.6%, respectively. Only one adult Monogenea species, *Macrouridophora macruri*, was found on the gills at a prevalence of 11.4%. Two larval (Grillotia *erinaceus*, Tetraphyllidea indet. = *Scolex pleuronectis*) and one adult Cestoda (*Parabothriocephalus macruri*) were isolated from the liver, pyloric caeca and intestine, with low infestation rates of 2.9%, 2.9% and 6.7%. With eight identified species, *Anisakis* sp. (53.3%), *Ascarophis* sp. (55.2%), *Capillaria gracilis* (51.4%), *Hysterothylacium aduncum* (45.7%), *Ichthyophilaria bergensis* (1.9%), *Neoascarophis macrouri* (73.3%), *Pseudoterranova decipiens* (32.4%) and *Spinitectus oviflagellis* (60.0%), the Nematoda was the most species-rich taxon. *Anisakis* sp., *H. aduncum* and *P. decipiens* were isolated as larval stages from the body cavity and liver, whereas the other nematodes as well as *H. aduncum* were in their adult stages. The adult Nematoda were located in the stomach (-wall), pyloric caeca and intestine. The adult stage of *Echinorhynchus gadi* and the larval *Corynosoma wegneri* (Acanthocephala) were located in the intestine (94.3% and 1.9%, respectively). Crustacea occurred only in their adult forms, with *Clavella adunca* and *Chondracanthodes radiatus* located on the gills (31.4 and 3.8%) and *Nectobranchia producta* and *Peniculus clavatus* on the body surface (5.7 and 1.0%).

The parasite infestation between years was similar for most of the parasites, such as *Lepidapedon* sp., *P. macruri*, *Anisakis* sp. and *E. gadi*. Differences could be observed for the digeneans *D. varicus* and *G. laticaudata*, both of which increased from 2001 to 2003. The prevalence of infestation for the nematodes *S. oviflagellis* and *H. aduncum* decreased in 2002 and increased again in 2003. In general, the parasite fauna appeared stable among the years. The prevalence, intensities and site of infestation for each parasite species and year are given in Table 1.

The characterisation of the isolated parasites identifies five host-specific species in *M. berglax*, four of them in the adult form (Fig. 1). A further species has so far only been recorded from another *Macrourus* species, and two species

are known to infest the Macrouridae (Klimpel et al., 2001). The less host-specific species have been recorded in gadiform fish or other teleosts, the latter partly in the adult (five species) and partly in the larval form (four species). According to the evaluation of the higher fish parasite taxa in macrourid fish (data after Klimpel et al., 2001), the distribution of the parasite fauna closely corresponds between the four macrourid genera, *Coryphaenoides*, *Coelorhynchus*, *Macrourus* and *Nezumia* (Fig. 2). The digeneans, followed by the nematodes and cestodes, are the predominant fish parasites in macrourid deep-sea fish.

#### 4. Discussion

The benthopelagic *M. berglax* is a widely distributed fish species from temperate and Arctic waters in the North Atlantic Ocean, living at depths between 100 and 1000 m but with a preference for a depth range of 300–500 m (Froese and Pauly, 2006). Earlier investigations (Zubchenko, 1981; Klimpel et al., 2001, 2006a) also reported that the isolated parasite fauna of *M. berglax* was species rich, with an infracommunity range between three and 11 parasites in each infested fish. Zubchenko (1981) also reported 20 parasite species compared to the 24 identified species or 26 taxa that were collected during the present study. The core species, e.g., species that reached a prevalence above 60%, were the adult digenean *G. phycidis* (maximum 63%), the nematodes *C. gracilis* (66%), *N. macrouri* (89%) and *S. oviflagellis* (83%) as well as the acanthocephalan *E. gadi* (97%). Only two species, the nematodes *Anisakis* sp. (63%) and *H. aduncum* (60%), occurred as larval forms in relative high numbers. According to Klimpel et al. (2001), the parasite fauna of deep-sea macrourids consists of 65% of species that have been recorded in a wide depth range, inhabiting other teleosts or related gadiforms from the continental shelf (Fig. 1). Twenty-six percent of the species are known only from *Macrourus* or are highly host-specific to *M. berglax*.

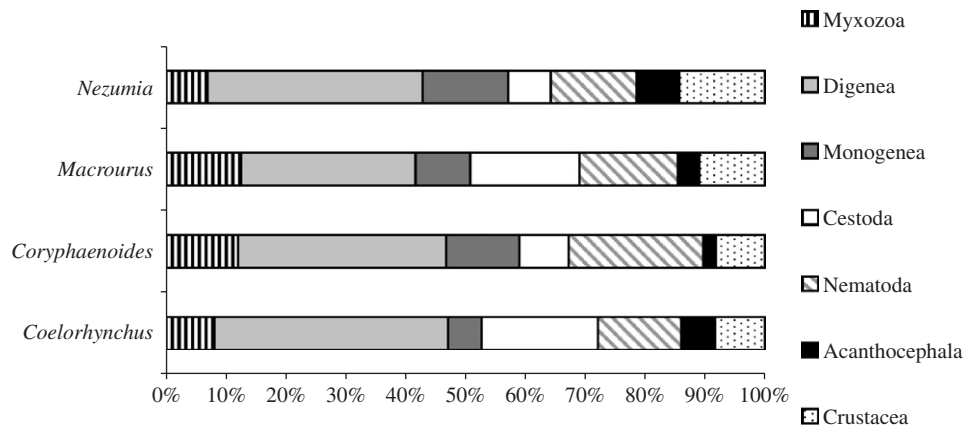


Fig. 2. Distribution of higher fish parasite taxa in macrourid fish genera (data from Klimpel et al., 2001).

Fish parasite prevalence and intensity can vary significantly over time due to irregular availability of the suitable final and intermediate hosts or seasonal or long-term changes of the environment (e.g., MacKenzie, 1987; Palm, 2004). This is the first parasitological study on the interannual variation of the fish parasite composition in a deep-sea macrourid from the North Atlantic. Of the 26 parasite taxa isolated over the 3-year period, 19 were recorded in all 3 years, and the prevalence and intensity of infestation as well as the community structure and diversity was similar between years. Those taxa that were missing in some years showed a low prevalence and intensity of infestation, indicating that they could be present in a study utilising a larger sample size. Consequently, the deep-sea parasite fauna of *M. berglax* was relatively uniform between 2001 and 2003, and showed no distinct inter-annual variation.

Most of the parasites collected within the present and earlier studies are known or believed to use planktonic and/or benthic invertebrates as first or second intermediate hosts (see Klimpel et al., 2006a,b). Consequently, they may have been acquired and accumulated by *M. berglax* as paratenic or final hosts through predation on infected macro-invertebrates and small fish. The function of *M. berglax* mainly as a final host for most of its deep-sea parasites can explain the large number of adult parasites encountered within the present study. This infestation pattern is very different to meso- and bathypelagic fish, where only a small number of parasites, often larval, occur (Klimpel et al., 2006a). The parasite fauna of the cod *Gadus morhua*, a typical gadiform of the North Atlantic continental shelf, is dominated by generalist parasites (Hemmingsen and MacKenzie, 2001). The Antarctic rock cod *Notothenia coriiceps* of the Southern Ocean (shallow water) harbours 22 different parasite species; however, most of them are larval stages and no adult nematodes are found (Palm et al., 1998). In contrast, the Antarctic deep-sea macrourid *M. whitsoni* harbours 22 parasite species of a similar composition to *M. berglax* (Walter et al., 2002). The tropical deep-water fishes *Trichiurus lepturus* and *Gempylus serpens* from the southern Java coast, both

known to reach a depth of 600 m, harboured 17 and 16 parasite taxa, respectively; however, most of them in their larval stages (Jakob and Palm, 2006). Only a few larval parasite species known to occur in shallow as well as deep water environments, such as the nematodes *Anisakis* sp., *Pseudoterranova decipiens* and the trypanorhynch cestode *G. erinaceus* (depth range see in Klimpel et al., 2001, 2004; Palm, 1999, 2004), were isolated during the present study. In summary, the occurrence of many adult and also several host-specific parasite species together with few less host-specific helminth species in the larval form with a wide depth range characterise the parasite fauna of *M. berglax* in the Irminger Sea.

According to Palm (2004) and Palm and Klimpel (2007), generalists are the driving force in the evolution of marine fish parasites. On the continental shelf, many predatory fish show overlapping parasite infestation patterns, hosting various different, and often generalist parasites. The feeding ecology determines the parasite composition rather than the host phylogeny (e.g., Klimpel et al., 2003). A large part of the fish parasite fauna consists of larval forms that are in the process of being transmitted through the food web into other teleost, mammalian, elasmobranch or bird final hosts. Many of these potential final hosts are absent in the deep-sea environment, where large predatory, benthopelagic fishes offer the most suitable final host system. Recent phylogenetic studies indicate that none of the common deep-sea fish digeneans are likely to be basal for their group (Cribb et al., 2001), indicating that the group is unlikely to have arisen in deep water (Bray et al., 1999). Based on the results of the present study and the above observations, we propose that many helminth parasites have exploited deep-sea macrourids from distinct lineages originating on the continental shelf. These were generalist species that most probably infested gadiform fish as their main final hosts, and have followed the macrourids into the deep sea (Fig. 3). The most successful groups are digeneans and some nematodes that are able to complete the entire life cycle in this deep-sea habitat. Together with their macrourid hosts, further parasite specialisation resulted in new, typical deep-sea species that do not occur in their

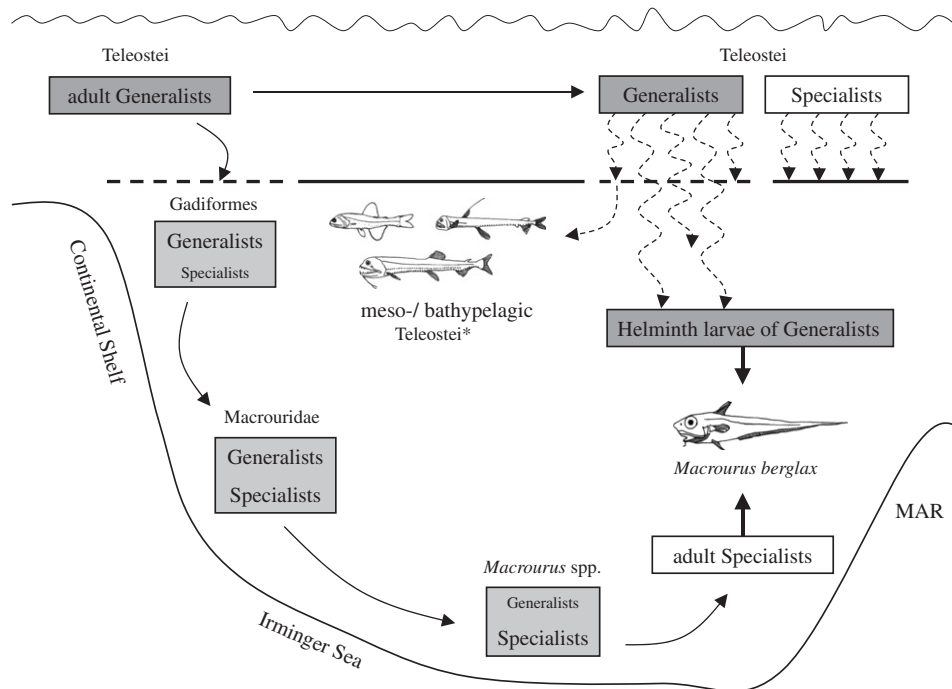


Fig. 3. Schematic illustration of the invasion of the deep sea by parasites of macrourid fishes. According to Palm (2004) and Palm and Klimpel (2007), generalist parasites are the driving force in the exploitation of new hosts and habitats in the oceanic system. The parasite fauna of *Macrourus berglax* from the Irminger Sea is dominated by adult specialists and generalists, and generalist helminth larvae occur in a lower number. The same species also accidentally infest meso- and bathypelagic fish (\*data published by Klimpel et al., 2006a). It can be expected that the parasite fauna of *M. berglax* from the Mid-Atlantic Ridge is composed of diverse adult deep-sea specialists and larval oceanic generalists (see further explanation in the text).

shallow-water fish relatives. Continuous radiation in deeper waters off the continental shelf led to the characteristic deep-sea parasite fauna consisting of a combination of generalists and specialists that we observe today (Fig. 3). In some cases, deep-sea generalists secondarily can also reinvade shallower water habitats, such as in some species of the digenean genera *Lepidapedon* and *Steringophorus* (Bray et al., 1999). These species typically infest the macrourid related gadiform fish of the continental shelf.

A different fish fauna and complete habitat separation of the epipelagic and the near-bottom environments most likely prevents any invasion of oceanic specialists into the deep sea (Fig. 3). In contrast, many fish parasitic helminth larvae are widespread, and several oceanic parasites are able to penetrate into the deep sea (Klimpel et al., 2001). They are known to infest meso-, bathy- and also bathypelagic deep-sea fish (Klimpel et al., 2006a). Therefore, on the basis of the parasite fauna of *M. berglax* from the Irminger Sea, the typical helminth fauna of bathypelagic fish from the MAR will consist of specialised adult digeneans and nematodes together with some generalistic helminth larvae that originate from the upper water layers. They typically belong to the nematodes and some cestodes.

Fish parasitological studies on and in the vicinity of the MAR are scarce (Bray et al., 1999). Recently, Justine et al. (2002) studied the zoarcid deep-sea hydrothermal vent fish *Pachycara thermophilum* from the MAR and described a new nematode species. Klimpel et al. (2008)

studied the halosaur *Halosauropsis macrochir* from the northern part of the MAR, and collected nine different parasite species. *H. macrochir*, along with the macrourids, is one of the most abundant fish in that region. Although the number of parasite species is smaller than that described for *M. berglax*, it is similar in that most of the parasites were adults (six species) rather than in the larval stages (three species). This is further evidence for the assumption of many adult, often host-specific parasites and some larval nematodes or cestodes with a wide depth range also might characterise the macrourid fish parasite fauna from the MAR. In the case of host-parasite co-evolution, our data suggest that the penetration of the deep-sea environment originated from the continental shelf regions, for the parasites and consequently also for their teleost hosts. Further studies with more detailed data especially on macrourids and meso- and bathypelagic fish of the MAR are needed in order to test the hypotheses presented above.

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