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Fish parasites in the bathyal zone: The halosaur *Halosauropsis macrochir* (Günther, 1878) from the Mid-Atlantic Ridge

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Abstract

A total of 42 *Halosauropsis macrochir* from a single position on the Mid-Atlantic Ridge (MAR) were collected for studies on parasites and feeding ecology. A total of 9 different parasite species were found, with most of them belonging to the Digenea (4 species) and Nematoda (3). The host specific *Degeneria halosauri*, (Digenea) and Cystidicolidae indet. (Nematoda) were the predominant species, reaching a prevalence of 100.0% and 57.1% with intensities of infection of 1–12 and 1–10, respectively. Less host specific parasites such as *Gonocerca phycidis* (Digenea) and Tetraphyllidea indet. (Cestoda) occurred at low rates of infection. The parasite fauna of this bathyal fish can be described as predominantly adult and host specific, with larval and less host specific components. A total of 16 different food groups were identified, most of them of benthic origin or associated with the benthopelagial. The predominant prey organisms belonged to the Crustacea (e.g., Copepoda, Gammaridea, Amphipoda and Isopoda), which serve as main parasite vectors for *H. macrochir*. This deep-sea fish seems to follow a general pattern of fish parasites in the deep sea, with most isolated parasites belonging to the digeneans, nematodes and a cestode. The parasite composition is caused by the narrow depth range of the species and the restricted distribution of the fish family Halosauridae. The species richness was found to be lower than other demersal fish from the deep sea and shallow waters, however, higher than those from deep-sea fish living in the pelagial.

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1. Introduction

It is difficult to separate the deep sea from other oceanic habitats on the basis of their typical inhabitants. The distributions of organisms are not universally correlated with temperature, depth or geomorphological features (edge of the continental shelf). At low latitudes, the typical shelf fauna may inhabit the continental slope to a depth of more than 1000 m, and characteristic deep-sea taxa can be found at depths of a few hundred metres in polar regions. The transition from the continental shelf to the deep sea is formed by the bathyal region. At lower latitudes this zone is situated between 1000 and 3000 m (tropical submergence), and has few species in common with the fauna of the neighbouring shelf and abyssal regions. At high latitudes, the bathyal fauna has strong affinities to both the

shelf and the deep-sea fauna, constituting the so-called archibenthic transition zone. It is difficult to define clearly the conditions that determine the distribution of deep-sea organisms in the world's oceans (see Ott, 1996).

Macrourid fishes and the halosaur *Halosauropsis macrochir* are dominant deep-sea benthopelagic fishes of the Mid-Atlantic Ridge (MAR). *H. macrochir* is relatively large, abundant and potentially important apex predator, feeding on bottom invertebrates (including, e.g., bivalves, gastropods, polychaetes, various crustaceans) and small fish (Sedberry and Musick, 1978; Gordon and Duncan, 1987). The Halosauridae are entirely marine and have their greatest diversity on the upper continental and insular slopes, down to at least 5000 m but with most species occurring between 1100 and 3300 m water depth (Campbell et al., 1980; Froese and Pauly, 2006). The helminth fauna of *H. macrochir* is characterized by nine different parasite species belonging to the Digenea (6 species), Cestoda (1) and Nematoda (2) (Klimpel et al., 2001). Most of them

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are in their adult (6 species) rather than in their larval (3) stages (see Palm and Klimpel, 2008).

Parasitological studies together with an analysis of the stomach contents can give information on the feeding ecology and behaviour of the host fish. This methodology is useful for fish that are difficult to study in vivo, because they live in inaccessible and extreme environments. In addition, the occurrence of fish parasites associated with specific prey organisms in the host can help to identify the life-cycles of the parasite species involved. For example, an analysis of the parasites and the stomach contents of the pearlside *Maurolicus muelleri* from the Norwegian Deep revealed the typical life-cycle of the anisakid nematode *Anisakis simplex* (Klimpel et al., 2004). Klimpel and Rückert (2005) analysed the stomach contents and nematode fauna of three commercially important gadiform fish species in the central and northern North Sea. They described the life-cycle of the fish nematode *Hysterothylacium aduncum* and clearly demonstrated an influence of mixed and stratified waters on the life-cycle. Palm and Schröder (2001) showed, from a study of the cestode parasites, that the elasmobranchs of the genus *Deania* can serve as food fish for larger oceanic sharks around the Great Meteor Seamount in the central North Atlantic Ocean.

The purpose of the present study is to describe the parasite fauna of *H. macrochir* collected from the MAR. Using the patterns of infection and an analysis of the stomach contents of *H. macrochir*, information is provided on the ecology of the host and on the life-cycles of its parasites. The parasite fauna of the halosaur from the bathyal is compared with the parasite fauna of other deep-sea fish in order to understand the characteristic infestation pattern in that deep-sea habitat. Implications for the importance of the MAR for the zoogeographic distribution of marine fish parasites especially the nematodes are discussed.

2. Materials and methods

2.1. Sample collection

Fish were sampled in July 2004 along the MAR on board of the Norwegian research vessel G.O. Sars as an element of MAR-ECO, a field project under the Census of Marine Life. Sampling was conducted with a bottom trawl as described in Wenneck et al. (2008). At superstation 40 (local station 367; position 42°54.91'N 30°20.37'W; trawling depth range 2660–2670 m; bottom depth ca. 2960 m) a total of 42 specimens of *H. macrochir* were captured in order to study their stomach contents and metazoan parasites. All fishes were deep frozen at –40 °C immediately after capture for subsequent examination. In the ship's laboratory, the total length (TL, to the nearest 0.1 cm) and total weight (TW, to the nearest 0.1 g) were determined.

2.2. Parasitological examination

The eyes, skin, fins, gills, nostrils and mouth cavity of each fish were examined for ectoparasites. The body cavity was opened to examine the liver, stomach, pyloric caeca, intestine and gonads microscopically for endoparasites, and the stomach contents were removed.

The 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. Parasite identification literature included original descriptions. The terms prevalence, mean intensity, intensity (see Palm and Klimpel, 2008) and abundance (total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of hosts of that species examined, including both infected and uninfected hosts) follow the recommendations of Bush et al. (1997). Furthermore, we use the following parasitological terms and definitions: (i) final host—where a parasite reaches sexual maturity, (ii) intermediate host—required by a parasite to complete its life-cycle, usually it undergoes considerable morphological or physiological change and (iii) paratenic host/transport host—not required by a parasite to complete its life-cycle, without detectable morphological change.

2.3. Stomach contents analysis

The stomach contents were sorted and food items were identified to the lowest possible taxon and grouped into taxonomic categories. In order to determine the relative importance of food items, the frequency of occurrence of each prey item i ($\%F_i$) and its percentage by number ($\%N$) was calculated (Hyslop, 1980; Amundsen et al., 1996). $\%F_i$ was determined as the number of stomachs with prey item i compared to all non-empty stomachs. $\%N$ was calculated as the number of prey item i compared to the total number of all prey items (Hyslop, 1980; Fock et al., 2002).

3. Results

The analysis of 42 *H. macrochir* with total lengths between 30.0 and 58.9 cm (mean 48.9 cm) and total weight ranging from 14.4 to 206.2 g (mean 100.9 g) from a single position of the MAR revealed a rich parasite fauna. A total of 9 different parasite species were found. The prevalence, intensity, mean intensity, abundance and site of infection for each parasite species are given in Table 1. Five different groups of prey items were identified, belonging to the Protozoa, Annelida, Crustacea, Mollusca and Echinodermata. Table 2 provides detailed information on the stomach contents of the examined fish.

Table 1
Prevalence (*P*), intensity (*I*), mean intensity (mI), abundance (*A*) and site of infestation of *Halosauropsis macrochir* from the Mid-Atlantic Ridge

Parasite species	Stage	<i>P</i> (%)	<i>I</i>	mI	<i>A</i>	Site
Digenea						
<i>Degeneria halosauri</i>	a	100.0	1–12	3.6	3.64	Ureter
<i>Gaevskajatrema halosauropsi</i>	a	9.5	1–3	1.8	0.17	Intestine
<i>Gonocerca phycidis</i>	a	7.1	1	1.0	0.07	Stomach
<i>Steringophorus</i> sp.	a	54.8	1–3	1.4	0.79	Intestine
Digenea indet.	a	7.1	1–2	1.5	0.07	Pyloric caeca
Cestoda						
Tetraphyllidea indet. (*) (<i>Scolex pleuronectis</i>)	1	16.7	1–3	1.4	0.24	Intestine
Nematoda						
<i>Anisakis</i> sp. (*)	1	9.5	1	1.0	0.10	Body cavity
<i>Hysterothylacium</i> sp.	1	14.3	1–3	1.5	0.21	Intestine
Cystidicolidae indet. (*)	a	57.1	1–10	2.6	1.48	Stomach
Nematoda indet.	1	7.1	1	1.0	0.07	Pyloric caeca
Acanthocephala						
<i>Echinorhynchus</i> sp. (*)	a	2.4	2	20	0.05	Intestine

a, adult; 1, larva and (*), new host record.

Table 2
Frequency of occurrence (F_i) and numerical percentage of prey i (N) of the food items identified from the stomach contents of *Halosauropsis macrochir* from the Mid-Atlantic Ridge

Prey item	F_i (%)	N (%)
Protozoa		
Foraminifera indet.	15.79	28.21
Annelida		
Polychaeta indet.	34.21	3.75
Crustacea		
Copepoda (Calanoida)	74.19	8.04
Euphausiacea	7.89	0.71
Hyperiididae	10.53	0.89
Gammaridea	81.58	11.79
Amphipoda	73.68	10.89
Sergestidae	2.63	0.18
Decapoda	23.68	2.32
Tanaidacea	28.95	4.29
Isopoda	81.58	15.54
Cumacea	7.78	0.89
<i>Gigantocypris</i> sp.	42.11	7.14
Ostracoda	13.16	0.89
Crustacea indet.	36.84	3.21
Mollusca		
Bivalvia	5.26	0.54
Echinodermata		
Echinodermata indet.	5.26	0.36
Other		
Stones	5.26	0.36

3.1. Parasite composition

The parasite species collected in this study belonged to the Digenea (4 species), Cestoda (1), Nematoda (3) and

Acanthocephala (1) (Table 1). All represent new locality records and 4 species represent new host records. The predominant parasites were the digeneans *Degeneria halosauri* and *Steringophorus* sp. and the nematode species of the family Cystidicolidae. The relationship between total fish length and the total number of the three dominant parasite species in each fish specimen is shown in Fig. 1A–C. Each individual *H. macrochir* usually carried 1–4 different parasite species (mean 2.6). The number of parasite species increased with increasing fish length (Fig. 1D).

The Digenea species (*D. halosauri*, *Gaevskajatrema halosauropsi*, *Gonocerca phycidis*, *Steringophorus* sp.) were adult and located in the digestive tract. The highest infestation rates were calculated for *D. halosauri* and *Steringophorus* sp. (Table 1). Only one species of larval Cestoda (Tetraphyllidea indet.) was detected in the intestine with low infestation rates. Three Nematoda, *Anisakis* sp., *Hysterothylacium* sp. and Cystidicolidae indet. were found. *Anisakis* sp. and *Hysterothylacium* sp. were only isolated as third and fourth larval stages. The larval *Anisakis* sp. and *Hysterothylacium* sp. were found exclusively in or on the organs of the body cavity and in the intestine, while the adult stages of Cystidicolidae indet. were isolated from the stomach. The adult stages of *Echinorhynchus* sp. (Acanthocephala) were located in the intestine at low rates of infestation. The parasite fauna of *H. macrochir* on the MAR is characterised by 3 specialised and 6 generalist parasite species.

3.2. Stomach contents

Of the 42 stomachs examined 38 contained food. A total of 16 different food items or groups belonging to five major prey groups were identified (Table 2). Almost all of the

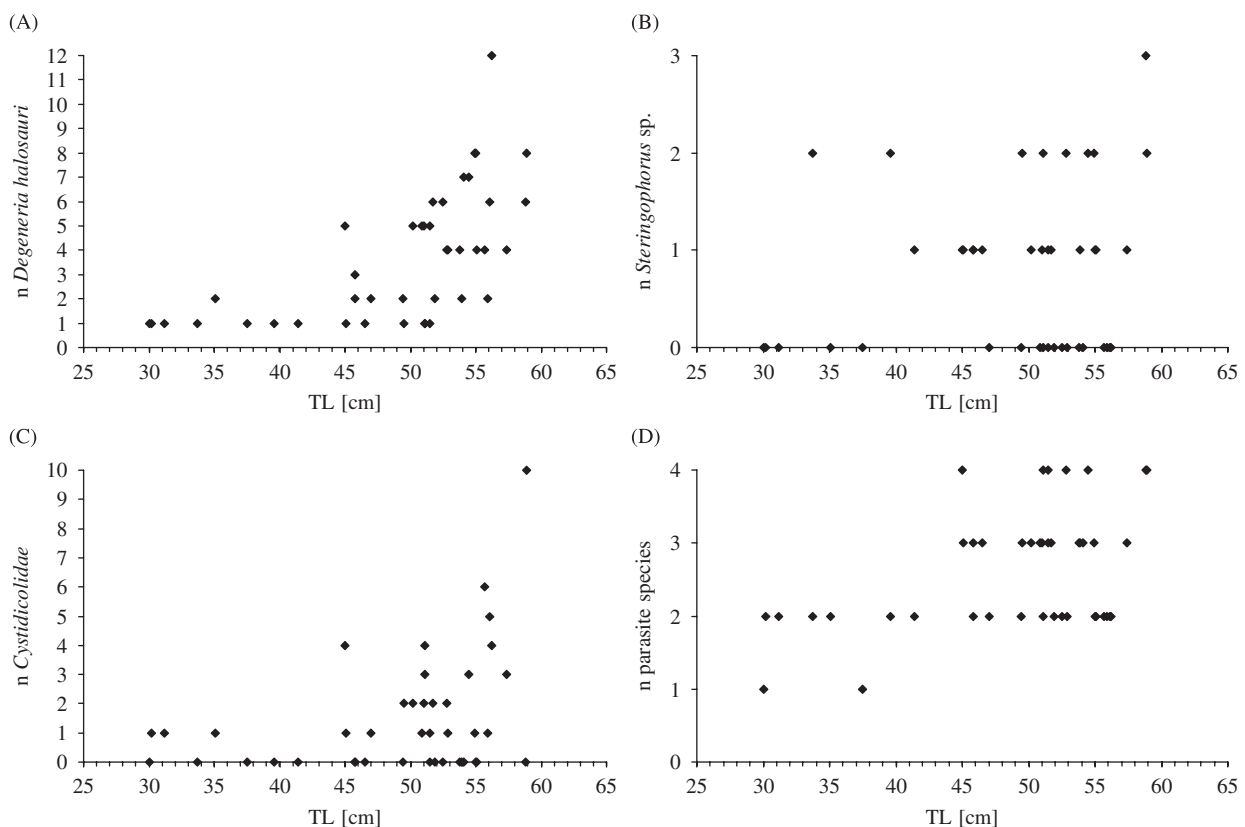


Fig. 1. Number (n) of different parasite species in comparison to the total fish length (TL) of *Halosaurus macrochir* from the Mid-Atlantic Ridge. (A) *Degeneria halosauri*, (B) *Stringophorus* sp., (C) Cystidicolidae indet. and (D) total number of different parasite species.

food organisms were of benthic origin or associated with the bathypelagic (bathypelagic) environment. The most frequent (F_i) prey organisms were the Crustacea (e.g., Gammaridea, Isopoda, Amphipoda and Copepoda), while the other prey groups were of lower importance. With regard to numerical percentage of prey (N), the most abundant prey items were Foraminifera, followed by Isopoda, Gammaridea and Amphipoda. In terms of prey species composition crustaceans were dominant.

4. Discussion

The parasite fauna of *H. macrochir* was found to be diverse, consisting of 9 different species, most of them belonging to the Digenea and Nematoda. With a total of 12 parasite species known so far, the parasite fauna of the halosaur from the bathyal is less species rich than observed for the macrourids (Palm and Klimpel, 2008), but more species rich than known from meso- and bathypelagic fish (Klimpel et al., 2006). According to Klimpel et al. (2006), the parasite fauna of marine fishes is influenced by the feeding ecology, the availability of intermediate and final hosts, and the depth range and host migration. The reduced diversity of the halosaurs compared to the macrourids that share the same environment, cannot be explained by the diversity of the prey items in their diet and different host availability (present study, Klimpel et al.,

2006). A further explanation is the lack of related halosaurs on the continental shelf compared with macrourids, where the related Gadiformes are numerous and harbour a species rich parasite fauna on the continental shelf.

Palm and Klimpel (2008) analysed the parasite fauna of the deep-water macrourid, *Macrourus berglax*, from the East Greenland Sea. They reported that the occurrence of many adult and also several host specific parasite species, together with a few less host specific helminth species in the larval form, characterized the parasite fauna of this species. A similar pattern is obvious also for *H. macrochir* from the MAR; however, with less species richness and more host specific parasites. Most of its 12 known parasite species are host specific, consisting of several adult and few larval forms, the latter having low host specificity. This also seems to be a typical parasite fauna for other deep-sea fish (see below).

This is the first parasitological and feeding ecology study of a demersal predator in the bathyal environment at the MAR. The prey organisms were dominated by crustaceans, which are typical second intermediate hosts for digeneans and first or transport hosts for the nematodes and cestodes. Consequently, *H. macrochir* functions as final as well as transport host through ingesting the larval parasite stages. Trematodes were the dominant parasites, followed by nematodes and cestodes. The benthic feeding of *H. macrochir* is reflected by the numerous isolated

digeneans of *D. halosauri*, typically encountered for this host. *D. halosauri* is highly host specific for *H. macrochir* and only distributed in 1500–2500 m water depths (Bray, 2004). *G. halosauropsi* is the most distinct species in terms of host specificity and depth range, infesting only *H. macrochir* in deep waters between 2000 and 3000 m in the northern Atlantic Ocean (Bray and Campbell, 1996; Bray, 2004). Most of the putative species of the genus *Gaevskajatrema* occur in perciform fish inhabiting shallower marine waters or from Cypriniform fishes in freshwater (Bray and Campbell, 1996). The genus *Gonocerca* has a wide or cosmopolitan distribution pattern, and *G. phycidis* shows a wide host and depth range, infesting members of various fish families in the deep sea (Bray et al., 1999; Klimpel et al., 2001). The genus *Steringophorus* is the largest genus of the digenean family Fellodistomidae in the deep sea, and its species were suggested to have radiated predominantly in deep waters (Bray et al., 1999; Klimpel et al., 2001; Bray, 2004). The life-cycle includes the bivalve genus *Nuculana*, one of the most common molluscs in the deep sea, as obligatory first intermediate host (Køie, 1979; Bray et al., 1999). According to Bray et al. (1999), the genus *Steringophorus* has a broad range of second intermediate hosts, indicating the possibility of a large number of final fish hosts of different trophic levels.

The presence of Cestoda of the order Tetrphyllidea is not surprising, since these parasites are common in large numbers and in different fish species (e.g., Palm et al., 1999; Klimpel et al., 2001). These larvae are circumpolar with a proposed marine life-cycle, including Crustacea (Copepoda) as probably first intermediate hosts and different elasmobranchs as final hosts. Further identification of these larvae is not possible without strobila characters, specific knowledge of the life-cycle and genetic analysis.

The Nematoda belong to the families Anisakidae (*Anisakis* sp.), Raphidacaridae (*Hysterothylacium* sp.) and Cystidicolidae. Anisakid nematodes are associated with aquatic vertebrates as typical definitive hosts. Transmission pathways are water dependent and usually involve a broad spectrum of invertebrates and intermediate or paratenic fish hosts. Adults of *Anisakis* sp. are parasites of the digestive tract of cetaceans and sometimes pinnipeds (e.g., Klimpel et al., 2004). The eggs are passed in faeces and sink in sea water where they develop and hatch in a few days. The third-stage larvae emerge from the eggs, sheathed with the cuticle of the second-stage larva, and float and drift in the pelagic water column under natural conditions (Klimpel et al., 2004). They infect planktonic crustaceans (e.g., copepods, euphausiids) as intermediate hosts, where they invade the haemocoel and develop into the infective third-stage larvae (Anderson, 2000). After ingestion by a teleost, they penetrate the intestine and encapsulate in the internal organs. Marine mammals acquire and accumulate larvae mainly from eating infected fish and larger crustaceans. The observed low infestation rates in the present study reflect the life-cycle of *Anisakis* sp., which originates in the pelagial, where the final hosts occur.

H. macrochir in the deep-sea environment can therefore be considered as an accidental intermediate host. Species of *Hysterothylacium* are found in the adult stages in the digestive tract of teleosts. The larval stages have been reported from a variety of invertebrates (crustaceans) and fish (Palm et al., 1999; Klimpel and Rückert, 2005). Members of the fish parasitic family Cystidicolidae are found in marine and freshwater. Though the life-cycles of most members are still unresolved, the eggs also are passed into sea water with the faeces and are ingested by various demersal crustaceans (e.g., Amphipoda, Decapoda), serving as intermediate hosts (Anderson, 2000). The family is typically found in demersal or benthopelagic fish. The isolated specimens of Cystidicolidae indet. from *H. macrochir* might represent a new species in this often host specific genus (Moravec et al., 2006).

Most host records for deep-sea specimens of *Echinorhynchus* are recorded for the Macrouridae. This is because this deep-sea fish family has received more extensive parasitological study than any other fish family, and all of the known hosts follow a demersal or benthopelagic distribution over the continental slopes and rises (Wayland et al., 1999; Klimpel et al., 2001). The life-cycles of acanthocephalans include benthic crustaceans as obligatory hosts. To date, no information on the life-cycle pathways of deep-sea acanthocephalans exist. At least 11 crustaceans (e.g., amphipods) can serve as intermediate hosts for *E. gadi* on the North Atlantic continental shelf (Marcogliese, 1994). The diversity of *Echinorhynchus* species in the deep-sea environment might be rather considerable (Wayland et al., 1999; Klimpel et al., 2001).

Individual species of deep-sea fishes can show marked differences in the composition of their parasite faunas directly related to their diet (Klimpel et al., 2006). *H. macrochir* has a generalized feeding behaviour, preying mainly on invertebrates residing on the sediments or swimming close to the sea floor. Therefore, the helminth fauna of this deep-sea fish is well represented by digeneans, cestodes and larval nematodes (see above). The digeneans are clearly the predominant parasite taxon, with 4 out of 12 species ($\approx 33\%$) occurring in the adult form. This ratio appears very similar to the 8 out of 24 identified digeneans ($\approx 33\%$) in *M. berglax* (Palm and Klimpel, 2008).

According to Marcogliese (2002) and Klimpel et al. (2006) the parasite diversity decreases with water depth to increase again close to the sea floor. According to food availability and consequently feeding ecology, pelagic and demersal deep-sea fishes follow different habits. This is reflected also in the parasite fauna and diversity between 200 and 5500 m water depths (Fig. 2). The most abundant parasite diversity is between 200 and 1000 m. From 1000 to 3000 m parasite richness decreases and the predominant parasite groups are the digeneans, cestodes and nematodes. Below 3000 m, only few records exist, but the diversity of all metazoans except the digeneans rapidly decreases (Fig. 2). The parasite diversity of fish from the meso- and bathypelagic zones is less (Klimpel et al., 2006). In the

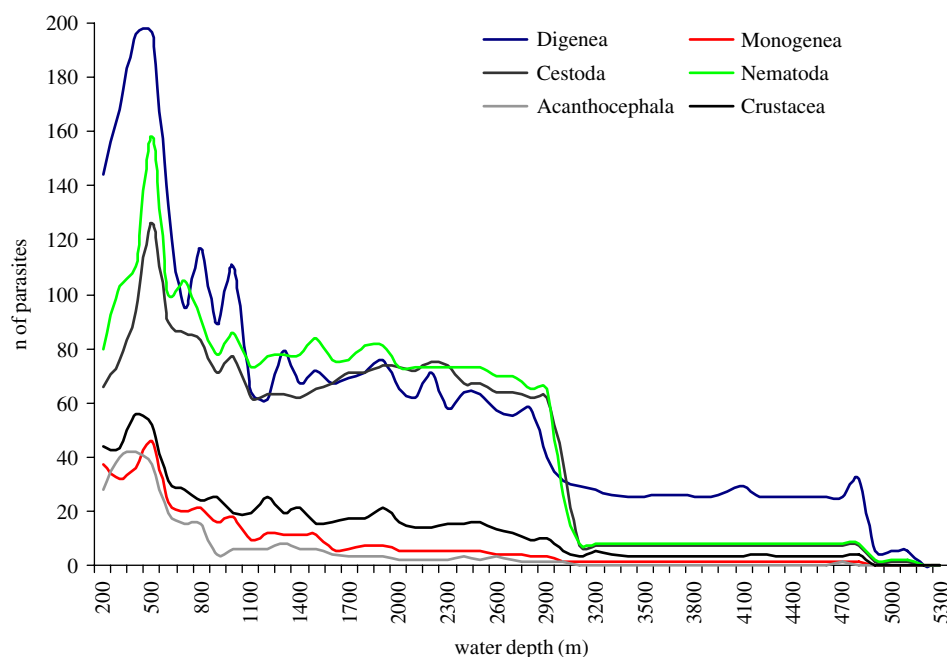


Fig. 2. Depth distribution of higher fish parasite taxa in deep-sea fish world wide (data from Klimpel et al., 2001).

present study, *H. macrochir* at a water depth of 2600 m seems to follow this pattern. Most isolated parasites belonged to the digeneans, nematodes and a cestode, and the species richness is reduced when compared to other demersal fish from shallower waters, however, higher when compared to pelagic deep-sea fish. More studies on demersal as well as pelagic deep-sea fish of the MAR are needed to test this hypothesis.

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