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VERSITA

Parasite fauna of the Mediterranean grenadier *Coryphaenoides mediterraneus* (Giglioli, 1893) from the Mid-Atlantic Ridge (MAR)

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Abstract

A total of 38 *Coryphaenoides mediterraneus* from the Charlie-Gibbs Fracture Zone (CGFZ), a part of the Mid-Atlantic Ridge (MAR), was studied for parasites and feeding ecology. Sixteen different parasite species were found, most of them belonging to the Digenea (6 species) and Nematoda (6). Twelve new host and 11 new locality records were established, and 8 deep-sea generalists and 5 deep-sea specialists were found. Twelve adult and 3 larval parasites occurred, with *Allopodocotyle margolisi* (Digenea), Tetraphyllidea indet. (*Scolex pleuronectis*, Cestoda) and *Ascarophis longiovata* (Nematoda) being the predominant species. These parasites reached a prevalence of 50.0%, 86.8% and 68.4% with an intensity of infection of 1–10, 1–91 and 1–74, respectively. The food consisted of crustaceans and cephalopods; no further prey items such as fish could be identified. *Coryphaenoides mediterraneus* demonstrates a parasite fauna similar to that of other deep-sea macrourids. No MAR-specific parasite species were found, and the collected helminths are common fish parasites of the North Atlantic deep-sea basin and the adjacent continental shelf regions. Only few larval epipelagic generalists such as ascaridoid nematodes were found, due to the deep origin of the studied fish between 1700–3500 m. The recorded species rich parasite fauna reflects the wide depth range and opportunistic feeding behaviour of *C. mediterraneus* on benthopelagic food. The recorded parasite species composition around the MAR appears to be similar to other deep-sea locations in the Atlantic Ocean, demonstrating the wide zoogeographical distribution of these deep-sea metazoans. Consequences of the MAR, the CGFZ and the homogeneous deep-sea environmental conditions for the parasite species distribution are discussed.

Keywords

Macrouridae, *Coryphaenoides mediterraneus*, parasites, life-cycles, stomach analysis, zoogeography, Charlie-Gibbs Fracture Zone, Mid-Atlantic Ridge

Introduction

The open ocean has been compared with terrestrial deserts, due to a lack of information on species diversity and composition caused by the far distance from any mainland. Compared with shallow coastal regions, relatively little is known about the ecology of the high seas. One characteristic, however, is the lack of available nutrients, resulting in low primary production with less zooplankton and nekton biomass (Noble 1973, Marcogliese 2002). Along the Mid-Atlantic Ridge system (MAR) in the Central Atlantic, local upwelling, complex currents and frontal systems create favourable conditions for increased primary and secondary production in the water column. Thus, this mountainous system might have an important role in the turnover of nutrients and the distribution of organisms between the epipelagial and the deep-sea.

The bathyal, meso- and upper bathypelagic nekton community from 200 to 2500 m water depth is usually dominated by benthopelagic fishes of the family Macrouridae, by small pelagic fishes of the Myctophidae, Microstomatidae and Gonostomatidae, and by different Crustacea (e.g. Foxton 1970, Gjøsaeter and Kawaguchi 1980, Sutton *et al*. 2008). The majority of these organisms exhibit extensive diurnal vertical migration, from water depths below 1500 m at daytime into the more productive surface layers during night (e.g. Pusch *et al*. 2004). Studies on the diet and food composition of meso- and bathypelagic fishes have been concentrated on the abundant myctophids, gonostomatids, stomiids and sternoptychids (e.g.

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Gartner and Zwerner 1989, Klimpel *et al*. 2006), those on benthopelagic species on the macrourids (Houston and Haedrich 1986).

One of the most abundant fish species in the open waters of the North Atlantic Ocean and the Charlie-Gibbs Fracture Zone (CGFZ, a part of the MAR) is the benthopelagic deep-sea macrourid *Coryphaenoides mediterraneus* (Bergstad *et al*. 2008, Froese and Pauly 2008). Deep-sea macrourids of the genus *Coryphaenoides* consist of more than 46 species (Morita 1999). *Coryphaenoides mediterraneus* frequently occurs along the MAR and prefers a depth range of 1200–2800 m. It can be also found deeper down to 4262 m, and feeds mostly on invertebrates such as polychaetes, cephalopods and crustaceans and also small fishes (Bergstad *et al*. 2008, Froese and Pauly 2008). The Mediterranean grenadier is commonly found together with other macrourids, such as *C. brevibarbis*, *C. rupestris*, and *C. carapinus*, in the northern and middle part of the MAR (e.g. Bergstad *et al*. 2008).

Parasitological studies on *C. mediterraneus* are scarce (e.g. Klimpel *et al*. 2001). Bray (1995), Gibson (1995) and Bray and Gibson (1995) studied the digenean parasite fauna from the Rockall Trough (Atlantic Ocean), and identified *Steringophorus thulini*, *Allopodocotyle margolisi* and *Lepidapedon beveridgei*. Mauchline and Gordon (1984) recorded cestodes and nematodes of 98 *C. mediterraneus* also from the Rockall Trough at a prevalence of 24.0% and 9.0%, respectively.

The purpose of the present study is to investigate the parasite fauna and food composition of *C. mediterraneus* from the CGFZ. An analysis of prey items determines the position of this macrourid species within the benthopelagic food web along the MAR. A comparison with the parasite fauna of other deep-sea fish is made in order to better understand the characteristic infection pattern within this unique deep-sea habitat. The importance of the CGFZ for the zoogeographical distribution of marine fish parasites is discussed.

Materials and methods

Sample collection

Fish were sampled in July 2004 on board the Norwegian research vessel G.O. Sars along the MAR. This underwater mountain range runs along the centre of the Atlantic Ocean in north-south direction of 16000 km length and separates the North American and Eurasian Plates. At 52°–53°N and 30°–35°E it is divided by the CGFZ into a northern and southern part. Samplings were conducted with a bottom trawl at a trawling speed between 1.5–2.5 knots and a towing time of approximately 60 min (Wenneck *et al*. 2008). Stations were located around the CGFZ covering an area between 42°46′–53°16′N and 28°52′–35°31′W. A sub-sample of 38 *C. mediterraneus* were caught in 1700 to 3500 m water depths. 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) of each fish was determined. All fish were deep frozen at –40°C for subsequent examination.

Parasitological examination

The eyes, skin, fins, gills, nostrils and buccal 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 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 100.0% glycerine (Riemann 1988). Digenea, Monogenea and Cestoda were stained with acetic carmine, dehydrated, cleared with eugenol or creosote, and mounted in Canada balsam. Crustacea were dehydrated and transferred into Canada balsam. Parasite identification literature included original descriptions as well as Campbell and Munroe (1977) and Gibson (1995) for Digenea, Kritsky and Klimpel (2007) for Monogenea, Khalil *et al*. (1994) and Palm (2004) for Cestoda, Anderson (2000) and Moravec and Klimpel (2009) for Nematoda, and Boxshall (pers. com.) for Crustacea. The terms prevalence (P), mean intensity (mI), intensity (I) and mean abundance (A) follow the recommendations of Bush *et al*. (1997). Prevalence 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); mean intensity is the average intensity of infection, 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; intensity of infection is the number of individuals of a particular parasite species in a single infected host (expressed as a numerical range); mean abundance is the 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.

Stomach content analysis

The stomach contents were sorted and food items were identified to the lowest possible taxon and grouped into taxonomic categories. 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, Amundsen *et al.* 1996). 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. In some fish specimens, the stomach was extruded into the buccal cavity. In these cases, the stomach contents together with some stomach parasites might have been lost.

Results

The analysis of 38 *Coryphaenoides mediterraneus* with total lengths between 29.8 to 58.5 cm (mean 42.9 cm) and total weight ranging from 81.4 to 950.0 g (mean 323.9 g) revealed a rich parasite fauna. A total of 16 different species was found,

Table I. Metazoan parasites in/on *Coryphaenoides mediterraneus* from the Charlie-Gibbs Fracture Zone (CGFZ), a part of the Mid-Atlantic Ridge (MAR)

Parasite species	P (%)	I	mI (± SD)	A
Monogenea				
Cyclocotyloides bergstadi	5.3	1	1.0 (± 0.22)	0.05
Digenea				
Allopodocotyle margolisi	50.0	1–10	2.9 (± 1.6)	1.45
Glomericirrus macrouri	42.1	1–3	1.5 (± 0.87)	0.63
Gonocerca minuta	36.8	1–3	1.5 (± 0.82)	0.50
Lepidapedon beveridgei	7.9	2–3	2.7 (± 0.73)	0.21
Steringophorus thulini	18.4	1–5	2.3 (± 1.12)	0.42
Steringotrema sp.	18.4	1–7	3.3 (± 1.48)	0.61
Digenea indet.	7.9	1	1.0 (± 0.26)	0.08
Cestoda				
Grillotia rowei	44.7	1–16	2.8 (± 2.82)	1.26
Tetraphyllidea indet. (*Scolex pleuronectis*)	86.8	1–91	17.3 (± 20.7)	15.21
Nematoda				
Anisakis simplex s. l.	23.7	1–5	2.0 (± 1.12)	0.47
Ascarophis longiovata	68.4	1–74	13.8 (± 2.63)	9.42
Capillaria sp.	2.6	2	2.0 (± 0.32)	0.05
Hysterothylacium aduncum	10.5	1–4	2.0 (± 0.73)	0.21
Neoascarophis longispicula	23.7	1–13	3.9 (± 2.74)	0.92
Spinitectus oviflagellis	2.6	2	2.0 (± 0.32)	0.05
Nematoda indet.	15.8	1–2	1.2 (± 0.45)	0.18
Crustacea				
Chondracanthodes deflexus	5.3	1	1.0 (± 0.22)	0.05

P – prevalence, I – intensity, mI (± SD) – mean intensity ± (standard deviation) and A – mean abundance.

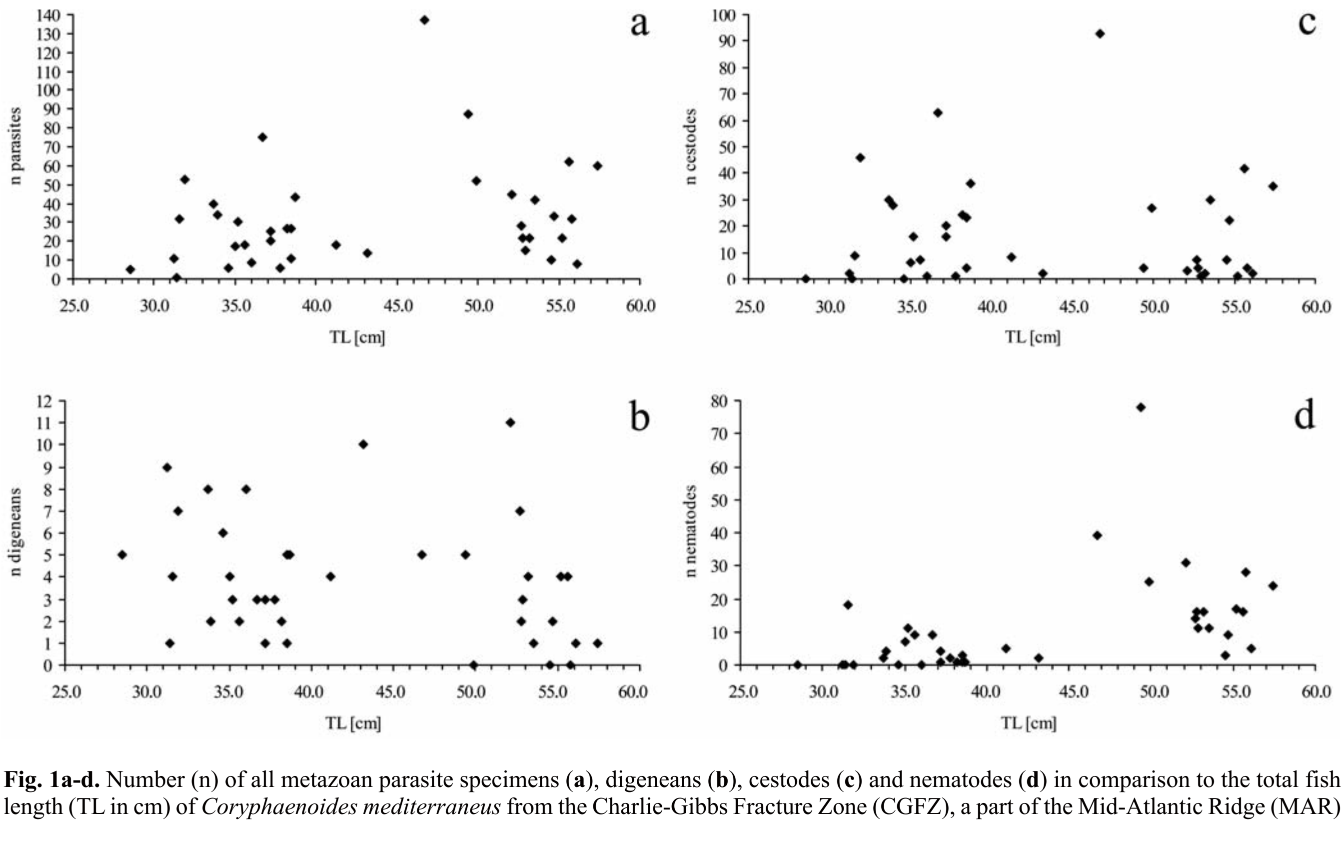

Fig. 1a-d. Number (n) of all metazoan parasite specimens (**a**), digeneans (**b**), cestodes (**c**) and nematodes (**d**) in comparison to the total fish length (TL in cm) of *Coryphaenoides mediterraneus* from the Charlie-Gibbs Fracture Zone (CGFZ), a part of the Mid-Atlantic Ridge (MAR) of similar composition in smaller and larger sized specimens (see Fig. 1). The prevalence, intensity, mean intensity, and abundance for each parasite species are given in Table I. Only two different prey item groups, Crustacea and Cephalopoda, were identified.

Parasite composition

Parasites belonged to the Digenea (6 species), Monogenea (1), Cestoda (2), Nematoda (6) and Crustacea (1) (Table I). All represent new locality records and 13 species represent new host records. The predominant parasites belonged to the digeneans, cestodes and nematodes. All digeneans were adult and located in the digestive tract. The highest prevalence was calculated for *Allopodocotyle margolisi* (50.0%), *Glomericirrus macrouri* (42.1%) and *Gonocerca minuta* (36.8%). Adults of the monogenean *Cyclocotyloides bergstadi* were isolated from the gills at a prevalence of 5.3%. Plerocerci of the trypanorhynch cestode *Grillotia rowei* (44.7%) were isolated from the body cavity, liver and intestine, while larval Tetraphyllidea indet. (*Scolex pleuronectis*) (86.8%) were located in the pyloric caeca and intestine. Along with digeneans, the nematodes represented the most species rich parasite taxon in *C. mediterraneus*. *Anisakis simplex s.l.* (23.7%) and *Hysterothylacium aduncum* (10.5%) were isolated as larval stages from the organs of the digestive tract, while *Ascarophis longiovata* (68.4%), *Capillaria* sp. (2.6%), *Neoascarophis longispicula* (23.7%), *Spinitectus oviflagellis* (2.6%) and *H. aduncum* were isolated as adults from the stomach and intestinal contents. The only crustacean on the gills of *C. mediterraneus* was *Chondracanthodes deflexus* at a prevalence of 5.3%. The relationship between the number of all metazoan parasite specimens, digeneans, cestodes and nematodes in comparison to the total fish length is given in Figure 1. The number of nematode specimens seems to increase with fish length.

Stomach contents

Of the 38 stomachs examined 19 contained feed in a digested state. Only two prey item groups were identified. The most frequent prey organisms belonged to the Crustacea (F = 75.0%, N = 75.0%, W = 98.9%, IRI = 13042.5), while the Cephalopoda were of lower importance (F = 25.0%, N = 25.0%, W = 1.1%, IRI = 652.5).

Discussion

This study represents the first parasitological and feeding ecological study of the deep-sea grenadier *Coryphaenoides mediterraneus* from the Charlie-Gibbs Fracture-Zone (CGFZ) of the Mid-Atlantic Ridge. In contrast to earlier studies (Mauchline and Gordon 1984) and single parasite records (Bray 1995, Bray and Gibson 1995), we recorded a species rich parasite fauna, consisting of 16 different helminths and crustaceans. Predominant parasite species at the CGFZ were the digenean *Allopodocotyle margolisi*, cestode larvae of Tetraphyllidea indet. (*Scolex pleuronectis*) and the nematode *Ascarophis longiovata*. Previously reported parasites of *C. mediterraneus* were the digeneans *A. margolisi*, *Lepidapedon beveridgei* and *Steringotrema thulini* as well as unidentified cestodes and nematodes (Klimpel *et al*. 2001). *Glomericirrus macrouri*, *Gonocerca minuta*, *Steringotrema* sp. (Digenea), *Cyclocotyloides bergstadi* (Monogenea), *Grillotia rowei*, Tetraphyllidea indet. (*Scolex pleuronectis*, Cestoda), *Anisakis simplex s.l.*, *A. longiovata*, *Capillaria* sp., *Hysterothylacium aduncum*, *Neoascarophis longispicula*, *Spinitectus oviflagellis* (Nematoda) and *Chondracanthodes deflexus* (Crustacea) represent new host records. Most parasites occurred as adults, demonstrating an important role of *C. mediterraneus* in the life cycle for the observed deep-sea parasites.

The digenean life-cycle is complex, including molluscs as obligatory first and in the case of deep-sea parasites teleosts as final hosts (e.g. Marcogliese 1995). In *C. mediterraneus* Digenea was the most predominant taxon at the MAR, represented by the families Lepocreadiidae, Hemiuridae, Derogenidae, Opecoelidae and Fellodistomidae (Klimpel *et al*. 2001, present study). Houston and Haedrich (1986) identified 5.8% benthic vs 27.8% pelagic digenean trematodes in deep sea fish from the Carson Canyon region, North Atlantic. The authors propose common feeding of demersal fishes in the pelagial, suggesting a pelagic life cycle of many of these digeneans.

Tetraphyllidea indet. (*S. pleuronectis*) and the trypanorhynch cestode *G. rowei* are known from a variety of different fish species (e.g. Klimpel *et al*. 2001, Palm 2004). They mature in the stomach or spiral valve of elasmobranchs, and both taxa are known for low host specificity especially in the teleost intermediate hosts (Khalil *et al*. 1994, Palm and Caira 2008). Crustacea (e.g. copepods) are first and larger invertebrates or fish second intermediate/paratenic hosts (Khalil *et al*. 1994, Palm 2004). In the case of *G. rowei*, deep-sea rays most probably serve as final hosts, suggesting the entire life cycle of this species within the deep-sea (other host records see Palm 2004). *Hysterothylacium aduncum* is the most abundant and least host specific fish nematode in the North Atlantic and uses various planktonic and benthic invertebrates as obligatory intermediate hosts (Køie 1993, Klimpel 2005). Teleosts are common final hosts for this species (Balbuena *et al*. 1998, Klimpel and Rückert 2005), and *C. mediterraneus* adds to the known final host spectrum. It is important to note that the life cycle of this species functions in a wide range of hosts and from shallow waters into the deep-sea.

Similar to the cestodes, the nematode *A. simplex s. l.* uses invertebrates as first and larger crustaceans or teleosts as second intermediate hosts (Klimpel *et al*. 2004, 2008a). However, *Anisakis* matures in marine mammals such as cetaceans (Anderson 2000, Køie 2001a), and these generalist larvae penetrate into deep waters through vertically migrating hosts (Palm and Klimpel 2008). Considering the deep origin of the *C. mediterraneus*, the infection of these fish most probably results in a dead-end for the nematode *A. simplex s. l.* The nematodes *N. longispicula* and *S. oviflagellis* are currently known only from *C. mediterraneus* (Moravec and Klimpel 2009), while the genus *Capillaria* uses oligochaetes as first intermediate and teleosts as obligatory second intermediate hosts (Køie 2001b). The ectoparasites *C. bergstadi* (Monogenea) and *C. deflexus* (Crustacea) are specific for macrourids (Klimpel *et al*. 2001, Kritsky and Klimpel 2007). Consequently, *C. mediterraneus* plays an important role especially as final host in the life cycle of a diversity of deep-sea fish parasites, getting infected mainly through crustacean intermediate hosts at the sampled water depth below 1700 m at the MAR.

The MAR exhibits a diversity of fish species, such as the Bathylagidae, Melamphaidae, Myctophidae, Sternoptychidae and Stomiidae as representatives for the pelagial and the Macrouridae and elasmobranch family Dalatiidae as representatives for the benthal (Bergstad *et al*. 2008, Sutton *et al.* 2008). The bathylagid *Bathylagus euryops* had 5 different parasites, the digeneans *Lecithaster* sp., *Lecithophyllum botryophorum* and a hemiurid, a bothriocephalidean cestode and the nematode *Anisakis* sp. (Busch *et al*. 2008). The sternoptychid *Maurolicus muelleri* was infected with unidentified cestodes (Tetraphyllidea indet.) and the nematode *Anisakis simplex* (*s. s.*) (Klimpel *et al*. 2007). The myctophids *Myctophum punctatum* and *Notoscopelus kroyeri* were both infected with the digeneans *Gonocerca phycidis*, *Lethadena* sp., tetraphyllidean cestodes and *A. simplex* (*s. s.*) (Klimpel *et al.* 2008a). The parasite fauna of the benthal representative *C. mediterraneus* was the most species rich, with 16 different parasite species and including 6 adult digeneans and 5 adult nematodes (present study). A wide depth range combined with a variety of prey species enable *C. mediterraneus* to accumulate a species rich parasite fauna (see Walter *et al.* 2002), dominated by adult digeneans and nematodes. Similarly, the halosaurid *Halosauropsis macrorchir* was host for 9 different parasite species, including 4 adult digeneans and 1 adult nematode (Klimpel *et al*. 2008b). This seems to be the common pattern of fish parasite infection along the MAR (Central Atlantic), in correspondence to general deep-sea fish parasite patterns as described by Campbell *et al*. (1980), Campbell (1983) and Marcogliese (2002).

The observed parasite fauna of *C. mediterraneus* at the MAR reflects a similar parasite composition to that described from other macrourids in different parts of the world oceans. Palm and Klimpel (2008) compared the parasite fauna of *Macrourus berglax* from the Central North Atlantic with the macrourid genera *Macrourus*, *Coryphaenoides*, *Coelorhynchus* and *Nezumia*, and recognized a similar infection pattern amongst these deep-sea fish, consisting of the same or closely related species. This observation led to the conclusion that the parasite life-cycles in these benthodemersal deep-sea fishes follow similar pathways independent of geographical location. Concurring habitat and food preference of macrourids results in a similar parasite fauna. *Macrourus berglax* and the best studied *Coryphaenoides* species *Coryphaenoides armatus*, *C. carapinus* and *C. rupestris* from different North and Central Atlantic localities harboured 39 and between 18–37 metazoan parasite species, respectively. Amongst these parasites are many taxa that occur in different macrourids and regions, such as the cestode *G. rowei*, and the nematodes *A. simplex s. l.* and *H. aduncum*. The digenean *G. macrouri* was earlier recorded from *C. rupestris*, *G. minuta* from *Nezumia bairdii*, and *G. phycidis* from different macrourids (e.g. Klimpel *et al.* 2001). Most representatives of *Macrourus* and *Coryphaenoides* occur in a wide depth range (Froese and Pauly 2008), enabling them to get access to a wide range of parasites. Palm and Klimpel (2008) proposed that the macrourids from the Mid-Atlantic Ridge harbour a similar parasite fauna and infection pattern to macrourids from other parts of the world oceans. This can be confirmed based on the presented results of *C. mediterraneus* from the MAR.

The MAR is a mountainous underwater system in the middle of the Atlantic Ocean and rises more than 4 km above the deep-sea plains. In combination with the CGFZ (two main parallel deep rift valleys, running perpendicular to the main MAR axis with a depth between 700 and 4500 m), this underwater system might serve as a geological barrier or filter for the zoogeographical distribution of some parasite species. For example, in the pelagic ecosystem, Klimpel *et al*. (2007) could demonstrate a poor parasite fauna of *M. muelleri* at the MAR compared with the NE Atlantic continental shelf region. However, the recorded parasitation of the benthodemersal *C. mediterraneus* from the MAR indicates an even parasite distribution in the benthic zone of the deep-sea, suggesting no separating function of the MAR between the eastern and western deep-sea plains. Detailed analyses of the parasite fauna of macrourids from the different Atlantic regions is needed to support this assumption.

The present study complements our analyses of the fish parasite fauna from the MAR (e.g. Klimpel *et al*. 2007, 2008a, b; Kritsky and Klimpel 2007; Moravec and Klimpel 2007; Busch *et al*. 2008; Palm and Klimpel 2008). A species poor bathypelagic zone that is composed of cestodes, larval nematodes and some digeneans changes towards the deep-sea floor into a diverse parasite fauna, clearly dominated by adult nematodes and digeneans. So far, we could not identify any specific fish parasitation at the MAR in terms of the species composition and distribution. A homogeneous water body in the deep-sea or the extensive depth range of the studied fish species might be possible reasons for the observed fish parasitation. More comparative studies on possible ecological differences (such as prevalence of infection and parasite abundance) are needed to detect any influence of the MAR system on the life cycles and evolution of deep-sea fish parasites.

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