

# Demersal fish parasite fauna around the South Shetland Islands: high species richness and low host specificity in deep Antarctic waters

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**Abstract** A total of nine Antarctic fish species belonging to five families were examined for their endohelminth parasite fauna. The fishes *Parachaenichthys charcoti* (Bathydraconidae), *Chaenocephalus aceratus* (Channichthyidae), *Paradiplospinus gracilis* (Gempylidae), *Muraenolepis microps* (Muraenolepididae), *Gobionotothen gibberifrons*, *Lepidonotothen larseni*, *L. nudifrons*, *L. squamifrons*, and *Trematomus eulepidopus* (Nototheniidae) were caught between 80 and 608 m trawling depth off the Antarctic Peninsula (Elephant Island, King George Island) in 1996. Nineteen different parasites species comprising five Digenea, two Cestoda, four Nematoda, and eight Acanthocephala were found. Pseudophyllidean cestodes, the nematodes *Contracaecum radiatum* and *C. osculatum* as well as the acanthocephalan *Corynosoma bullosum* were the most common, infesting eight of the fish species studied with prevalences reaching 100%. *Pseudoterranova decipiens* s.l. was the only parasite that was isolated from all studied fish species; however, at a lower intensity. The observed parasite host specificity was low, and the species richness in a single fish ranged from one to eleven in a *C. aceratus*. This icefish and the moray cod *M. microps* were the most heavily infested fish, harbouring many adult and larval parasitic stages. The benthodemersal *P. gracilis* had only two larval parasite species, while the nototheniids had very similar parasite communities, harbouring a total of 8–14 species.

Larval mammalian parasites were found to utilize fish, especially the nototheniids and channichthyids, as a common transmission route into their final hosts. The fish parasites parallel explored different benthic host systems to reach the most suitable host. In contrast to the coast and continental shelf, the meso/bathypelagic zone appears to be species poor and is inhabited by few larval forms. The fish parasite fauna off the South Shetland Islands can be characterized by generalistic parasites that distribute within Antarctic waters according to the feeding ecology and depth range of their teleost hosts, not only horizontally but also extending vertically into the deep sea.

**Keywords** Antarctic fishes · Distribution · Endemic parasites · Cosmopolitan parasites · Generalist · Parasite diversity · Host specificity · South Shetland Islands · Transmission · Zoogeography · Food web

## Introduction

The Southern Ocean consists of the southern parts of the Pacific, Indian and Atlantic oceans, with the southern boundary being the Antarctic continent. The northern border is not physio-geographically fixed, but the Antarctic Polar Frontal Zone (APFZ) with its sharp and strong horizontal gradients in a number of parameters is taken as the northern boundary. Since the locations of the continents and the deep-sea ridges directly influence circulation patterns and water exchange below 3,000 m between basins, they may have a decisive influence on the biogeography of some of the typical Antarctic fish species (Gon and Heemstra 1990) as well as their parasite fauna.

One of the basins is situated at the Antarctic Peninsula with their Islands such as Elephant and King George Island

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(both in the South Shetlands Islands Group), located north of the peninsula. They are parts of the low-Antarctic province or seasonal pack-ice zone (Kock 1992). Krill and Antarctic fish species are considered the key species of the marine food web in the area. With currently 322 recognized fish species, the Antarctic fish fauna is generally dominated by the perciform suborder Notothenioidei (Kock 2005a, b; Froese and Pauly 2007), which dominates species in shelf waters down to 500 m water depth (Flores et al. 2004). The composition of the inshore and offshore coastal fish fauna in the vicinity of Elephant Island consists of two ichthyofaunistic elements, (1) species of the low-Antarctic and (2) species of the high-Antarctic environment. Low-Antarctic nototheniids and some channichthyids are the predominant bottom fish fauna, and high-Antarctic species are quite abundant in water depths below 300 m (Kock and Stransky 2000).

The composition of the inshore and offshore fish fauna, fish biomass, zoogeographical distribution, feeding ecology and reproduction is comparatively well known (e.g. Kock and Stransky 2000; Flores et al. 2004; Bushula et al. 2005; Eastman 2005; Kock 2005a, b). In contrast, the knowledge on high Antarctic fish parasites in the Southern Ocean is missing information on the parasite ecology, life-cycle strategies and parasite distribution (e.g. Holloway and Spence 1980; Klöser et al. 1992; Palm et al. 1994, 1998; Palm 1999). Furthermore, most studies have been carried out on notothenioids from shallow coastal waters or the open sea shelf (e.g. Zdzitowiecki 1991a, 1997), and only a portion of the known Antarctic fish fauna has been studied for parasites. Fish parasitological investigations along the Antarctic continental slope and the deep-sea are restricted to single species, such as the rattail *Macrourus whitsoni* (Walter et al. 2002) or the horizontal and vertical distribution of *Pseudoterranova decipiens s.l.* (Palm et al. 1994; Palm 1999; Zhu et al. 2002). Most recent parasitological studies from the Antarctic Peninsula and the eastern Weddell-Sea revealed a rich parasite fauna in some nototheniid and channichthyid fish that include endemic and non-cosmopolitan parasite species (e.g. Palm et al. 1998; Zdzitowiecki and Laskowski 2004; Brickle et al. 2005; Rocka 2006).

Other examples of parasitological investigations of different Antarctic fish species are the recent publications of e.g. Rocka (2002, 2003, 2004), Rocka and Zdzitowiecki (1998), Wojciechowska (1991), Wojciechowska et al. (1994), Zdzitowiecki (1990, 1991b, 1996), Zdzitowiecki and Laskowski (2004) and Zdzitowiecki and Pisano (1996). The Polish researchers characterized the digenean, cestode, nematode and acanthocephalan parasite fauna of different bony fishes and elasmobranchs. Rocka (2006) summarised the available information about the life-cycle biology, specificity and geographical distribution of the parasitic helminth groups Digenea, Cestoda, Nematoda and

Acanthocephala of Antarctic bony fishes and elasmobranchs. The author stated that almost all of the helminth species maturing in Antarctic bony fishes are endemic, whereas only extremely few parasite species are cosmopolitan or bipolar. Specificity in the intermediate or paratenic hosts of the majority of Antarctic helminths is wide, whereas it is often narrower for the definitive host (Rocka 2006). However, the overall distribution pattern of the fish parasites within the different Antarctic fish species and regions was not addressed, allowing no further judgement on the patterns and processes of inner Antarctic parasite species distribution. In addition, information on the annual and seasonal variability of fish parasitic infestation in the high Antarctic is completely missing.

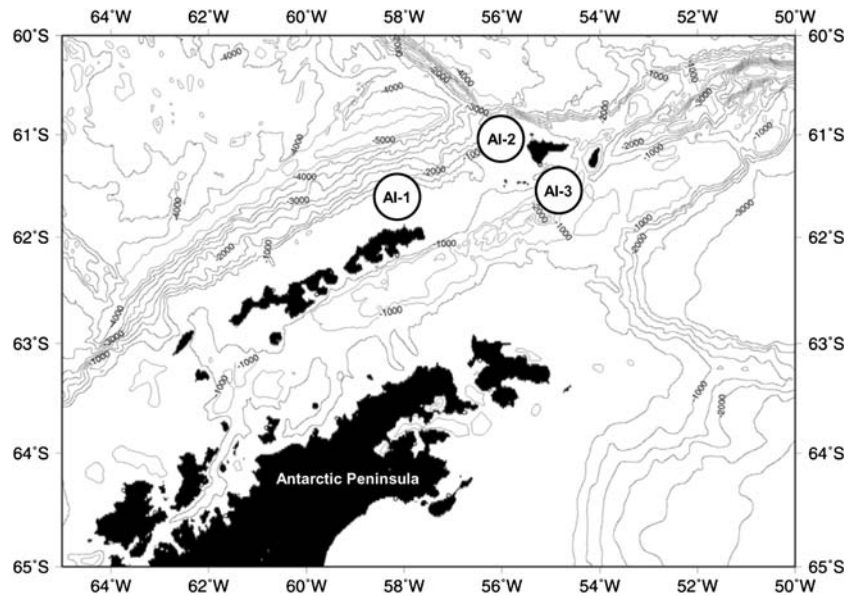
The purpose of the present study is the description and analysis of the endohelminth parasite fauna of nine different fish species from the South Shetland Islands. This will enable future comparative studies on the long-term variation of parasite infestation patterns within that region. Special attention is given to the overlapping infestation patterns of the detected parasite species, allowing comments to be made on the host specificity and life cycle ecology. A model is developed to illustrate the common pathways and transmission routes of parasitic helminths through the Antarctic food web, involving fish as intermediate as well as final hosts.

## Materials and methods

### Sample collection

A total of 199 fish belonging to 9 species and 5 families were sampled between November and December 1996 on board of the German research vessel Polarstern (research cruise ANT XIV/2) during the field phase of the international project "Convention for the Conservation of Antarctic Marine Living Resources" (CCAMLR) to the South Shetland Islands (King George Island (area of investigation AI-1) and Elephant Island (area of investigation AI-2 and AI-3)) (Fig. 1). The fishes were caught with a bottom trawl and a benthopelagic net with a towing time of 30 min. The following fishes were collected around Elephant Island between 80–480 m water depth: *Parachaenichthys charcoti* (Vaillant, 1906) (Bathydraconidae) in AI-2 and AI-3, *Chaenocephalus aceratus* (Lönnberg, 1906) (Channichthyidae) in AI-1 to AI-3, *Muraenolepis microps* Lönnberg, 1905 (Muraenolepididae) in AI-2 and AI-3, *Gobionotothen gibberifrons* (Lönnberg, 1905) in AI-2, *Lepidonotothen larseni* (Lönnberg, 1905) in AI-2, *L. nudifrons* (Lönnberg, 1905) in AI-2 and AI-3, *L. squamifrons* (Günther, 1880) in AI-3, and *Trematomus eulepidotus* Regan, 1914 (Nototheniidae) in AI-2 and AI-3. *Paradiplospinus gracilis* (Brauer, 1906) (Gempylidae) was

**Fig. 1** Map of the area of investigation (AI). AI-1 King George Island, AI-2 and AI-3 Elephant Island



collected North-west of King George Island between 555 and 608 m using a benthopelagic net in the AI-1. All fishes were deep frozen at  $-40^{\circ}\text{C}$  immediately after capture for subsequent examination. Prior to examination each fish specimen was defrosted to  $0-1^{\circ}\text{C}$ . Morphometrical data such as total length (TL) and total weight (TW) were recorded to the nearest 1 cm and 1 g (Table 1). Fishes were identified according to Gon and Heemstra (1990).

#### 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. Isolated parasites were fixed in 4% borax-buffered formalin and preserved in 70% ethanol/5% glycerine. Acanthocephalans were transferred to freshwater until the proboscis everted prior to fixation. For identification purposes, nematodes and acanthocephalans 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 parasitological terminology used follows Bush et al. (1997): where prevalence

**Table 1** Number ( $n$ ), mean total length, mean total weight (range in parentheses) and depth of the studied South Shetland fish species

Fish species	$n$ examined	Total length (cm)	Total weight (g)	Sampling depth (m)
Bathypagrus				
<i>Parachaenichthys charcoti</i>	12	17(11–26)	21(4–68)	80–212
Channichthyidae				
<i>Chaenocephalus aceratus</i>	21	36(22–49)	276(37–589)	120–410
Gempylidae				
<i>Paradiplospinus gracilis</i>	11	41(37–45)	81(45–103)	555–608
Muraenolepididae				
<i>Muraenolepis microps</i>	12	31(22–40)	317(84–650)	216–480
Nototheniidae				
<i>Gobionotothen gibberifrons</i>	12	37(31–43)	560(289–830)	167–173
<i>Lepidonotothen larseni</i>	51	14(8–19)	18(4–50)	145–171
<i>L. nudifrons</i>	40	12(6–17)	18(2–52)	157–212
<i>L. squamifrons</i>	31	18(11–24)	65(12–207)	280–300
<i>Trematomus eulepidopus</i>	9	22(20–25)	147(108–228)	216–355
Total	199			
Range				80–608

(P) is the number of infected fish with one or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined (expressed as a percentage); intensity (of infection, I) is the number of individuals of a particular parasite species in a single infected host (expressed as a numerical range); and mean intensity (of infection, mI) is the average intensity, in other words, it is the total number of parasites of a particular species found in a sample divided by the number of infected hosts. Furthermore, we use the following parasitological terms and definitions: (1) Final host—where a parasite reaches sexual maturity, (2) Intermediate host—required by a parasite to complete its life-cycle, usually it undergoes considerable morphological or physiological change, (3) Paratenic host/transport host—not required by a parasite to complete its life-cycle, without detectable morphological change.

## Results

The analysis of nine fish species belonging to five Antarctic fish families from the South Shetland Islands revealed a high parasite richness and host range. A total of 19 different parasite species/taxa were found, and most parasites infested more than one host species up to all nine studied fish species. The real parasite number might be even higher, considering that pseudophyllidean and tetraphyllidean cestodes are a composite of species, and *Metacanthocephalus* spp. and *Corynosoma* spp. represent acanthocephalan specimens with inverted proboscides that also might represent additional species. The number (*n*), mean total length, mean total weight (range) and depth of the studied fish species as well as the prevalence, intensity, and mean intensity of infestation for each parasite and fish species are given in Tables 1 and 2.

### Parasite composition

#### *Muraenolepis microps*

The parasite fauna of *M. microps* consisted of 14 different parasite species (Table 2). The predominant parasites were adult Acanthocephala and larval Nematoda. The digeneans *Discoverytrema gibsoni* and *D. markowskii* were adult and located in the digestive tract. Two larval Cestoda (Pseudophyllideae indet., Tetraphyllideae indet. (*Scolex pleuronectis*)) were detected with low infestation rates in the digestive tract. Species identification, however, cannot be provided in the larval stage due to the lack of a fully developed scolex and genitalia. The genetic identification of these larval stages is still at the beginning. Three Nematoda, *Contracaecum osculatum*, *C. radiatum* and *Pseudoterranova decipiens* s.l. (or *P. decipiens* sibling species E, after Zhu et al. 2002) were found. All nematodes were isolated as larval stages and

were found exclusively in or on the organs of the body cavity. The adult stages of *Aspersentis megarhynchus*, *Echinorhynchus petrotschenkoii*, *Heterosentis heteracanthus*, *Metacanthocephalus dalmori* and *Metacanthocephalus* spp. (Acanthocephala) and the larval stages of *Corynosoma bullosum* and *Corynosoma* spp. were located in the intestine and body cavity, respectively. *M. microps* usually carried 2–9 (mean 6.2) different parasite species (Fig. 2).

#### *Parachaenichthys charcoti*

Eleven parasite species were isolated from *P. charcoti* (Table 2). The adult stage of the Digenea *Lecithaster macrocotyle* was located in the intestine. Two larval Cestoda (Pseudophyllideae indet., Tetraphyllideae indet. (*Scolex pleuronectis*)) were detected in the stomach, intestine and on organs of the body cavity. Four Nematoda, *Ascarophis nototheniae*, *Contracaecum osculatum*, *C. radiatum* and *Pseudoterranova decipiens* s.l. were found. *A. nototheniae* were isolated as adult stages from the stomach lumen, while the other three nematodes were isolated exclusively as larval stages in or on the organs of the body cavity and in the liver. The Acanthocephala *Aspersentis megarhynchus* and *Metacanthocephalus* spp. were found as adults in the intestine; while the cystacanths of *Corynosoma bullosum* and *Corynosoma* spp. were isolated as larvae from the body cavity. *P. charcoti* usually carried 1–7 (mean 3.3) different parasite species (Fig. 2).

#### *Chaenocephalus aceratus*

A total of 16 parasite species were collected from the examined fish (Table 2). The predominant parasites were the Acanthocephala with seven identified species. The adult stages of the Digenea *Gonocerca phycidis*, *Lecithaster macrocotyle* and *Neolebouria antarctica* were isolated from the digestive tract. The both larval Cestoda (Pseudophyllideae indet., Tetraphyllideae indet. (*Scolex pleuronectis*)) were located in the body cavity, digestive tract and the liver. *Ascarophis nototheniae* (Nematoda) was adult and inhabited the stomach lumen, while the larval Nematoda *Contracaecum osculatum*, *C. radiatum* and *Pseudoterranova decipiens* s.l. were in or on the organs of the body cavity and in the liver. Specimens belonging to the Acanthocephala genus *Corynosoma* were isolated as cystacanths from the organs of the body cavity, while the species of the genus *Metacanthocephalus* were found as adult stages in the intestine. *C. aceratus* usually carried 1–11 (mean 7.1) different parasite species (Fig. 2).

#### *Paradiplospinus gracilis*

Only two parasite species were found in the *P. gracilis* examined: one larval Cestoda and one larval Nematoda

**Table 2** Prevalence (P), mean intensity (mI), and intensity (I) of infestation of the South Shetland fish species

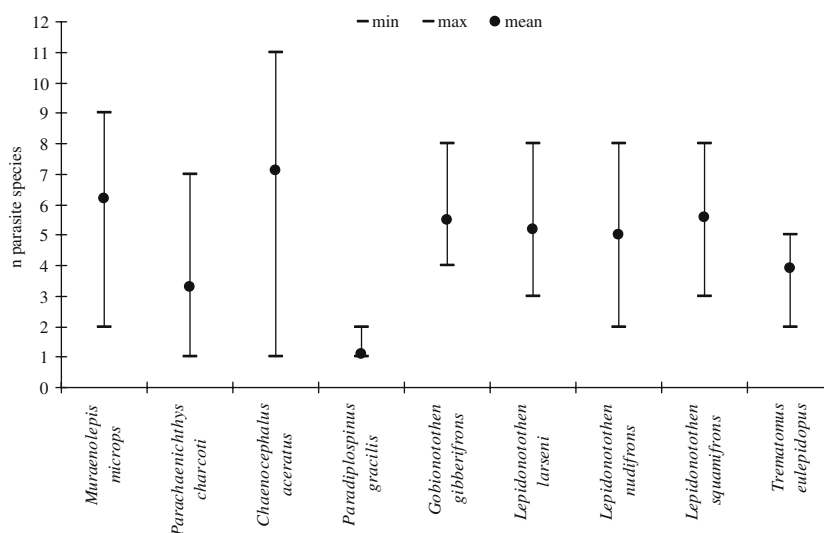
Parasite species	adult/		Fish species											
	larva		<i>Muraenolepis microps</i>	<i>Parachaenichthys charcoti</i>	<i>Chaenocephalus aceratus</i>	<i>Paradiplospinus gracilis</i>	<i>Gobionotothen gibberifrons</i>	<i>Lepidonotothen larseni</i>	<i>Lepidonotothen mudifrons</i>	<i>Lepidonotothen squamifrons</i>	<i>Trematomus eulepidotus</i>			
		P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	P%/ml (I)	
<b>Digenea</b>														
<i>Discoverytrema gibsoni</i>	a	92/15(1–54) <sup>b</sup>												
<i>Discoverytrema markowskii</i>	a	67/7(1–46) <sup>b</sup>												
<i>Gonocerca phycidis</i>	a		14/5(1–12)											
<i>Lecithaster macrocoyle</i>	a		9/4(1–7)				31/2(1–4)	33/2(1–5)						
<i>Neolebouria antarctica</i>	a		33/1(1–2)				2/3(3)	5/1(1)	6/1(1)			11/1(1)		
<i>Digenea indet.</i>	a	67/3(1–8)	5/2(2)				2/5(5)	33/2(1–4)				11/1(1)		
<b>Cestoda</b>														
<i>Pseudophyllidea indet.</i>	l	17/2(2) <sup>a</sup>	86/71(1–364)				92/19(1–100) <sup>a</sup>	25/2(1–4) <sup>a</sup>	19/1(1–2)			100/6(2–16) <sup>a</sup>		
<i>Tetraphyllidea indet</i>	l	25/4(1–8)	57/8(1–55)		100/11(2–30)		6/1(1–2)	8/1(1)				11/1(1)		
<b>Nematoda</b>														
<i>Ascarophis nototheniae</i>	a		38/2(1–9)	25/2(1–9) <sup>a</sup>			49/2(1–6) <sup>a</sup>	83/6(1–28) <sup>a</sup>	94/5(1–13)					
<i>Contracaecum osculatium</i>	l	42/1(1–3) <sup>a</sup>	71/29(1–91) <sup>a</sup>	8/1(1) <sup>a</sup>			39/2(1–3) <sup>a</sup>	15/1(1) <sup>a</sup>	74/3(1–7) <sup>a</sup>			78/3(1–5)		
<i>Contracaecum radiatum</i>	l	58/11(1–36) <sup>a</sup>	90/80(1–493) <sup>a</sup>	92/5(1–15) <sup>a</sup>			94/6(1–17) <sup>a</sup>	88/5(1–22) <sup>a</sup>	100/6(1–44) <sup>a</sup>			89/6(1–21)		
<i>Pseudoterranova decipiens</i>	l	50/10(1–26)	95/55(2–194)	83/6(1–15)	9/1(1)		94/4(1–12)	43/1(1–2)	55/1(1–3)			22/1(1–3)		
<i>Nematoda indet.</i>	l	33/6(1–14)	43/8(1–37)	17/1(1–2)			92/6(1–31)	90/8(1–41)	97/8(1–21)			100/13(3–27)		
<b>Acanthocephala</b>														
<i>Aspersentis megarhynchus</i>	a	8/1(1) <sup>a</sup>		8/1(1)					6/1(1)					
<i>Corynosoma arctocephali</i>	l		29/2(1–5)						10/1(1)					
<i>Corynosoma bullosum</i>	l	92/7(1–45)	76/14(1–63)	33/1(1–2)			59/2(1–7)	55/2(1–8)	100/9(1–25)			11/1(1)		
<i>Corynosoma hammami</i>	l		10/1(1)				2/1(1)							
<i>Corynosoma shacletoni</i>	l		5/1(1)				2/1(1)							
<i>Corynosoma</i> spp.	l	92/19(2–47)	62/17(1–70)	17/1(1)			10/2(1–5)	5/1(1)	81/73(1–6)			11/1(1)		
<i>Echinorhynchus petrotschenkoi</i>	a	17/5(1–8)												
<i>Heterosentis heteracanthus</i>	a	8/1(1) <sup>a</sup>												
<i>Metacanthocephalus dalmani</i>	a	8/6(6) <sup>a</sup>	29/3(1–5)				22/2(1–6)	80/4(1–14)						
<i>Metacanthocephalus</i> spp.	a	25/5(3–9)	20/3(1–7)	8/2(2)			8/1(1)	35/3(1–8)	13/1(1)			22/1(1)		

Data for *Pseudoterranova decipiens* taken from Palm (1999)

<sup>a</sup> New host record, <sup>b</sup> new locality record



**Fig. 2** Number of parasite species ( $n$ ) in mean (filled circle), minimum and maximum value (verticle line) are given



(Table 2). The predominant parasite was Tetracystidae indet. (*Scolex pleuronectis*) (Cestoda), and was found to inhabit the pyloric caeca and the intestine. The third stage larvae of the anisakid Nematoda *P. decipiens s.l.* was encapsulated in the body cavity. *P. gracilis* usually carried 1–2 (mean 1.1) different parasite species (Fig. 2).

#### *Gobionotothen gibberifrons*

A total of eight species were recovered, interestingly the Digenea were not represented (Table 2). Only a single larval Cestoda (Pseudophyllidea indet.) was detected in the digestive tract and was isolated from the organs of the body cavity. Adult stages of the Nematoda *Ascarophis nototheniae* were located in the stomach lumen and the intestine, while the larval stages of *Contracaecum osculatum*, *C. radiatum* and *Pseudoterranova decipiens s.l.* were found in or on the organs of the body cavity. Cystacanths of the Acanthocephala *Corynosoma bullosum* and *Corynosoma* spp. were found in the body cavity, and adult *Metacanthocephalus dalmori* were located in the intestine. *G. gibberifrons* usually carried 4–8 (mean 5.5) different parasite species (Fig. 2).

#### *Lepidonotothen larseni*, *L. nudifrons*, *L. squamifrons*

The parasite fauna of the three *Lepidonotothen* species were similar and reflected the same ecological requirements, such as similar feeding behaviour, depth range and habitat. The parasite fauna varied from 14 parasite species in *L. larseni*, 12 in *L. nudifrons* and 11 in *L. squamifrons* (Table 2). The adult Digenea *Lecithaster macrocotyle* and *Neolebouria antarctica* were located in the pyloric caeca and the intestine. Two larval Cestoda (Pseudophyllidea indet., Tetracystidae indet. (*Scolex pleuronectis*)) were detected in the stomach lumen, the intestine or on the

organs of the body cavity. Three larval (*Contracaecum osculatum*, *C. radiatum*, *Pseudoterranova decipiens s.l.*) and one adult Nematoda (*Ascarophis nototheniae*) were found. The larval stages were found exclusively in or on the organs of the body cavity, while the adult stages were isolated from the stomach lumen. Larval Acanthocephala stages (cystacanths) of the genus *Corynosoma* were isolated from the body cavity and adult *Metacanthocephalus* spp. and *Aspersentis megarhynchus* were located in the intestine. *L. larseni*, *L. nudifrons* and *L. squamifrons* usually carried 3–8 (mean 5.2), 2–8 (mean 5.0) and 3–8 (5.6) parasite species, respectively (Fig. 2).

#### *Trematomus eulepidopus*

The parasite fauna of *T. eulepidopus* consisted of 9 parasite species (Table 2). Only the digenean *Neolebouria antarctica* was found as an adult in the pyloric caeca. Both Cestoda larvae Pseudophyllidea indet. and Tetracystidae indet. (*Scolex pleuronectis*) were isolated from the organs of the body cavity and the intestinal lumen, respectively. Larval Nematoda, *Contracaecum osculatum*, *C. radiatum* and *Pseudoterranova decipiens s.l.* were isolated exclusively from the organs of the body cavity. Cystacanths of the Acanthocephala *Corynosoma bullosum* and *Corynosoma* spp. were found in the body cavity, and adult *Metacanthocephalus* spp. were isolated from the intestine. *T. eulepidopus* usually carried 2–5 (mean 3.9) different parasite species (Fig. 2).

## Discussion

The nine fish species studied from the South Shetland Islands revealed high parasite diversity. A total of 19 different parasite species/taxa were found, belonging to the Dige-

nea (5), Cestoda (2), Nematoda (4), and Acanthocephala (8). The fish were infested with both, larval and adult parasites, thus being the final host for the digeneans, the nematode *Ascarophis nototheniae*, and four acanthocephalans. While the tetraphyllidean cestode larvae infest Antarctic elasmobranchs as adults (e.g. *Amblyraja* spp. and *Bathyraja* spp.), the pseudophyllideans are typical parasites of seals and whales (Rocka 2003; Balbuena and Raga 2006). The acanthocephalans *Corynosoma* spp. as well as the nematodes *Contracaecum* spp. and *Pseudoterranova decipiens* s.l. are typical parasites of the abundant seals in the area, such as the Weddell seal *Leptonychotes weddellii* (e.g. Burns et al. 1998; Klöser et al. 1992; Klöser and Plötz 1992; Palm 1999).

The parasite species richness of the fish studied varied from 1 to 2 in *Paradiplospinus gracilis* to a mean of 7 in the icefish *Chaenocephalus aceratus*. In general, the marine fish parasite fauna is determined by the feeding ecology, the availability of intermediate and final hosts, the host's depth range and migration (Klimpel et al. 2003, 2006a, b), and less importantly by the host's phylogeny (Jakob and Palm 2006). The high species richness with up to 11 different parasite species in a single *C. aceratus* consequently reflects its less specialized, predatory feeding behaviour that reaches from shallower waters into the deep-sea (5–770 m, Froese and Pauly 2007). The nototheniids *Lepidonotothen* spp. and *Gobionotothen gibberifrons* had a very similar parasite fauna but was less species rich. Palm (1999) compared the infestation of *Chaenocephalus aceratus* and *L. larseni* around the South Shetland Islands with the seal-worm *Pseudoterranova decipiens* s.l. A much higher prevalence and intensity of infestation in the icefish compared to the nototheniid was explained by the different role of these fish in the life cycle of the parasite. While *C. aceratus* is a common fish feeder that can accumulate these parasites as a paratenic host from other fish, the nototheniids serve as second intermediate hosts that acquire the parasites directly through the infested crustacean first intermediate host. A similar situation is illustrated within the present study. Though sharing the same fish parasites, the prevalence and especially the intensity of infestation for all larval fish helminths was much higher in the icefish compared with the nototheniids. Consequently, the latter must be the predominant prey for the former, explaining its high parasite burden.

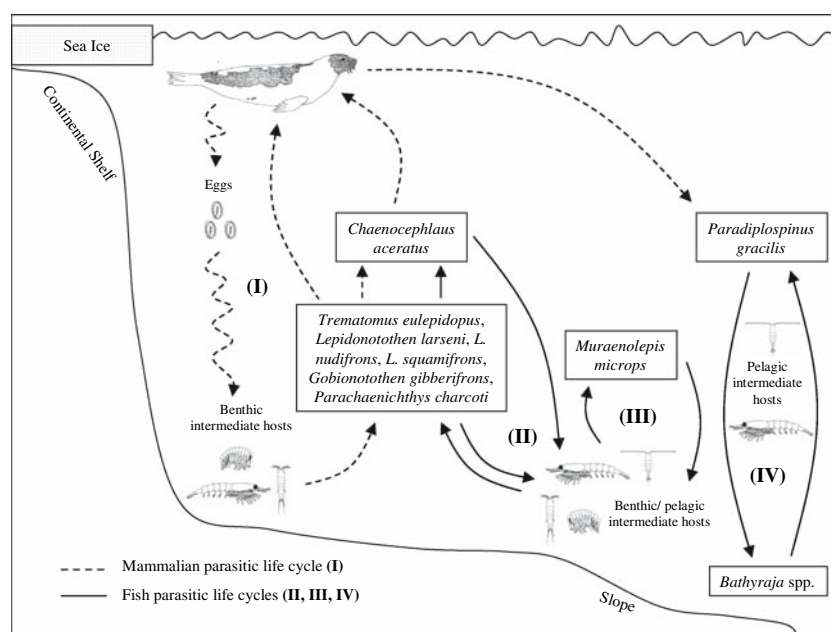
Together with *Trematomus eulepidotus* and *Gobionotothen gibberifrons*, all three *Lepidonotothen* species had a similar parasite fauna, in terms of species composition and abundance. The reason for this is a similar benthodemersal feeding ecology and depth range giving access to the same intermediate hosts in the region. According to Froese and Pauly (2007), *L. larseni* (30–750 m), *L. nudifrons* (3–400 m), *L. squamifrons* (10–900 m), *G. gibberifrons* (6–

429 m) and *T. eulepidotus* (70–650 m) have an overlapping depth range, and mainly feed on zooplankton, such as krill, amphipods, copepods and mysids. They become infested through invertebrate first intermediate hosts, and can transfer parasites either into fish paratenic hosts (such as channichthyids) or directly into the mammalian top predators along the Antarctic Peninsula (Fig. 3). Consequently, these nototheniids play a decisive role in the transmission of the mammalian parasites, as already stated for *Contracaecum* spp. (Klöser et al. 1992) and *Pseudoterranova decipiens* (Palm et al. 1994; Palm 1999). More complex life cycles include parasites that can utilize fish as final hosts (Fig. 3). *Muraenolepis microps* has a similar function as intermediate host for mammalian parasites (as described for the nototheniids), indicated by a similar species richness and abundance to that observed for *C. aceratus*. This muraenolepidid obviously has a wide range of prey items, including fish. However, two digenean and two acanthocephalan parasite species solely infest this host. *M. microps* consequently represents another possible host cycle for fish parasites in Antarctic waters around the South Shetland Islands.

The fish parasite fauna of the bathydraconid *Parachae-nichthys charcoti* was very similar to those isolated from the nototheniid fish. In contrast to the channichthyid *C. aceratus*, however, the prevalence and intensity of infestation was similar. This suggests that the studied *P. charcoti* in the small size range between 11 and 26 cm is a less important fish predator in the region, also relying on crustaceans or other macro-invertebrates as its main diet. A similar feeding ecology and wide depth range (5–400 m) can explain a highly corresponding parasite fauna compared to *Lepidonotothen* spp., *Gobionotothen gibberifrons* and *Trematomus eulepidotus*. Zdzitowiecki (2001) recorded a higher species richness of 18 parasite species in *P. charcoti* in Admiralty Bay and the Bransfield Strait, off the South Shetland Islands. The parasite fauna differed in both localities, with a higher species richness in Admiralty Bay and an increasing level of infestation parallel with the fish size up to more than 40 cm. Obviously, this bathydraconid changes towards a piscivorous behaviour with a larger size, followed by an increase in parasite uptake as a paratenic host in the region. A similar situation has been recorded for the channichthyid *C. aceratus* around the South Shetlands by Palm (1999).

The mesodemersal gempylid *Paradiplospinus gracilis* with a depth range of 368–626 m was only infested with two parasite species, *P. decipiens* s.l. and larval tetraphyllideans. Both are deep ranging larval parasitic stages that can invade the deep sea even through the open pelagial (Palm and Klimpel 2007). Because gempylids have been recorded to harbour a wide variety of fish parasites in other geographical regions (e.g. Jakob and Palm 2006), this level of

**Fig. 3** Suggested parasitic life cycles in coastal waters off the South Shetland Islands, Antarctica. Mammalian parasites (I) and fish parasites (II, III, IV), utilize similar pathways to reach the final hosts. Benthic and/or pelagic invertebrates and the different studied fish species serve as intermediate or final hosts. Most parasite species demonstrate low host specificity and a wide range of distribution also vertically into the deep-sea (further explanation in the text)



infestation is low, and comparable to meso- and bathypelagic fish species from the North and Mid-Atlantic (Klimpel et al. 2006a, b). Gusev (1958) similarly reported low or missing parasitization of the bathypelagic fish *Bathylagus* and *Cyclothone* in the Antarctic region. Despite the potential role of *P. gracilis* as an important paratenic host or top predator in the region, the studied fish specimens might have originated from the Antarctic mesopelagic zone and not from the vicinity of the continental shelf, giving an explanation for the observed low parasite diversity.

The demersal fish parasite fauna from Antarctic deep waters between 80 and 608 m around the South Shetland Islands is species rich, and can be compared to other geographical regions. The diversity is lower than observed for *Notothenia coriiceps* from shallow South Shetland waters (Palm et al. 1998) as well as from the benthodemersal deep sea fish *Macrourus whitsoni* from the Weddell Sea (Walter et al. 2002) or from other North Atlantic macrourids (Palm and Klimpel 2007; Klimpel et al. 2006a). The diversity is higher compared to meso- and bathypelagic fish in the central North Atlantic (Klimpel et al. 2006b), and similar to a bathydemersal deep sea fish *Halosaurus macrorchir* at the Mid-Atlantic Ridge (Klimpel et al. 2007b). The observed parasite fauna of the demersal Antarctic fish is determined by the enriched biomass along the sea floor that is utilized by notothenoid fish with an opportunistic feeding ecology. The wide depth range from shallow waters into the deep-sea gives access to the available generalistic parasite fauna that is obviously not negatively influenced by changing water conditions. In South Shetland waters, the temperature, salinity, and pressure have no influence on the parasite composition in the studied depth range between around 100 and 600 m water depth.

According to our knowledge, not a single record reported a nematode belonging to the cosmopolitan genus *Anisakis* from a teleost in the high Antarctic, though several, mostly demersal fish species and from different regions have been studied (also present study). This is astonishing because the cetacean final hosts are highly abundant and can transport this parasite into Antarctic waters. Mammalian hosts have been recorded to be infected with *A. similis* and *A. physeteris*, although their real identity must still be clarified (Rocka 2006). Two possible reasons might explain the missing evidence for *Anisakis* in fish in higher latitudes. Besides the pelagic *Pleuragramma antarcticum* (e.g. Bartsch 1985) and *Paradiplospinus gracilis* (present study), mainly demersal fish species have been studied and the suitable intermediate hosts are yet unknown. Another possibility is the lacking ability of Antarctic *Anisakis* to penetrate into the benthodemersal food web in high Antarctic waters, due to the lack of suitable intermediate hosts or environmental factors such as the extremely cold-water temperatures. This is astonishing because e.g. the most common North Atlantic *Anisakis simplex* is considered to have a pelagic life cycle in the cold waters of the East Greenland Sea, however, also occurs in 278–1,650 m water depth at the Mid-Atlantic Ridge and the East Greenland Sea (Kellermanns et al. 2007; Klimpel et al. 2007a). This also contrasts the development of an Antarctic *Pseudoterranova decipiens* s.l. sibling species that still follows a benthic life cycle even in the Weddell-Sea, and also reaches into 880 m water depth (Palm 1999). Studies on further pelagic fish species are needed to clarify the identity and to detect the intermediate hosts of this important and cosmopolitan fish parasite genus in high Antarctic waters.



## Conclusions

The parasite fauna of the studied demersal deep-water fish was species rich and consisted of a combination of teleost and mammalian (especially seals) parasites in the adult and larval stage, respectively. Several different life cycle strategies can be recognized. The mammalian parasites utilize the various fish second intermediate or paratenic hosts, especially the nototheniids and channichthyids, as a common route into the final hosts (Fig. 3). The fish parasites, in parallel, explored different benthic host systems to reach the most suitable teleost host. The meso/bathypelagic zone appears to be species poor (in contrast to the coastal or continental shelf), and is inhabited by few larval forms (such as *Pseudoterranova decipiens* s.l.) that either accidentally reach the fish host or originate from e.g. deep-sea elasmobranchs (*Amblyraja* spp. and *Bathyraja* spp.). The host specificity of most Antarctic fish parasites is low, especially within the intermediate hosts. This is in agreement with Palm et al. (1998) who attributed low host specificity of fish parasites in the more shallow water nototheniid *Notothenia coriiceps* to the close phylogenetic relationship combined with a circumpolar distribution among the typically notothenoid hosts. Thus, a combination of generalistic parasites according to the feeding ecology and depth range of the various fish hosts seems to be the typical parasite infestation pattern in high Antarctic waters, not only horizontally but also extending vertically into the deep sea.

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