Meso- and bathy-pelagic fish parasites at the Mid-Atlantic Ridge (MAR): Low host specificity and restricted parasite diversity

Sven Klimpel [a,b,*], Markus Wilhelm Busch [a], Tracey Sutton [c], Harry Wilhelm Palm [a]

[a] Heinrich-Heine-University Düsseldorf, Institute of Zoomorphology, Cell Biology and Parasitology, Universitätsstr. 1, D-40225 Düsseldorf, Germany
[b] Biodiversity and Climate Research Centre (BiK-F), Johann Wolfgang Goethe-University, Georg-Voigt-Str. 14-16, D-60325 Frankfurt am Main, Germany
[c] Virginia Institute of Marine Science, College of William and Mary, PO Box 1346, Gloucester Point, VA 23062, USA

ARTICLE INFO

ABSTRACT

Seven meso- and bathy-pelagic fish species from the Mid-Atlantic Ridge (MAR) were firstly studied for fish parasites and feeding ecology. With a total of seven parasite species, the 247 meso- and bathy-pelagic deep-sea fish specimens belonging to the families Melamphaidae (3 spp.), Myctophidae (3 spp.) and Stomiidae (1 sp.) revealed low parasite diversity. The genetically identified nematodes *Anisakis simplex* (s.s.) and *Anisakis pegreffii* from the body cavity, liver and muscles of *Myctophum punctatum* were the most abundant parasites, reaching a prevalence of 91.4% and mean intensity of 3.1 (1–14). *Anisakis* sp. (unidentified) infected *Chauliodus sloani* and *Poromitra crassiceps*. Bothriocephalidean and tetraphyllidean cestode larvae infected *Benthosema glaciale*, the latter also occurring in *C. sloani* and *Scopelogadus beanii*, at low prevalences. Adult parasites at low infection rates included the digenean *Lethadena* sp. (2.9%), and the two copepod species *Sarcotretes scopeli* (5.7%) and *Tautochondria dolichoura* (5.3–11.4%). The myctophid *Lampanyctus macdonaldi* and the melamphaid *Scopelogadus mizolepis mizolepis* were free of parasites. Analyses of the stomach contents revealed crustaceans, especially copepods and euphausiids for the myctophids and also amphipods for the melamphaids as predominant prey items. While all stomachs showing distinct content comprising often unidentified 'tissue' (possibly gelatinous zooplankton), only *C. sloani* preyed upon fish. Though this feeding habit would enable transfer of a variety of crustacean-transmitted parasites into the fish, the parasite fauna in the meso- and bathy-pelagic fish was species poor. All observed parasites showed low host specificity, demonstrating no distinct pattern of host–parasite co-evolution. The MAR is no barrier for the parasite distribution in the North Atlantic meso- and bathy-pelagial.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Meso-pelagic fishes require various adaptations to cope with high pressure, cold temperatures, missing light and the immense space with an extremely scarce food supply. Consequently, their behaviour including extensive diurnal migration and characteristic feeding ecology affect the oceanic food web, and the pathways of parasite transmission in the deep sea. Meso-pelagic fishes represent a major component of the oceanic nekton community and are fundamental prey for piscivorous fish and commercially important species such as tunas and mackerels (e.g. Fock et al., 2004) or dolphins and other whales (Fiedler et al., 1998; Wang et al., 2003).

First investigations on the parasite fauna of meso- and bathy-pelagic fish have been carried out e.g. by Noble (1973), Mauchline and Gordon (1984), Gartner and Zwerner (1989) and Campbell (1990). Klimpel et al. (2009) summarized the literature on fish parasites from deep-sea habitats and recorded over 789 parasite species in the so far studied 511 fish species (1.5 parasite species per fish species). With the existence of about 3800–4200 different deep-sea fishes (~10–12% of the known fish fauna, Froese and Pauly, 2009), only a fraction of deep-water fishes have been studied for parasites.

The Mid-Atlantic Ridge (MAR) is an extensive mountainous underwater system in the centre of the Atlantic Ocean, rising from the abyssal plains of about 4500–7500 m water depth up to several 100 m below or even above the sea surface (e.g. Iceland, Azores). It separates the North American and Eurasian Plates, and is divided at 52–53°N and 30–35°E by the Charlie-Gibbs Fracture Zone (CGFZ). The CGFZ consists of two main parallel deep rift valleys, 16–24 km wide, running perpendicular to the main ridge axis with a depth between 700 and 4500 m. The water masses are

---

the result of recirculation and mixing of northeastern and northwestern deep waters (Vinogradov, 2005). The CGFZ creates a north–south divide for benthic and pelagic fish species. This is caused in particular by the vicinity of the Sub-Polar Front, enhancing the turnover in the food web from planktonic organisms up to the whale and seabird consumers, and appears to be an important whale feeding area (e.g. Dotinga and Molenaar, 2008).

The MAR consequently might constitute a biogeographical barrier for east–west dispersal, limiting the distribution of deep-sea biota either to the eastern or western side. On the other hand, seamounts or mountainous structures may exhibit increased biological productivity, caused by unique currents and upwelling situations, bringing nutrient-rich deep water into the light-flooded productive surface layers (Sutton et al., 2008). Sutton et al. (2008) detected a maximum biomass in the bathy-pelagial at the MAR and connected this with the influence of the ridge. Usually it is assumed that biomass and species richness decline with depth in the pelagic environment and rise again towards the deep-sea floor (e.g. Marcogliese, 2002).

Recent biological surveys of the structure of the deep-sea fish assemblages at the MAR by Fock et al. (2004) and the Census of Marine Life Mar-Eco project (Bergstad et al., 2008; Sutton et al., 2008) revealed a diverse fish fauna and a high biomass. The authors, however, did not find any distinct differences on either side of the MAR. Studies on the vertical and horizontal structure, biomass and topographic association of zooplankton (e.g. copepods, decapods, amphipods, cnidarians) along the MAR also supported these results (Gaard et al., 2008; Stemmann et al., 2008). Multivariate analyses of the different physical and biological data that were sampled during the Mar-Eco surveys indicate that species composition and abundance along the ridge vary especially with the dominant water masses and more importantly with water depth.

Fish parasites on the MAR are largely unexplored, and we are just beginning to understand the marine parasite biodiversity in the area. Recently, Busch et al. (2008), Kellermanns et al. (2009) and Klimpel et al. (2007, 2008a, b) analysed the fish parasite fauna, identifying several new species (Moravec and Klimpel, 2007, 2009; Kritsky and Klimpel, 2007) and speculating about the parasite composition of deep-sea macrourids at the MAR (Palm and Klimpel, 2008). The present study adds parasitological data on seven dominant meso- and bathy-pelagic fish species. Comments are made on the host specificity of the recorded parasites, and the ecology of the hosts and their importance for parasite transmission are analysed.

2. Material and methods

2.1. Sample collection

Fishes were sampled in June 2004 on board the Norwegian research vessel G.O. Sars along the MAR (Fig. 1). The stations were located on the MAR in the area 41°31′–53°05′N and 29°13′–36°43′W. The fish originated from different stations, because they were shared among different research groups prior examination and depending on catch composition. A total of 247 deep-sea fishes belonging to three families were examined for the parasite fauna and stomach contents. Benthosema glaciale (Reinhardt, 1837) (70 specimens caught at Super station 26, Local station 355), Chauliodus sloani Bloch & Schneider, 1801 (34 specimens caught at Super station 20, Local station 348), Lampanyctus macdonaldi (Goode & Bean, 1896) (34 specimens caught at Super station 12, Local station 339), Myctophum punctatum Rafinesque, 1810 (35 specimens caught at Super station 14, Local station 341), Poromitra crassiceps (Günther, 1878) (19 specimens caught at Super station 32, Local station 361), Scopelogadus beanii (Günther, 1887) (35 specimens caught at Super station 31, Local station 360) and S. m. mizolepis (Günther, 1878) (20 specimens caught at Super station 34, Local station 364) were caught with pelagic trawls in water depths between 340 and
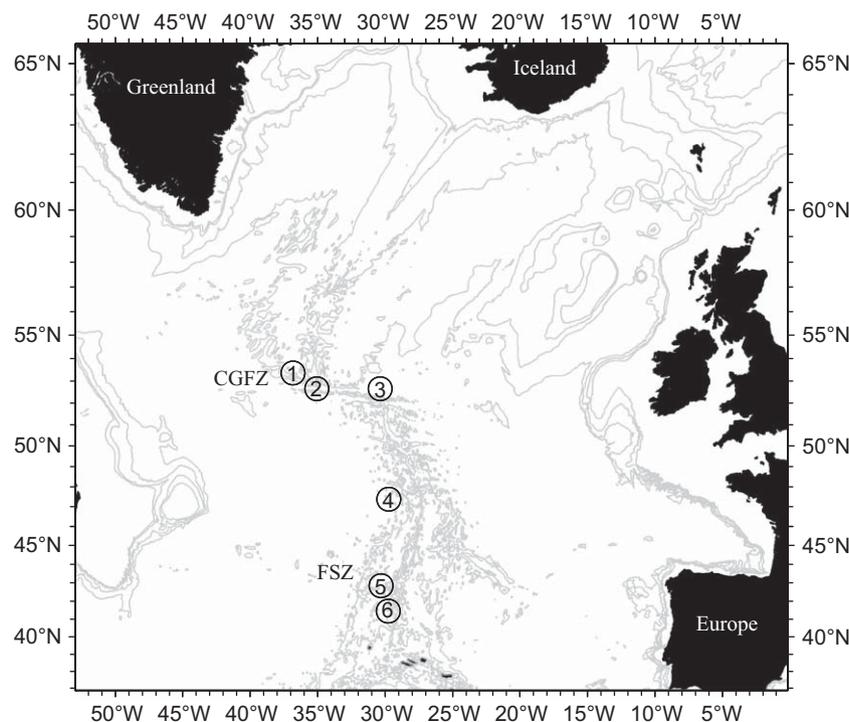

Fig. 1. Map of the area of investigation with sample stations 1–6 (Station 1. Myctophum punctatum, 2. Lampanyctus macdonaldi, 3. Chauliodus sloani, 4. Benthosema glaciale, 5. Poromitra crassiceps, Scopelogadus beanii, 6. Scopelogadus mizolepis mizolepis). CGFZ=Charlie-Gibbs Fracture Zone, FSZ=Faraday Seamount Zone.

2300 m as described by Wenneck et al. (2008). All fish specimens examined were deep frozen at −40 °C immediately after catch. Prior to examination each fish was defrosted by 0–1 °C. Morphometrical fish data, standard length (SL) 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 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 gradated ethanol series and transferred to 100% glycerine. Digenea 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 Bray (pers. com.) for Digenea, Euzet (1994) and Kuchta et al. (2008) for Cestoda, Anderson (2000) for Nematoda and Boxshall (pers. com.) for Crustacea. The terms prevalence (P), mean intensity (mI), intensity (I) and mean abundance (mA) follow the recommendations of Bush et al. (1997). Host specificity at the species level was assessed using the specificity index (HSs) of Caira et al. (2003). Host specificity values ranging between 1 and ~10 and were calculated using the software available at http://darwin.eeb.uconn.edu/specificity/specificity.html.

2.3. 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.

2.4. PCR amplification and sequencing of ITS-1, 5.8S and ITS-2 of Anisakis simplex (s.s.)

All nematodes were identified morphologically by existing keys and descriptions. Only nematodes isolated from the examined M. punctatum were identified genetically. After isolation and identification the anisakid nematodes were fixed and stored in absolute ethanol (~100%). Genomic DNA was isolated and purified from individual larvae by using a genomic DNA extraction kit (Peqlab Biotechnology GmbH, Erlangen, Germany) according to the instructions of the manufacturer. The rDNA region comprising the ITS-1, 5.8S, ITS-2 and flanking sequences (=ITS+) was amplified by using the previously described primers NC5 (5′-GTA GGT GAA CCT GCG GAA GGA TCA TT-3′) and NC2 (5′-TTA GTT TCT TTT CCT CCG CT-3′) (Zhu et al., 2000). PCR-reactions (26 µl) included 13 µl Master-Mix (Peqlab Biotechnology GmbH, Erlangen, Germany) containing dNTP, MgCl₂, Buffer and Taq-Polymerase, 3 µl of each primer, 2 µl dest. water and 5 µl genomic DNA. Each PCR reaction was performed in a thermocycler (Biometra, Germany) under the following conditions: after initial denaturation at 95 °C for 15 min, 30 cycles of 94 °C for 1 min (denaturation), 55 °C for 1 min (annealing), 72 °C for 1 min (extension), followed by a final extension at 72 °C for

5 min. Samples without DNA were included in each PCR run. PCR products were checked on 1% Agarose gels. A 100-bp ladder marker (peqGOLD, Erlangen, Germany) was used to estimate the size of the PCR products. In order to identify the anisakid nematodes, the PCR products were purified with E.Z.N.A. Cycle-Pure Kit (Peqlab Biotechnology GmbH, Erlangen, Germany). Afterwards a total volume of 7 µl, including 2 µl primer (individually) and 5 µl of the PCR product (250 ng/µl) was sequenced by Seqlab (Goettingen GmbH, Germany). Both spacers and the 5.8S gene were sequenced in both directions from each PCR product, using primers NC5, NC13 (forward; 5′-ATC GAT GAA GAA CGC AGC-3′), NC13R (reverse; 5′-GCT GCG TTC TTC ATC GAT-3′), XZ1R (reverse; 5′-GGA ATG AAC CCG ATG GCG CAA T-3′) and NC2. The obtained sequences were identified via GenBank and aligned with previously characterized sequences of the A. simplex complex, using CLUSTAL W (1.83) Multiple Sequence Alignments (Thompson et al., 1994).

3. Results

The analysis of the 247 meso- and bathy-pelagic fishes belonging to three different families from the deep sea along the MAR revealed low parasite diversity. Seven parasite species including three new locality records could be established, adding to the known number of fish parasites around the MAR. Including the present study, 34 parasite species have been collected so far from deep-sea fish species of different trophic levels at the MAR. Nine groups of prey items were identified, belonging to Mollusca, Crustacea and Teleostei.

3.1. Parasite composition and stomach contents

3.1.1. Myctophidae (Tables 1 and 2)

The studied myctophids showed low parasite richness, with three, three and no parasite species in B. glaciale, M. punctatum and Lampanyctus macdonaldi, respectively. Only the anisakid nematodes A. simplex (s.s.) and Anisakis pegreffii occurred in high numbers, while the other parasites had low infestation rates.

Three parasite species were isolated from B. glaciale. A single tetraphyllidean cestode larva was located in the pyloric caecum, and a single bothriocephalidean cestode larva was detected in the stomach lumen. Specimens of the mesoparasitic copepod Sarcotretes scopeli were isolated from the skin and musculature. All prey items in B. glaciale belonged to the Crustacea. The frequency of occurrence (F %) was highest for 'tissue', followed by Crustacea indet., Copepoda and Euphausiacea. In wet weight (W %) Euphausiacea were followed by 'tissue', Crustacea indet. and Copepoda. Numerically (N %) 'tissue' was dominant, followed by Crustacea indet., Copepoda and Euphausiacea. The proportion of empty stomachs was 67.1%.

Three parasite species were isolated from M. punctatum. A single specimen of the hemiurid digenean Lethadena sp. occurred in the stomach lumen. Third-stage larvae (L3) of the nematodes A. simplex (s.s.) and A. pegreffii (genetic identification see below) were detected in the body cavity, liver and muscles. The stomach contents varied, consisting of Mollusca, Crustacea and 'tissue'. The frequently (F %) dominant prey group was Crustacea, followed by 'tissue' and Gastropoda. Regarding the wet weight (W %) Copepoda and Hyperiidae exceeded 'tissue', Crustacea indet. and Gastropoda. Numerically (N %) Copepoda and Hyperiidae were the most consumed food items, while Gastropoda, Euphausiacea, Decapoda, Crustacea indet. and 'tissue' were of minor importance. All examined stomachs contained food.

Lampanyctus macdonaldi was free of parasites. Three prey groups could be identified: 'tissue', Mysidacea and Crustacea

Table 1
Prevalence (P), mean intensity (mI), intensity (I) and mean abundance (mA) of with parasites infested deep-sea fishes.

Fish family		Myctophidae											Stomiidae						Melamphaidae									
Fish species		Benthosema glaciale					Myctophum punctatum						Chauliodus sloani						Poromitra crassiceps						Scopelogadus beanii				
Parasite species	HS s	Adult/larval	P (%)	mI	I	mA	Adult/larval	P (%)	mI	I	mA		Adult/larval	P (%)	mI	I	mA		Adult/larval	P (%)	mI	I	mA		Adult/larval	P (%)	mI	I	mA
Digenea																													
Lethadena sp.	5.574						a	2.9	1.0	1.0	0.03																		
Cestoda																													
Tetraphyllidea indet.	8.724	l	1.4	1.0	1	0.01							l	2.9	1.0	1	0.03								l	2.9	1.0	1	0.03
Bothriocephalidea indet.		l	1.4	1.0	1	0.01																							
Nematoda																													
Anisakis simplex complex*	9.461						l	91.4	3.1	1–14	2.83																		
Anisakis sp.	9.485												l	2.9	1.0	1	0.03		l	5.3	1.0	1	0.05						
Crustacea																													
Sarcotretes scopeli	7.960	a	5.7	1.0	1	0.06																							
Tautochondria dolichoura	7.659																		a	5.3	1.0	1	0.05		a	11.4	1.3	1–2	0.14

a, adult; l, larval; HS s, host specificity index; *, genetically identified Anisakis simplex (s.s.) and A. pegreffii.

indet. The frequencies of occurrence (F %) and the numerical percentage of prey (N %) were highest for 'tissue', followed by Crustacea indet. and Mysidacea. In wet weight (W %) Crustacea indet. exceeded Mysidacea and 'tissue'. 50.0% of the analysed stomachs were empty.

3.1.2. Stomiidae (Tables 1 and 2)

Two parasite species were found in C. sloani, one larval cestode and one larval nematode. The tetraphyllidean cestode was isolated from the lumen of the intestine and a third-stage larva of Anisakis sp. was located in the body cavity. The occurrence of unidentified 'tissue' among the contents was high and exceeded the Teleostei fragments by frequency of occurrence (F %), numerically (N %) and weight (W %) percentage of prey. The proportion of empty stomachs was 17.6%.

3.1.3. Melamphaidae (Tables 1 and 2)

Two parasite species were isolated from P. crassiceps. A single larval stage of the nematode Anisakis sp. was found in the body cavity and one adult specimen of the copepod Tautochondria dolichoura on the gills. All examined stomachs contained exclusively unidentifiable 'tissue'.

In S. beanii two parasite species were identified: one cestode and one copepod. In the pyloric caeca, one tetraphyllidean cestode larva was found. The adult copepod T. dolichoura was located on the gills. Scopelogadus beanii serves as intermediate host for the detected Cestoda and as final host for the Copepoda. Unidentified 'tissue' occurred in 86.7% of the stomachs with food (F %). Amphipoda and Crustacea indet. were of minor importance to both weight (W %) and numerical (N %) percentage. The proportion of empty stomachs was 57.1%.

No parasites were found in Scopelogadus m. mizolepis. The stomach content consisted mainly of unidentifiable 'tissue' and a small proportion of Crustacea indet. The frequency of occurrence (F %), the weight percentage (W %) of prey and the numerical (N %) percentage of prey was highest for 'tissue'. The proportion of empty stomachs was 35.0%.

3.2. Genetic identification

The ITS-1, 5.8 S and ITS-2 rDNA sequences were determined for 15 anisakid nematodes isolated from M. punctatum. The identification via GenBank showed that 12 samples belonged to A. simplex (s.s.) and three to A. pegreffii. The lengths of the PCR products including the three regions were ~919 bp long, depending on the species (A. simplex (s.s.) 916–922 bp, A. pegreffii 918–919 bp). The G+C contents for the three regions of rDNA of all individuals ranged from 44.77% to 45.43% (A. simplex (s.s.)) and from 44.94% to 45.32% (A. pegreffii). The length of the ITS-1, 5.8S and ITS-2 sequences was 365, 157, respectively, 306 bp (A. simplex (s.s.) and A. pegreffii). The obtained sequences were compared with sequences of anisakid nematodes (EU624342 A. simplex (s.s.) from Japan, 0–5 positions difference (0.0–0.6%); EU624342 A. pegreffii from Japan and 2–5 positions difference (0.2–0.6%)).

4. Discussion

The present study is the first comprehensive parasitological and ecological study on seven meso- and bathy-pelagic fish species from the MAR. It adds to earlier investigations of bentho-demersal and bathy-pelagic fish species (e.g. Justine et al., 2002; Busch et al., 2008; Klimpel et al., 2008a, b; Kellermanns et al.,

Table 2

Number (no. examined), mean standard lengths (SL in cm) and total weights (TW in g) (range in parentheses) and food items of the studied deep-sea fish species. F %: frequency of occurrence, W %: weight percentage of prey, N %: numerical percentage of prey, IRI: index of relative importance.

Fish family	Myctophidae												Stomiidae				Melamphaidae											
Fish species	Benthosema glaciale				Lampanyctus macdonaldi				Myctophum punctatum				Chauliodus sloani				Poromitra crassiceps				Scopelogadus beanii				Scopelogadus m. mizolepis			
No. examined	70				34				35				34				19				35				20			
SL mean (range)	6.0 (4.3–7.4) cm				11.6 (7.5–15.3) cm				7.6 (6.3–9.5) cm				17.6 (11.4–25.0) cm				14.2 (13.2–15.3) cm				10.8 (10.0–11.7) cm				10.8 (9.7–12.7) cm			
TW mean (range)	2.6 (1.0–4.9) g				16.9 (3.3–36.5) g				6.5 (3.4–14.5) g				12.0 (3.1–32.9) g				44.1 (30.3–61.8) g				22.5 (19.0–27.1) g				20.2 (17.3–25.1) g			
Prey category	F%	W%	N%	IRI	F%	W%	N%	IRI	F%	W%	N%	IRI	F%	W%	N%	IRI	F%	W%	N%	IRI	F%	W%	N%	IRI	F%	W%	N%	IRI
Mollusca																												
Gastropoda									5.7	0.4	0.3	4																
Crustacea																												
Copepoda	4.4	0.2	4.2	19					91.4	30.8	55.7	7906																
Euphausiacea	4.4	55.2	4.2	244					28.6	9.0	1.2	292																
Decapoda									5.7	2.4	0.2	15																
Hyperiidae									94.3	28.5	41.6	6610																
Amphipoda																					6.7	3.6	6.7	69				
Mysidacea					11.8	39.4	10.0	583																				
Crustacea indet.	34.8	17.0	33.3	1751	35.2	42.8	30.0	2563	25.7	9.7	0.3	257									6.7	4.7	6.7	76	30.8	42.9	30.8	2270
Teleostei																												
Teleostei indet.													3.6	34.2	3.6	136												
Tissue	60.9	27.6	58.3	1737	70.6	17.8	60.0	5493	62.9	19.2	0.7	1252	96.4	65.8	96.4	15636	100	100	100	20000	86.7	91.7	86.6	15459	69.2	57.1	69.2	8740
Empty stomachs	47 (67.1%)				17 (50.0%)				0 (0.0%)				6 (17.6%)				0 (0.0%)				20 (57.1%)				7 (35.0%)			

2009) in order to characterize the fish parasite fauna at this deep-sea ecosystem in the mid-Atlantic Ocean.

4.1. Myctophidae

4.1.1. Benthosema glaciale

The examined specimens of B. glaciale contained three parasite species. Two cestode larvae, one tetraphyllidean and a bothriocephalidean, occurred with low infestation rates. The synonym 'Scolex pleuronectis' combines larvae of different final hosts. However, typical for marine cestodes, these larvae probably use crustaceans (Copepoda) as first intermediate host. Final hosts are elasmobranchs such as sharks and rays where they mature in the spiral valve (Euzet, 1994). Larger invertebrates and marine fishes harbour the plerocercoids and act as second intermediate or paratenic hosts (e.g. Euzet, 1994).

Sarcotretes scopeli belongs to a group of two parasitic copepod species that has been recorded from deep-sea pelagic fishes (Cherel and Boxshall, 2004). It utilizes only one host during its life cycle, different from most other members of the family Pennelidae. Boxshall (1998) reported 11 deep-sea fish hosts, primarily from the Atlantic Ocean, and stated low host specificity for this species. Regarding the size of the midwater habitat, this adaptation enhances the chance to find a suitable host (Boxshall, 1998). The low infestation rate in the present study seems to be common for this parasite. Hogans (1988) reported low infestation rates from deep-sea fishes from the northwest Atlantic (P=2.82%, I=1 on B. glaciale). Studies from the Norfolk Submarine Canyon showed a prevalence of 8.3% for S. scopeli (Gartner and Zwerner, 1989). Myctophid fishes get infected in the upper water column during their diel migrations (Boxshall, 1998). B. glaciale enters the epi-pelagic layer (< 200 m) during the night.

According to Froese and Pauly (2009), B. glaciale frequently preys upon calanoid copepods and euphausiids. Examinations of Sameoto (1989) off the subarctic region detected prey selectivity for copepods, especially Calanus finmarchicus and Calanus hyperboreus, which they hunt in the epi-pelagic zone during night. In this study two fish specimens contained calanoid copepods and euphausiids within their stomachs, together with unidentifiable crustacean fragments. Copepods serve as intermediate host for the tetraphyllidean cestode larvae and presumably for the bothriocephalidean cestode larvae, but regarding the low number of copepods and also a low prevalence of infection, B. glaciale seems to have minor importance within their life cycle.

4.1.2. Lampanyctus macdonaldi

Lampanyctus macdonaldi is a typical diurnal migration fish species, and Sutton et al. (2008) captured L. macdonaldi frequently between 1500 and 2300 m at the MAR. The examined specimens had no parasites. Parasite infestation is generally low in L. macdonaldi. Mauchline and Gordon (1984) recorded a single unidentified nematode in the stomach of 23 specimens at the Rockall Trough, while Gartner and Zwerner (1989) documented only one parasitic cyst in L. macdonaldi from the Norfolk Submarine Canyon. Klimpel et al. (2006) studied L. macdonaldi from the Irminger Sea and detected larval cestodes (Tetraphyllidea) and nematodes with low infestation rates. The absence of fish parasites in the specimens during the present study might be caused by the smaller size of our studied specimens from the MAR (11.6 cm mean SL) compared with those from the Irminger Sea (13.0 cm mean SL) and by a less diverse prey spectrum (e.g. Klimpel et al., 2006). This myctophid is an offshore species that is less exposed to fish parasites either from the shelf or from the sea floor (Klimpel et al., 2006).

4.1.3. Myctophum punctatum

Parasitological studies on the meso-pelagic M. punctatum are scarce (Klimpel et al., 2009). Hogans (1988) isolated the copepod S. scopeli on M. punctatum from Newfoundland waters. Recently, Klimpel et al. (2008b) investigated the parasite fauna of M. punctatum from the MAR and recorded four parasite species. The digenean genus Lethadena (Hemiuridae) occurred in the present study with only a single specimen. The life cycle of Lethadena species is entirely unknown. However, a heteroxenous life cycle with gastropods (molluscs) as first intermediate and pelagic invertebrates (e.g. copepods, euphausiids, chaetognaths) as second intermediate hosts is most common in the family Hemiuridae (Gibson, 2002).

Anisakis simplex (s.s.) and A. pegreffii, both A. simplex-complex, have been earlier recorded from northern and central parts of the MAR. Kellermanns et al. (2007) and Klimpel et al. (2007) found A. simplex (s.s.) in the deep-sea fishes Macrourus berglax (Fam. Macrouridae) and Maurolicus muelleri (Fam. Sternoptychidae), respectively. Mattiucci and Nascetti (2008) listed A. pegreffii and A. simplex (s.s.) from Trachurus spp. (Fam. Carangidae) and Scomber spp. (Fam. Scombridae) at the Azores and north-eastern Atlantic. Final hosts for both anisakids are cetaceans, seldom pinnipeds. Anisakis simplex (s.s.) parasitizes in the whale families Delphinidae, Monodontidae, Phocoenidae and Balaenopteridae, and has been genetically identified mainly in the North Atlantic and Pacific Oceans. Anisakis pegreffii utilizes the families Delphinidae, Ziphiidae, Physeteridae and Neobalaenidae as final hosts, with the main zoogeographical distribution in the entire Atlantic Ocean and Mediterranean Sea (Klimpel et al., 2008b; Mattiucci and Nascetti, 2008). These cetacean families frequently occur at the MAR during the studied sampling period (Doksæter et al., 2008; Skov et al., 2008).

4.2. Stomiidae

4.2.1. Chauliodus sloani

At the MAR C. sloani is frequently caught at a depth range between 750 and 2300 m (Sutton et al., 2008). Only a single larval tetraphyllidean cestode and one larval nematode Anisakis sp. (possibly A. simplex (s.s.) or A. pegreffii, see above) were found in the examined C. sloani. Gartner and Zwerner (1989) (Norfolk Submarine Canyon) and Klimpel et al. (2006) (Irminger Sea) documented also tetraphyllidean larvae, but with higher prevalences and intensities of infestation. The prevalence of 8.3% by Gartner and Zwerner (1989) for the Nematoda genus Anisakis is similar to our findings.

Chauliodus sloani prefers a piscivorous diet (Sutton and Hopkins, 1996). Williams et al. (2001) recorded Myctophiformes and Stomiiformes in the stomachs of C. sloani from the Sargasso Sea and adjacent waters, while Klimpel et al. (2006) found unidentified teleosts and cephalopods. Hopkins et al. (1996) concluded that juveniles of the genus Chauliodus feeds also on crustaceans. In the present study teleosts occurred with minor importance. Nearly all stomachs with prey (F=96.4%) contained unidentifiable 'tissue'. Chauliodus sloani might get infected with tetraphyllideans and Anisakis sp. as a paratenic host through preying upon fish.

4.3. Melamphaidae

4.3.1. Poromitra crassiceps

At the MAR this melamphaid species occurred with a high biomass in depths between 750 and 2300 m (Sutton et al., 2008). Parasitological records from P. crassiceps are still missing (Klimpel et al., 2009). Noble (1984) studied 17 specimens from the

Southern Ocean and could not detect any parasites. Our results also record a poor infection with metazoan parasites.

Hopkins et al. (1996) stated for the congener *Poromitra gibbsi* a mostly non-crustacean invertebrate prey preference. This corresponds with our data, because all stomachs contained unidentifiable 'tissue'. Following our record of L3 *Anisakis* sp. larvae (possibly *A. simplex* (s.s.) or *A. pegreffii*, see above) we can assume that *P. crassiceps* ingested Crustacea (e.g. calanoid copepods, euphausiids) that serve as obligatory intermediate hosts (Klimpel et al., 2004). The low infection rate indicates only minor importance of *P. crassiceps* for the life cycle of this nematode.

4.3.2. Scopelogadus beanii

Gartner and Zwerner (1989) examined 69 specimens from the western North Atlantic and detected seven different parasite species, including fungi, digeneans and nematodes. They isolated tetraphyllidean plerocercoid cestodes with a prevalence of 4.3%. Compared with the data from *S. beanii* from the MAR, tetraphyllidean larvae occurred at a similar low infestation rate. *S. beanii* gets infected with tetraphyllidean larvae while preying upon Crustacea and serves as intermediate host.

Gartner and Musick (1989) examined the stomach content of *S. beanii* from the western North Atlantic and found no evidence for vertical migration or ontogenetic difference in diet. The prey consisted mostly of Amphipoda and gelatinous zooplankton. Studies from the eastern North Atlantic (Rockall Trough) had been done by Mauchline and Gordon (1984). They found besides Crustacea (mainly Copepoda and Amphipoda) unidentifiable 'soft tissue' ($F=88.9\%$), which they assumed to be gelatinous zooplankton, such as salps. Our area of investigation (MAR) lies between these sample stations. Besides a small proportion of Amphipoda and unidentified Crustacea, unidentified 'tissue' occurred with a frequency of occurrence of 86.7% and supports the results of Mauchline and Gordon (1984) and Gartner and Musick (1989).

4.3.3. Scopelogadus mizolepis mizolepis

In the eastern Gulf of Mexico *S. m. mizolepis* preys on crustaceans (amphipods) and gelatinous zooplankton (e.g. tunicates, siphonophores). While smaller specimens mainly prefer crustaceans, this proportion shifts to gelatinous prey in the adult stage (Hopkins et al., 1996). *Scopelogadus m. mizolepis* from the MAR confirmed these results. While our examined specimens are larger than those of Hopkins et al. (1996) the stomach content consists mainly of unidentifiable 'tissue', maybe remains of gelatinous zooplankton, and to a smaller part of well digested crustaceans. Interestingly, in contrast to the related *S. beanii*, no parasites were found within the present study.

5. Conclusion

The host specificity of the recorded seven parasites from meso- and bathy-pelagic fishes was low, ranging from 5.574 (still metastenoxenous) to 9.485 (highly euryxenous). The only fish significant for accountable numbers of parasites was the mycto-phid *M. punctatum*, with a high prevalence of infestation for the both anisakid nematode species *A. simplex* (s.s.) and *A. pegreffii*. All other recorded fish helminths occurred only at very low numbers, appearing to be cases of accidental infection at the studied deep-sea locality. Consequently, while *M. punctatum* might play an important role for the completion of the life cycle of both *Anisakis* species in the mid-Atlantic, all other studied fish species have only a minor role for the existence of oceanic mid- and deep-water helminths at the MAR.

In general this result confirms earlier studies from other deep-sea localities on meso- and bathy-pelagic fishes, revealing only low numbers of parasites and species. So far, the MAR has not generated a specific parasite fauna within these hosts. One of the important questions to ask for fish parasitological studies within the region was the importance of the MAR for the distribution and possibly evolution of fish-specific parasites (see Palm and Klimpel, 2008). According to our results from the meso-/bathy-pelagic realm, the fishes from these environments harbour low host-specific parasites, without any distinct pattern of host–parasite co-evolution. Consequently, these fishes become accidentally infected through their extensive diel migrations.

Similar to recent results concerning invertebrate and fish distribution surrounding the MAR (e.g. Bergstad et al., 2008; Sutton et al., 2008), the possession of only low host specific parasites seems to be a common pattern in the deep Atlantic (compare Klimpel et al., 2009), and thus not locally restricted. Larvae of generalist parasite species can penetrate from the oceanic epi-pelagial into the deep-sea environment, not necessarily enhancing their success to complete their natural cycles (see Palm and Klimpel, 2008). Consequently, the MAR does not appear to be a barrier for the recorded parasite distribution within the meso- and bathy-pelagial of the North Atlantic, and parasitism seems to be more dependent on chance and accident than local biomass distribution. However, in the case of *M. punctatum* and both *Anisakis* species of the *A. simplex*-complex, this meso-pelagic fish might contribute to the parasite transfer of these nematodes into the cetacean final hosts, reflecting its uptake of the first intermediate host as well as its importance as prey organism (for cetaceans) in the central Atlantic Ocean. Consequently, the combination of fish feeding ecology, depth zonation and respective water masses still might play a significant role for specific meso- or bathy-pelagic fish parasite species distribution.

References

Amundsen, P.A., Gabler, H.M., Staldvik, F.J., 1996. A new approach to graphical analysis of feeding strategy from stomach contents data-modification of the Costello (1990) method. J. Fish Biol. 48, 607–614.

Anderson, R.C., 2000. Nematode Parasites of Vertebrates. Their Development and Transmission. CAB International, Wallingford, pp. 267–290.

Bergstad, O.A., Menezes, G., Høines, Å.S., 2008. Demersal fish on a mid-ocean ridge: distribution patterns and structuring factors. Deep-Sea Res. II 55, 185–202.

Boxshall, G.A., 1998. Host specificity in copepod parasites of deep-sea fishes. J. Mar. Syst. 15, 215–223.

Busch, M.W., Klimpel, S., Sutton, T., Piatkowski, U., 2008. Parasites of the deep-sea smelt *Bathylagus euryops* (Argentiniformes: Microstomatidae) from the Charlie-Gibbs Fracture Zone (CGFZ). Mar. Biol. Res. 4, 313–317.

Bush, O., Lafferty, A.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83, 575–583.

Caira, J.N., Jensen, K., Holsinger, K.E., 2003. On a new index of host specificity. In: Combes, C., Jordan, J. (Eds.), Taxonomy, Ecology, and Evolution of Metazoan Parasites. Tome I (Livre hommage à Louis Euzet). PUP Presses, Perpignan, France, pp. 161–201.

Campbell, R.A., 1990. Deep water parasites. Ann. Parasitol. Hum. Comp. 65, 65–68.

Cherel, Y., Boxshall, G.A., 2004. *Sarcotretes* (Copepoda: Pennelidae) parasitizing myctophid fishes in the Southern Ocean: new information on seabird diet. J. Parasitol. 90, 1288–1292.

Doksæter, L., Olsen, E., Nøttestad, L., Fernö, A., 2008. Distribution and feeding ecology of dolphins along the Mid-Atlantic Ridge between Iceland and the Azores. Deep-Sea Res. II 55, 243–253.

Dotinga, H., Molenaar, E.J., 2008. The Mid-Atlantic Ridge: A Case Study on the Conservation and Sustainable Use of Marine Biodiversity in Areas Beyond National Jurisdiction. IUCN, Gland, Switzerland.

Euzet, L., 1994. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, pp. 149–194.

Fiedler, P.C., Barlow, J., Gerrodette, T., 1998. Dolphin prey abundance determined from acoustic backscatter data in eastern Pacific surveys. Fish. Bull. 96, 237–247.

Fock, H.O., Pusch, C., Ehrich, S., 2004. Structure of deep-sea pelagic fish assemblages in relation to the Mid-Atlantic Ridge (45–50°N). Deep-Sea Res. I 51, 953–978.

Froese, R., Pauly, D., 2009. Fishbase. World Wide Web electronic publication. Available from: ⟨www.fishbase.org⟩, version (09/2009).

Gaard, E., Gislason, A., Falkenhaug, T., Søiland, H., Musaeva, E., Vereshchaka, A., Vinogradov, G., 2008. Horizontal and vertical copepod distribution and abundance on the Mid-Atlantic Ridge in June 2004. Deep-Sea Res. II 55, 59–71.

Gartner, J.V., Musick, J.A., 1989. Feeding habits of the deep-sea fish, *Scopelogadus beanii* (Pisces: Melamphaidae), in the western North Atlantic. Deep-Sea Res. 36, 1457–1469.

Gartner, J.V., Zwerner, D.E., 1989. The parasite faunas of meso- and bathypelagic fishes of Norfolk Submarine Canyon, western North Atlantic. J. Fish Biol. 34, 79–95.

Gibson, D.I., 2002. In: Gibson, D.I., Jones, A., Bray, R.A. (Eds.), Keys to the Trematoda, vol. 1. CAB International, Wallingford pp. 305–340.

Hogans, W.E., 1988. Review of *Sarcotretes* Jungersen, 1911 (Copepoda: Pennellidae) from midwater and demersal fishes in the North Atlantic Ocean. Can. J. Zool. 66, 1371–1375.

Hopkins, T.L., Sutton, T.T., Lancraft, T.M., 1996. The trophic structure and predation impact of a low latitude midwater fish assemblage. Prog. Oceanogr. 38, 205–239.

Hyslop, E.J., 1980. Stomach content analysis – a review of methods and their application. J. Fish Biol. 17, 411–429.

Justine, J.L., Cassone, J., Petter, A., 2002. *Moravecnema segonzaci* gen. et sp. n. (Nematoda: Cystidicolidae) from *Pachycara thermophilum* (Zoarcidae), a deep-sea hydrothermal vent fish from the Mid-Atlantic Ridge. Folia Parasitol. 49, 299–303.

Kellermanns, E., Klimpel, S., Palm, H.W., 2007. Molecular identification of ascaridoid nematodes from the deep-sea onion-eye grenadier (*Macrourus berglax*) from the East Greenland Sea. Deep-Sea Res. I 54, 2194–2202.

Kellermanns, E., Klimpel, S., Palm, H.W., 2009. Parasite fauna of the Mediterranean grenadier *Coryphaenoides mediterraneus* (Giglioli, 1893) from the Mid-Atlantic Ridge (MAR). Acta Parasitol. 54 (2), 158–164.

Klimpel, S., Palm, H.W., Rückert, S., Piatkowski, U., 2004. The life cycle of *Anisakis simplex* in the Norwegian Deep (northern North Sea). Parasitol. Res. 94, 1–9.

Klimpel, S., Palm, H.W., Busch, M.W., Kellermanns, E., Rückert, S., 2006. Fish parasites in the Arctic deep-sea: poor diversity in pelagic fish species vs. heavy parasite load in a demersal fish. Deep-Sea Res. I 53, 1167–1181.

Klimpel, S., Kellermanns, E., Palm, H.W., Moravec, F., 2007. Zoogeography of fish parasites of the pearlside (*Maurolicus muelleri*), with genetic evidence of *Anisakis simplex* (s.s.) from the Mid-Atlantic Ridge. Mar. Biol. 152, 725–732.

Klimpel, S., Palm, H.W., Busch, M.W., Kellermanns, E., 2008a. Fish parasites in the bathyal zone: the halosaur *Halosauropsis macrochir* (Günther, 1878) from the Mid-Atlantic Ridge. Deep-Sea Res. II 55, 229–235.

Klimpel, S., Kellermanns, E., Palm, H.W., 2008b. The role of pelagic swarm fish (Myctophidae: Teleostei) in the oceanic life cycle of *Anisakis* sibling species at the Mid-Atlantic Ridge, Central Atlantic. Parasitol. Res. 104, 43–53.

Klimpel, S., Busch, M.W., Kellermanns, E., Kleinertz, S., Palm, H.W., 2009. Metazoan deep-sea fish parasites. Acta Biologica Benrodis (Suppl. 11), Verlag Natur & Wissenschaft, Solingen, pp. 1–384.

Kritsky, D.C., Klimpel, S., 2007. *Cyclocotyloides bergstadi* n. sp. (Monogenoidea: Diclidophoridae: Diclidophoropsinae) from the gills of grenadier, *Coryphaenoides brevibarbis* (Teleostei: Macrouridae), in the northeast Atlantic Ocean. Comp. Parasitol. 74, 23–30.

Kuchta, R., Scholz, T., Bray, R., 2008. Suppression of tapeworm order Pseudophyllidea (Plathyhelminthes: Eucestoda) and the proposal of two new orders, Bothriocephalidea and Diphyllobothriidea. Int. J. Parasitol. 38, 49–55.

Marcogliese, D.J., 2002. Food webs and the transmission of parasites to marine fish. Parasitology 124, 83–99.

Mattiucci, S., Nascetti, G., 2008. Advances and trends in the molecular systematics of anisakid nematodes, with implications for their evolutionary ecology and host–parasite co-evolutionary processes. Adv. Parasitol. 66, 47–148.

Mauchline, J., Gordon, J.D.M., 1984. Incidence of parasitic worms in stomachs of pelagic and demersal fish at the Rockall Trough, northeastern Atlantic Ocean. J. Fish Biol. 24, 281–285.

Moravec, F., Klimpel, S., 2007. A new species of *Comephoronema* (Nematoda: Cystidicolidae) from the stomach of the abyssal halosaur *Halosauropsis macrochir* (Teleostei) from the Mid-Atlantic Ridge. J. Parasitol. 93, 901–906.

Moravec, F., Klimpel, S., 2009. Two new species of cystidicolid nematodes from the digestive tract of the deep-sea fish *Coryphaenoides mediterraneus* (Giglioli) (Macrouridae) from the Mid-Atlantic Ridge. Syst. Parasitol. 73, 37–47.

Noble, E.R., 1973. Parasites and fishes in a deep-sea environment. Adv. Mar. Biol. 11, 121–195.

Noble, E.R., 1984. Ecologic aspects of protozoan infections in Antarctic fishes. J. Protozool. 31 (4), 575–577.

Palm, H.W., Klimpel, S., 2008. Metazoan fish parasites of *Macrourus berglax* Lacepède, 1801 and other macrourids of the North Atlantic: invasion of the deep sea from the continental shelf. Deep-Sea Res. II 55, 236–242.

Pinkas, L., Oliphant, M.D., Iverson, I.L.K., 1971. Food habits of albacore, bluefin tuna and bonito in Californian Waters. Calif. Fish Game 152, 1–105.

Sameoto, D., 1989. Feeding ecology of the lantern fish *Benthosema glaciale* in a subarctic region. Polar Biol. 9, 169–178.

Skov, H., Gunnlaugsson, T., Budgell, W.P., Horne, J., Nøttestad, L., Olsen, E., Søiland, H., Víkingsson, G., Waring, G., 2008. Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. Deep-Sea Res. II 55, 254–268.

Stemmann, L., Hoisa, A., Youngbluth, M.J., Søiland, H., Picheral, M., Gorsky, G., 2008. Vertical distribution (0–1000 m) of macrozooplankton, estimated using the Underwater Video Profiler, in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge. Deep-Sea Res. II 55, 94–105.

Sutton, T.T., Hopkins, T.L., 1996. Trophic ecology of the stomiid (Pisces, Stomiidae) assemblage of the eastern Gulf of Mexico: strategies, selectivity and impact of a mesoelagic top predator group. Mar. Biol. 127, 179–192.

Sutton, T.T., Porteiro, F.M., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C.I.H., Horne, J., Søiland, H., Falkenhaug, T., Godø, O.R., Bergstad, O.A., 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. Deep-Sea Res. II 55, 161–184.

Thompson, J.D., Higgins, D.G., Gibson, T.J., 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. Nucleic Acids Res. 22, 4673–4680.

Vinogradov, G.M., 2005. Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible "Mir-1". Mar. Biol. 146, 325–331.

Wang, M.C., Walker, W.A., Shao, K.T., Chau, L.S., 2003. Feeding habits of the pantropical Spotted Dolphin, *Stenella attenuata*, off the eastern coast of Taiwan. Zool. Stud. 42, 368–378.

Wenneck, T.L., Falkenhaug, T., Bergstad, O.A., 2008. Strategies, methods and technologies adopted on the RV *G.O. Sars* MAR-ECO expedition to the Mid-Atlantic Ridge in 2004. Deep-Sea Res. II 55, 6–28.

Williams, A., Koslow, J.A., Terauds, A., Haskard, K., 2001. Feeding ecology of five fishes from the mid-slope micronecton community off southern Tasmania, Australia. Mar. Biol. 139, 1177–1192.

Zhu, X., Gasser, R.B., Jacobs, D.E., Hung, G.C., Chilton, N.B., 2000. Relationships among some ascaridoid nematodes based on ribosomal DNA sequence data. Parasitol. Res. 86, 738–744.