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The role of the rock cod *Notothenia coriiceps* Richardson, 1844 in the life-cycle of Antarctic parasites

Received: 11 September 1997 / Accepted: 12 January 1998

Abstract Fifty specimens of *Notothenia coriiceps* caught in Potter Cove, King George Island, were examined for ecto- and endoparasites. Of the 22 parasite species found, 18 were helminths, 2 were hirudineans and 2 were crustaceans. The isopod *Aega antarctica* and an unidentified hirudinean are reported for the first time from this fish host. Dominant parasites were the adults of *Aspersentis megarhynchus*, the invasive stage of *Corynosoma* spp. (cystacanth) and the adults of *Macvicaria pennelli*, with respective prevalences of infestation of 94, 76 and 74%. The preferred sites of infestation were the pylorus and intestine, where five different larval (nematodes and cestodes) and eight adult (digeneans and acanthocephalans) parasite species were found. No adult nematodes and cestodes were found and no parasites could be isolated from the musculature. The results of the present study are related to previous findings on the parasite fauna of *N. coriiceps*. The comparison implies a high parasite diversity in this benthic Antarctic fish species. Most parasites found appear to have a wide range of distribution within Antarctic waters together with a low host specificity. Besides its role as final host for several species of trematodes and acanthocephalans, *N. coriiceps* serves as transmitter of parasite larvae to piscivorous birds and seals. It is concluded that the parasite fauna in Antarctic fish species provides important insights into the different habitat use and trophic relationship of their fish hosts.

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Introduction

The Antarctic fish *Notothenia coriiceps* Richardson, 1844 is regarded as having a circumpolar distribution (De Witt et al. 1990) and is one of the dominant fish species in the waters around the South Shetland Islands (Casaux et al. 1990). *N. coriiceps* is primarily a benthic predator known for its feeding on polychaetes, thaliaceans, gammarid amphipods, molluscs, and fish such as *Harpagifer antarcticus* and *Trematomus newnesi* (see Blankley 1982; Casaux et al. 1990). The main predators of *N. coriiceps* are piscivorous birds, such as the cormorant *Phalacrocorax atriceps bransfieldensis* (see Coria et al. 1995), and seals (Everson 1970).

In the first investigation on the parasite fauna of *Notothenia coriiceps*, Railliet and Henry (1907) found encysted larval nematodes in the stomach wall. Later studies by Johnston (1937a,b), Johnston and Best (1937), Johnston and Mawson (1945), Mawson (1953) and Szidat (1965) revealed a rich parasite fauna including monogeneans, trematodes, cestodes, nematodes, acanthocephalans and hirudineans. This was followed up by more detailed work on the two most diverse groups, trematodes and acanthocephalans (Zdzitowiecki 1986a,b,c, 1988; Zdzitowiecki and Rokosz 1986; Zdzitowiecki and Pisano 1996; Zdzitowiecki and White 1996; Zdzitowiecki et al. 1997). The first protozoan parasite of *N. coriiceps*, *Haemogregarina nototheniae*, was isolated by Barber et al. (1987).

To date, the parasite fauna of *N. coriiceps* is one of the most extensively studied among Antarctic fish and allows first conclusions regarding the life-cycle ecology of its parasites. The examination of the parasite fauna of *N. coriiceps* in the South Shetland region in the context of earlier works was the purpose of the present study.

Materials and methods

N. coriiceps ($n = 50$) ranging from 20 to 58 cm standard length (median = 27.5, 27.7 cm) were caught with gill nets at a depth of

approximately 10 m at the entrance to Potter Cove, close to the Argentinean research station Teniente Jubany (62°14'S, 58°40'W) on King George Island, between 7 and 13 December 1994. Fish were examined for helminth and ectoparasite infestation either fresh ($n = 8$) or frozen ($n = 42$). Firstly, the skin and gills were examined for ectoparasites and then the body cavity and gastrointestinal tract were dissected using a stereomicroscope. Belly flaps and musculature were examined on a candling table.

All parasites were fixed in a 20% formaldehyde solution and stored in 75% ethanol with glycerine. Acanthocephalans were transferred to freshwater prior to fixation and left until projection of the proboscis occurred. In some cases the proboscis was extracted manually using needles. For identification purposes, nematodes were dehydrated in an alcoholic series, and then transferred to 100% glycerine (Riemann 1988). The transparency of the nematodes was increased by further treatment with a 1:1 glycerine/lactic acid solution. Trematodes and cestodes were stained with acetic carmine as described by Rausch (Reichenow et al. 1969). Reference literature used for the identification of parasites included original descriptions, as well as Gibson (1976) for Trematoda, Bartsch (1985) for Nematoda, Wägele (1987) and Rokicki et al. (1992) for Crustacea, Meyer and Bureson (1990) for Hirudinea and Zdzitowiecki (1991a) for Acanthocephala. The ecological terms prevalence and intensity of infestation and site are used according to Bush et al. (1997). To detect differences between fish length and intensity of infestation, 2.5-cm length classes were tested using ANOVA ($P = 0.95$). The prevalence of infestation was tested against host sex using the χ^2 -test ($P = 0.95$).

Results

Of the 22 parasite species found, 18 were helminths, 2 were hirudineans (including 1 unidentified species) and 2

were crustaceans (Table 1). The isopod *Aega antarctica* Hodgson, 1910 and an unidentified hirudinean are reported for the first time from *Notothenia coriiceps*. The dominant species found were the adults of *Aspersentis megarhynchus* (Linstow, 1892), the invasive stage of *Corynosoma* spp. (cystacanth) and the adult stage of *Macvicaria pennelli* (Leiper & Atkinson, 1914) with respective prevalences of infestation of 94, 76 and 74%. The preferred sites of infestation were the pylorus and intestine, where five different larval (nematodes and cestodes) and eight adult parasite species (digeneans and acanthocephalans) were found. No adult nematodes and cestodes were found and no parasites could be isolated from the musculature. The prevalences and intensities of infestation are summarised in Table 1. Details on the isolated parasites together with comments on their distribution in Antarctic waters are given below.

Monogenea

Adult monogeneans were represented by a single specimen of *Pseudobenedenia nototheniae* Johnston, 1931 found on the skin between the pectoral fins of one specimen of *N. coriiceps*. *Pseudobenedenia nototheniae* has been reported previously to occur on *N. colbecki* (Antipodes Island, Johnston 1931), *N. rossi* (Kerguelen, Dollfus and Euzet 1964) and *N. coriiceps* (South Orkney Islands, Zdzitowiecki et al. 1997), and has been detected

Table 1 Parasite species found in *Notothenia coriiceps* ($n = 50$)

Parasite species	Adult/larvae	Prevalence (%)	Mean intensity (range)	Site of infestation
Monogenea				
<i>Pseudobenedenia nototheniae</i>	a	2	1.0 (1)	Skin
Digenea				
<i>Elytrophalloides oatesi</i>	a	4	1.0 (1)	Stomach
<i>Genolinea bowersi</i>	a	62	4.6 (2–19)	Stomach, pyloric caeca
<i>Gonocerca phycidis</i>	a	8	1.5 (1–2)	Stomach
<i>Lepidapedon garrardi</i>	a	14	2.4 (1–4)	Intestine
<i>Macvicaria pennelli</i>	a	74	21.0 (1–164)	Pyloric caeca, intestine
Cestoda				
Tetraphyllidean larvae	1	4	19.0 (1–38)	Pyloric caeca, intestine
<i>Diphyllobothrium</i> sp.	1	4	1.0 (1)	Pyloric caeca
Nematoda				
<i>Contracaecum osculatum</i>	1	30	1.9 (1–12)	Liver, body cavity
<i>Contracaecum radiatum</i>	1	28	1.7 (1–9)	Stomach
<i>Pseudoterranova decipiens</i>	1	56	4.6 (1–58)	Liver, body cavity
Nematoda indet	1	12	1.2 (1–2)	Stomach
Acanthocephala				
<i>Aspersentis megarhynchus</i>	a	92	19.0 (3–154)	Intestine
<i>Corynosoma</i> spp. (cystacanth)	1	76	7.0 (1–102)	Body cavity, liver
<i>Corynosoma</i> cf. <i>hamanni</i>	a	30	3.1 (1–6)	Stomach, pyloric caeca
<i>Echinorhynchus petrotschenkoi</i>	a	8	2.0 (1–5)	Pyloric caeca, intestine
<i>Heterosentis heteracanthus</i>	a	2	1.0 (1)	Intestine
<i>Metacanthocephalus dalmori</i>	a	14	1.4 (1–2)	Pyloric caeca, intestine
<i>Metacanthocephalus johnstoni</i>	a	34	6.1 (1–17)	Pyloric caeca, intestine
Hirudinea				
<i>Notobdella nototheniae</i>	a	2	1.0 (1)	Mouth cavity
Hirudinea indet	a	2	1.0 (1)	Skin
Isopoda				
<i>Aega antarctica</i>	a	2	1.0 (1)	Operculum
<i>Gnathia calva</i>	1	14	1.0 (1–2)	Skin

in the waters around the Antarctic Peninsula (Lutnicka and Zdzitowiecki 1984).

Digenea

The two most abundant digeneans in the present study were *Macvicaria pennelli* (Leiper & Atkinson, 1914) and *Genolinea bowersi* (Leiper & Atkinson, 1914). *M. pennelli* was found in 74% of the fish studied and had a mean intensity of infestation of 21.0, range 1–164. Most specimens were found in the pyloric caeca, with the remainder in the upper intestine. *G. bowersi* was found in the stomach and had a prevalence of 62% and a mean intensity of infestation of 4.6, range 2–19. The three other digenean species also detected, *Lepidapedon garrardi* (Leiper & Atkinson, 1914), *Elytrophalloides oatesi* (Leiper & Atkinson, 1914) and *Gonocerca phycidis* Manter, 1925, were found in only a few fish and their mean intensities did not exceed 2.4 (Table 1). *E. oatesi* and *Gonocerca phycidis* were found in the stomach, whereas *L. garrardi* infested the proximal intestine. All trematodes described here were found as adults and have been described in a number of other fish species around the Antarctic Peninsula (Zdzitowiecki 1991b), as well as in *N. coriiceps* (Zdzitowiecki et al. 1997; Table 2).

Cestoda

Only larval specimens belonging to two or more different species were isolated. With the pseudophyllid *Diphyllobothrium* sp., a larval form without genitalia was present and identification at the species level was therefore not possible. The other specimens were identified as tetraphyllidean larvae, which were characterised by having an apical sucker and 4 suckers bearing 2 or 3 loculi, and thus they might represent more than a single species. Both were detected in two fish only and had intensities of infestation of 1–38 (tetraphyllidean larvae) and 1 (*Diphyllobothrium* sp.). The tetraphyllidean larvae were found in the intestinal lumen and *Diphyllobothrium* sp. occurred in the walls of the pyloric caeca. A single specimen of *Diphyllobothrium* sp. was observed in *N. coriiceps* caught in Commonwealth Bay (Johnston 1937a) and, according to Wojciechowska (1990), tetraphyllidean larvae of the *S. pleuronectis* complex have been found in fish of the order Notothenioidea [*Chaenocephalus aceratus*, *Notothenia rossi* and *N. neglecta* (= *N. coriiceps*)] caught in the South Shetland region.

Nematoda

The highest prevalence (56%) and mean intensity of infestation (4.6, range 1–58) were measured for third stage larvae (L3) of *Pseudoterranova decipiens* (Krabbe,

1878). Most specimens were found in the liver and some in the body cavity. L3 of *Contracaecum osculatum* (Rudolphi, 1802) and *Contracaecum radiatum* (Linstow, 1907) had respective prevalences of 30% and 28% and respective mean intensities of infestation of 1.9 (range 1–12) and 1.7 (range 1–9) (Table 1). Larval nematodes belonging to an unidentified species of nematode were also detected. Though the seven specimens found were in bad condition, some morphometrical characteristics corresponded to those described by Mawson (1953) for *Ascarophis nototheniae* Johnston & Mawson, 1945. Previously, *Dichelyne fraseri*, *Pseudoterranova decipiens*, *Ascarophis* spp. and *Contracaecum* spp. have been reported as parasites of *Notothenia coriiceps* in the South Shetland region (Reimer 1987; Chai et al. 1995; Zdzitowiecki and Cielecka 1996).

Acanthocephala

Aspersentis megarhynchus (Linstow, 1892) was the most abundant acanthocephalan and also had, overall, the highest prevalence of infestation (92%). The mean intensity reached 19.0 (range 3–154). *Aspersentis megarhynchus* was found mainly in the posterior part of the intestine, either free or attached to the intestinal wall. *Metacanthocephalus johnstoni* Zdzitowiecki, 1983 was detected in the pyloric caeca and in the anterior part of the intestine with a moderate prevalence of 34% and a low mean intensity of infestation of 6.1 (range 1–17). Three other species, *Echinorhynchus petrotschenkoi* (Rodjuk, 1984), *Heterosentis heteracanthus* (Linstow, 1896) and *Metacanthocephalus dalmori* Zdzitowiecki, 1983, were isolated from only a few fish, and the prevalence in this group did not exceed 14%. The highest mean intensity for any of the three species was 2.0, range 1–5 (*Echinorhynchus petrotschenkoi*). Beside adult acanthocephalans, invasive stages of *Corynosoma* spp. (cystacanth) occurred in the body cavity and in the liver, with a prevalence of infestation of 76% and a mean intensity of infestation of 7.0 (range 1–102). Due to the inverted proboscis, the specimens could not be identified to the species level. Additionally, pre-adults of *Corynosoma* cf. *hamanni* (Linstow, 1892) were found in the stomach and in the pyloric caeca (prevalence 30%, mean intensity of infestation 3.1, range 1–6). Out of approximately 30 different Antarctic acanthocephalans known, 18 have been recorded in the region of the South Shetland Islands and 16 from *Notothenia coriiceps*, including the acanthocephalans isolated in the present study (Table 2).

Hirudinea

Hirudineans were detected in only two fish studied. *Notobdella nototheniae* Benham, 1909 was found in the mouth cavity of a single fish. The second species was

Table 2 (continued)

<i>Echinorhynchus debenhani</i>		X			
<i>Echinorhynchus petroschenkoi</i>	8			66.7	0.4
<i>Heterosentis heteracanthus</i>	2		X	33.3	0.8
<i>Hyechinorhynchus magellanicus</i>					♀K
<i>Metacanthocephalus campbelli</i>	14				
<i>Metacanthocephalus dalmori</i>	34			100	27.0
<i>Metacanthocephalus johnstoni</i>					57.7
<i>Metacanthocephalus rennicki</i>					♀K
Hirudinea					X ^L
<i>Notobdella nototheniae</i>	2		X		
Hirudinea indet	2				
Isopoda					
<i>Aega antarctica</i>	2				
<i>Gnathia calva</i>	14				14.5 ^M

^a Detected in *Notothenia coriiceps* var. *macquariensis*

^b *Contracaecum*, *Phocanema* and *Anisakis* ? were isolated from the liver (92%) and the body cavity (54%)

^c In fishes from the South Shetlands

represented by a single specimen isolated from the skin behind the operculum of another fish. Due to the poor condition of the specimen, it was impossible to identify. Only *Notobdella nototheniae* have been earlier recorded from *N. coriiceps* and from different nototheniids from the South Shetland Islands (Meyer and Burreson 1990).

Crustacea (Isopoda)

One fish was found to carry a specimen of *Aega antarctica* Hodgson, 1910 on the inner part of the operculum. Larvae of *Gnathia calva* Vanhöffen, 1914, known as pranizae, were isolated from the lateral skin of the fish hosts. Two pranizae were also detected in the stomach of a larger piscivorous *Notothenia coriiceps*. Only the larvae of *Gnathia calva* parasitise fish. The prevalence of infestation was 14% and intensity was low with 1–2 specimens per fish. According to Rokicki et al. (1992), *Gnathia calva* has a circumpolar distribution on the Antarctic shelf but has only rarely been reported in the South Shetland region. It is mostly found in depths of 120–660 m.

There was no significant difference between intensity of infestation and length classes, as well as between prevalence of infestation and sexes of *Notothenia coriiceps* ($P = 0.95$).

Discussion

In the present study, *Notothenia coriiceps* was found to host a total of 22 species of parasites. Two of these, *Aega antarctica* and an unidentified hirudinean, have not been reported in *Notothenia coriiceps* before. The core species of *Notothenia coriiceps*, defined as occurring in over 60% of fish studied, are the digeneans *Macvicaria pennelli* and *Genolinea bowersi* and the acanthocephalan *Aspersentis megarhynchus*. A literature review shows that 13 parasite species may reach a prevalence of infestation of over 60% in *Notothenia coriiceps*, depending on locality and season (Table 2). However, the different numbers of fish examined in these studies (Hoogesteger and White 1981, $n = 117$; Zdzitowiecki and White 1992a,b, $n = 3$; Zdzitowiecki 1988, Zdzitowiecki and White 1996, $n = 248$) should be kept in mind.

For both the trematodes and acanthocephalans, the observed infestation rates were lower than those reported by Zdzitowiecki and Rokosz (1986), Zdzitowiecki (1988) and Zdzitowiecki and White (1996). A possible explanation for this difference could be that the occurrence of trematodes and acanthocephalans follows a seasonal pattern, as demonstrated for *Macvicaria pennelli* (Zdzitowiecki 1988). It seems as if the acanthocephalans *Corynosoma arctocephali*, *Echinorhynchus petroschenkoi*, *Heterosentis heteracanthus* and *Metacanthocephalus johnstoni* also follow a season-

ality, in contrast to *Aspersentis megarhynchus*, which had a similar prevalence of infestation during the present and previous studies (Zdzitowiecki 1988; Zdzitowiecki and White 1996). Interestingly, no significant difference between intensity of infestation and fish length, as well as between prevalence of infestation and sexes could be observed. However, this can be considered as an effect of having only 50 examined fish, most of them with a length between 20 and 30 cm ($n = 38$) and fewer in the upper length classes between 32.5 and 57.5 cm ($n = 12$).

At present, 37 parasite species are known to occur in *Notothenia coriiceps*, including 32 species of helminths and 5 species of ectoparasites (Table 2). Thus, the parasite fauna of *Notothenia coriiceps* is highly diverse and is comparable to the spectrum found in highly parasitised benthic and pelagic fish species from other localities (for example, see Margolis and Arthur 1979). Rohde (1993) and Rohde et al. (1995) stated that the environmental temperature appears to be of great significance in determining community richness of metazoan ectoparasites of fish. Similar to the smaller numbers of fish species found in the cold regions, the ectoparasite diversity in high latitudes is low (Rohde 1984). This pattern is confirmed by results of the present and previous studies (Table 2). In contrast to a rich endoparasite fauna, only one monogenean and four other ectoparasite species are known from *Notothenia coriiceps*. However, it has to be remembered that, because of the frozen material examined, some ectoparasites may have dropped off during the present study.

Most of the 37 species of parasite known to occur in *Notothenia coriiceps* have been detected in other localities and in other host species, often of the genera *Notothenia* and *Trematomus* (see Leiper and Atkinson 1915; Johnston 1931; Johnston and Mawson 1945; Szidat and Graefe 1967; Kagei and Watanuki 1975; Rodjuk 1985; Zdzitowiecki 1986a,b,c; Reimer 1987; Zdzitowiecki 1988; Meyer and Burreson 1990; Zdzitowiecki 1991a,b; Rokicki et al. 1992; Zdzitowiecki and White 1992a,b). In particular, the parasites *Diphyllobothrium* sp., *Scolex pleuronectis*, *Contracaecum osculatum*, *Contracaecum radiatum*, *Pseudoterranova decipiens*, *Gonocerca phycidis*, *Corynosoma bullosum*, *Echinorhynchus petrotschenkoi*, *Metacanthocephalus campbelli* and *Metacanthocephalus dalmori* are known from several fish species in the eastern Weddell Sea (Bartsch 1985; Zdzitowiecki 1996; Zdzitowiecki and Cielecka 1997). Specimens of the genus *Anisakis* have also been detected in Antarctic waters (Table 2) and can be considered as widely distributed. It appears that the parasite fauna of *Notothenia coriiceps* is characterised by a low host specificity and wide distribution within Antarctic waters. More host-specific parasites like monogeneans are rare and adult cestodes could not be detected. This would correspond to a low host specificity of parasites in higher latitudes, as proposed by Polyanskii (1955) for the northern marine fish of the Barents Sea, and in more general terms by Holmes (1990) for digeneans, acanthocephalans, nematodes and cestodes parasitising teleost fish. A possible explanation

for a low host specificity of northern, in comparison to warm water, digeneans was given by Appy and Burt (1982), who suggested that this reflects a trophic specialisation that has evolved within the different biocoenoses. Another reason might be a close relation of many Antarctic fish species belonging to the suborder Notothenioidei.

In coastal Antarctic fish communities, habitat separation is considered a more important factor in avoiding competition for food resources than either temporal separation or within-habitat prey separation (Targett 1981). To illustrate this point, *Notothenia coriiceps* and *Notothenia macrocephala* inhabit the 2- to 5-m and 5- to 20-m depth zone off the coast of sub-Antarctic Marion Island, and show a clear-cut difference in diet, both between one another and compared to an intertidal population of *Harpagifer gregorianus*. The reason for this difference is that the depth zones occupied by the fish correspond to a different range of prey species (Blankley 1982). Arai (1967) suggested that some digeneans tend to occur in hosts living in a specific type of environment; thus, the habitat of the fish host determines its parasite fauna. This seems to be a major factor for determination of the parasite fauna of *Notothenia coriiceps* from King George Island. Interestingly, the same model has been used to predict the presence or absence of the digenean *Genolinea leiperi* Byrd, 1963 in four species of *Trematomus* in McMurdo Sound (Holloway and Spence 1980). It would be expected that fish species occupying an ecological niche similar to *Notothenia coriiceps* would show a similar pattern of infestation with endoparasitic helminth species. This has been already demonstrated for *Trematomus centronotus* in McMurdo Sound by Holloway and Spence (1980).

Gusev (1958) proposed that the most varied fauna of fish parasites occurred in the shallow-water fish of the Antarctic, the Nototheniidae. He reasoned that this was a result of the great diversity of living conditions encountered by this group of fish, including variation of benthos composition, food availability, contact with other fish and various intermediate hosts. With 37 known larval and adult parasite species, the benthic predator *Notothenia coriiceps* has an important role in the transmission and distribution of Antarctic marine parasites. This may indeed be a consequence of its shallow water habitat, because frequently shallow-water snails are first intermediate hosts of parasites such as trematodes. For example, in snails of the genus *Margarella*, Graefe (1968, 1971) detected cercariae that were able to use the polychaete *Harmothoe spinosa* as their second intermediate host in the shallow-water zone. The cercariae were presumed to belong to *Macvicaria pennelli*. In the present study, *Macvicaria pennelli* was found to be highly abundant in *Notothenia coriiceps*. Another reason for the highly diverse parasite fauna of *Notothenia coriiceps* may be the potentially wide depth range between 0 and 550 m (Gon and Heemstra 1990), which enables the fish to come in contact with deep-water parasites. For example, life-cycle stages of two lepo-

creadiid trematode species were found in *Neobuccinum eatoni* and *Trematomus* spp. at a depth of 300 m (Graefe 1971), and third stage larvae of *Pseudoterranova decipiens* have been shown to follow a benthic life-cycle (Palm et al. 1994). The young pelagic stages of *Notothenia coriiceps* have a circum-Antarctic distribution (Gon and Heemstra 1990) and thus may be infected by parasites with pelagic life-cycles, such as the plerocercoids of pseudophyllidean cestodes found in the Antarctic midwater fish *Pleuragramma antarcticum* (see Bartsch 1985), and parasites associated with an open sea environment, such as *Corynosoma bullosum* (see Zdzitowiecki and White 1996). Thus, the important role of *Notothenia coriiceps* in the life-cycles of Antarctic parasites may be explained by a combination of two factors: the large depth range of *Notothenia coriiceps* with a large range of prey species, and the low host specificity of the parasites it encounters as a result.

The preferred sites of infestation in the present study were the pylorus and intestine, where five different larval (nematodes and cestodes) and eight adult (digeneans and acanthocephalans) parasite species were found. This may be an effect of the predominance of adult stages among the acanthocephalans and trematodes. Larval stages occur mostly in the liver, as well as the body cavity, the stomach and the stomach wall. According to Klöser et al. (1992) and Palm et al. (1994), these are preferred sites of infestation for the nematode species of the genera *Contracaecum* and *Pseudoterranova*. Musculature and belly flaps were free of parasites, and this is in agreement with findings of previous studies on *Notothenia* spp. off the coast of King George Island (Reimer 1987; Feiler 1990), as well as with investigations on the nematode fauna of fish in the eastern Weddell Sea (Klöser et al. 1992; Palm et al. 1994). However, this contrasts with the musculature infestation on nototheniid fish species from the sub-Antarctic islands (Johnson and Mawson 1943). A question that cannot be resolved at present is whether the difference in water temperature between high and sub-Antarctic regions influences a different site of infestation.

Acknowledgements Drs. R. Bray (Natural History Museum, London) and G. Hubold (Bundesforschungsanstalt für Fischerei, Hamburg) reviewed an earlier draft of the manuscript. Thanks are due to R. Eisert (Lincoln University, Canterbury, NZ) who improved the English and to Dr. E. Barrera Oro (Instituto Antártico Argentino, Buenos Aires) for obtaining the fish material. The study is part of the Argentinian-German cooperation programme "Research on Antarctic Shallow Coastal and Littoral Systems". This is Contribution No 1369 of the Alfred Wegener Institute for Polar and Marine Research.

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