ORIGINAL PAPER

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Ecology of *Pseudoterranova decipiens* (Krabbe, 1878) (Nematoda: Anisakidae) from Antarctic waters

Abstract The present study provides further data on the occurrence of *Pseudoterranova decipiens* in fish from two different sampling sites in the Antarctic. A total of 690 fish belonging to 33 species from the eastern Weddell Sea and 322 fish belonging to 12 species from the South Shetland Islands were examined. Altogether, 23 fish species were found to be infested and 11 new host records could be established. *P. decipiens* occurred at a water depth of between 80 and 820 m. *Chaenocephalus aceratus* and *Notothenia coriiceps* from the South Shetland Islands were the species with the highest prevalence (95%) and intensity (2–194 and 1–121, respectively) of infestation. Both are transport hosts, which mainly feed on benthic nototheniid fish species and accumulate the nematodes. Bathypelagic, pelagic, or mainly euphausid feeding fish species were only lightly infested, if at all. This demonstrates the benthic life cycle of *P. decipiens* in the Antarctic. The preferred site of infestation was the body cavity and the liver; no specimen could be isolated from the fish musculature. This might be explained by the low water temperatures. The infestation of fish from the Weddell Sea was distinctly lower than that of fish around the South Shetland Islands. Besides possible differences in final host populations at the two localities studied, the loss of eggs and larvae under the eastern Weddell Sea shelf ice and over the continental slope and differences in the availability of the first intermediate and macroinvertebrate hosts led to a lower level of infestation. Another role, although nondecisive, may be played by the reduced time of development and infectivity of eggs and larvae, respectively, in the extremely cold waters of the Weddell Sea. *P. decipiens* is not a rare but, rather a well-established parasite of the Antarctic fauna, which demonstrates the ability of this cosmopolitan species to complete its life cycle even under conditions of subzero temperatures.

Introduction

Pseudoterranova decipiens can be considered a cosmopolitan species, occurring in many aquatic hosts from the boreal to the Antarctic region (Kerstan 1991; Palm et al. 1994). *P. decipiens* matures in seals, and the first intermediate hosts are crustaceans, such as copepods, amphipods, shrimps, and isopods (Marcogliese 1996). Only when the worms reach a size of about 2 mm they can infest fish (McClelland 1995), which serve as second intermediate hosts (Kerstan 1991). This size is attained only in macroinvertebrates, such as mysids (Jackson et al. 1997), which are thus an essential step in the life cycle of *P. decipiens* (McClelland 1995). *P. decipiens* is considered to follow a benthic life cycle, with larvae not being able to swim. In contrast, the larvae of *Anisakis* spp. and *Contracaecum osculatum* can swim, having cuticular sheaths with lateral extremities that increase their buoyancy (McClelland 1982).

Within Antarctic waters, findings of *P. decipiens* go back to von Linstow, who first isolated this nematode from the seal *Arctocephalus gazella*. Later authors recognized the Weddell Seal *Leptonychotes weddellii* and the sea elephant *Mirounga leonina* as the main final host species. In addition, increasing numbers of fish species were found infested with the third-stage larvae (see Palm et al. 1994). The first comprehensive study on fish species from the Weddell Sea was carried out by Palm et al. (1994), who examined 11 different fish species of more than 75 species known in that region (Hubold 1992); they found 6 fish species, all demersal feeders, to be mainly lightly infested. The bathydraconid *Cygnodraco mawsoni* was considered to be the required intermediate host for *P. decipiens* in this region. The lack of a shallow coastal zone and the low water temperatures were considered the decisive factors for the distribution of the

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species in Antarctic waters. However, the data were too sparse to provide an understanding of the life cycle of this parasite in high Antarctic waters.

Paggi et al. (1991) divided the *P. decipiens* complex into three different sibling species in the North Atlantic, which were ecologically separated through their infestation of different final and second intermediate hosts. To date, only a single sibling species, *P. decipiens* E, has been identified from Antarctic waters (Bullini et al. 1992, 1997), indicating the presence of an endemic sibling for the Antarctic. However, before further studies on specimens from the Antarctic confirm this finding, in the present paper we continue to call it *P. decipiens* as discussed in Palm et al. (1994). In the present study the occurrence of *P. decipiens* in Antarctic waters was examined to provide a better understanding of the ecology of the species. Data on *P. decipiens* in fish of the Weddell Sea and the South Shetland Islands were obtained and compared. They were used for interpretation of the currently known distribution pattern in Antarctic hosts to explain both the occurrence and the abundance of *P. decipiens* in Antarctic fish.

Materials and methods

A total of 1012 fish were collected on board the research vessel FS POLARSTERN during the cruises ANT XIII/3 (EASIZ I) in the southeastern Weddell Sea and ANT XIV/2 (CCAMLR) around the South Shetland Islands (Arntz and Gutt 1997; Kattner 1998). The fish were caught between the periods of February 5 to March 5 and November 16 to December 9, 1996, using Agassiz trawlnets, bottom trawlnets, benthopelagic nets and dredging at various stations and depths. The alimentary tract and the body cavity of 400 specimens belonging to 32 species caught at various stations at depths ranging between 120 and 1560 m in the Weddell Sea were examined directly on board with the help of a stereomicroscope (Zdzitowiecki 1997). The body cavity, the viscera, all internal organs, and the musculature were examined in 290 specimens of 5 species from the Weddell Sea and in all specimens belonging to 12 species obtained from the South Shetland waters using a stereomicroscope and a candling table. The sampling depth around the South Shetland Islands varied between 80 and 820 m. Antarctic *Pseudoterranova decipiens* is easily identifiable by its large size, the presence of a cecum, the absence of an appendix, and the red color of many specimens (Palm et al. 1994). The fish species were identified directly on board the POLARSTERN by Balguerías and Morales-Nin (1997) and Kock (1998).

Results

Pseudoterranova decipiens was found to be abundant at both localities studied: the southeastern Weddell Sea and around the South Shetland Islands (Tables 1, 2). With *Artedidraco orianae*, *A. skottsbergi*, *Chionodraco myersi*, *C. rastrospinosus*, *Lepidonotothen larseni*, *L. nudifrons*, *Muraenolepis microps*, *Parachaenichthys charcoti*, *Paradiplospinus gracilis*, *Trematomus eulepidotus*, and *T. loennbergi*, 11 new host records were established. Fish from the South Shetland Islands had higher degrees of infestation than did those from the Weddell Sea. At the South Shetland Islands, four species reached a prevalence of over 80% and intensities of up to 194 (Table 2). In contrast, southeast Weddell Sea fish reached only up to 57% prevalence, and the highest intensity found was 8 (Table 1). *T. eulepidotus*, which was studied at both localities, had a 3-fold heavier infestation around the South Shetland Islands than along the eastern Weddell Sea coast (Tables 1, 2).

Eastern Weddell Sea

Of the 33 fish species examined, 11 were found to be infested with red-colored *P. decipiens*. Whereas the Bathydraconidae, Liparidae, Macrouridae, and Zoarcidae had no *P. decipiens*, 5 of 10 Nototheniidae, 3 of 6 Channichthyidae, and 3 of 7 Artedidraconidae were infested. The heaviest infestation occurred in the channichthyid *Cryodraco antarcticus* (57%), followed by the nototheniids *Trematomus scotti* (46%) and *T. hansoni* (40%; Table 1). The intensity of infestation was low and varied between 1 and 8, with the highest mean intensity being observed in the artedidraconid *A. skottsbergi* (2.3). The preferred site of infestation was the body cavity and liver surface; no *P. decipiens* could be isolated from the musculature. Few specimens were found in the liver.

P. decipiens occurred at all water depths investigated between 118 and 604 m (Table 3). No difference was observed in the abundance of *P. decipiens* within a fish species between different positions and water depths along the Weddell Sea coast. The abundance of *P. decipiens* in *T. scotti* varied only between 0.9 and 1.2 at depths ranging from 242 to 571 m. The nematode was similarly abundant within the eastern Weddell Sea between Kap Norvegia and south of Vestkapp. In all, 30 specimens of *T. scotti* caught between Vestkapp and Halley Bay harbored 29 *P. decipiens* as compared with the 27 worms found in 30 specimens collected Northeast of Kap Norvegia. The abundance in the most heavily infested fish species, *C. antarcticus*, *T. scotti*, and *T. hansoni*, ranged between 0.4 and 1.2. Due to the body cavity's being the preferred site for *P. decipiens* in the Weddell Sea, no difference was observed between fish examined only in the alimentary tract and body cavity in comparison with completely dissected fish.

South Shetland Islands

All of the 12 examined fish species belonging to 5 different families (Bathydraconidae, Channichthyidae, Gempylidae, Muraenolepididae, and Nototheniidae) were infested with *P. decipiens* (Table 2). The channichthyid *Chaenocephalus aceratus* (Fig. 1) and the nototheniid *Notothenia coriiceps* were the species with the highest prevalence (95%) and intensity (2–194 and 1–121, respectively) of infestation. Although the other nototheniids had a low mean intensity (between 1 and 4), the values recorded for the channichthyids *Pseudochaenichthys georgianus* and *C. rastrospinosus* were 78

Table 1 *Pseudoterranova decipiens* in fishes from the Weddell Sea

Fish species	Method of examination					
	Alimentary tract and body cavity			All internal organs, body cavity, and musculature		
	Number examined	Prevalence (%)	Mean intensity (range)	Number examined	Prevalence (%)	Mean intensity (range)
Artedidraconidae:						
Artedidraco loennbergi	20	0	0	–	–	–
A. orianae	7	14	1 (1)	–	–	–
A. skottsbergi	18	17	2.3 (1–3)	–	–	–
Dolloidraco longedorsalis[a]	44	5	1 (1)	93	3	1 (1)
Pogonophryne marmorata	6	0	0	–	–	–
P. permitini	3	0	0	–	–	–
P. ventrimaculata	1	0	0	–	–	–
Bathydraconidae:						
Bathydraco marri (?)	14	0	0	–	–	–
Gerlachea australis	20	0	0	–	–	–
Prionodraco evansii	3	0	0	–	–	–
Racovitzia glacialis	22	0	0	–	–	–
Channichthyidae:						
Chaenodraco wilsoni	4	0	0	–	–	–
Chionodraco hamatus	20	10	1.5 (1–2)	–	–	–
C. myersi	21	5	1	29	0	0
Cryodraco antarcticus[a]	7	57	1.8 (1–4)	–	–	–
Dacodraco hunteri	5	0	0	–	–	–
Pagetopsis maculatus[a]	2	0	0	–	–	–
Liparididae:						
Paraliparis antarcticus	12	0	0	–	–	–
P. meganchus	2	0	0	–	–	–
Macrouridae:						
Macrourus whitsoni	23	0	0	–	–	–
Nototheniidae:						
Aethotaxis mitopteryx	5	0	0	–	–	–
Pleuragramma antarcticum	–	–	–	58	0	0
Trematomus bernacchii (?)	1	0	0	–	–	–
T. eulepidotus	12	8	1 (1)	–	–	–
T. hansoni	5	40	1.5 (1–2)	–	–	–
T. lepidorhinus[a]	46	2	1 (1)	50	8	1.3 (1–2)
T. loennbergi	25	4	1	–	–	–
T. nicolai	4	0	0	–	–	–
T. pennelli	1	0	0	–	–	–
T. scotti[a]	28	46	1.4 (1–2)	60	48	2 (1–8)
Zoarcidae:						
Lycodichthys antarcticus	9	0	0	–	–	–
Ophthalmolycus amberensis	5	0	0	–	–	–
O. bothriocephalus	5	0	0	–	–	–
Totals	400			290		

[a] Infested in Palm et al. (1994)

and 7. The preferred site of infestation was the body cavity and the liver (Fig. 1); no *P. decipiens* could be isolated from the musculature (Table 2). Most specimens occurred freely, and only a few encapsulated parasites were found. In the channichthyids *C. aceratus* and *P. georgianus*, which showed high intensities (55 and 78, respectively), some specimens were also found in the stomach wall, and encapsulated specimens were observed in the liver of *Muraenoplepis microps*. The color of the worms varied from white to yellow to red.

P. decipiens occurred at all water depths investigated between 80 and 820 m. Within the channichthyid *C. aceratus* the intensity varied with fish length and water depth (Figs. 2, 3). Smaller *C. aceratus* with a body length of below 39 cm had 18 worms, and specimens measuring over 39 cm had 82 worms on average

(Fig. 2). Four specimens measuring 43–49 cm in body length that were caught at a water depth of 357–410 m were lightly infested in comparison with six specimens of similar size from more shallow localities. Whereas smaller *C. aceratus* (length below 40 cm) showed a similar degree of infestation between depths of 120–123 and 305–410 m, larger specimens were much more heavily infested in a shallow water locality (Fig. 3). In contrast to *C. aceratus*, the nototheniid *L. larseni* showed no difference in *P. decipiens* infestation with differing body length and water depth between 145 and 353 m (Fig. 4). The smallest infested fish was 8.1 cm long. A similar infestation pattern was observed for the lightly infested *L. nudifrons*, *L. squamifrons*, and *Gobionotothen gibberifrons*, with the intensity not exceeding 4.

Table 2 *P. decipiens* in fishes from the South Shetland Islands

Fish species	Number examined	Total length (cm)	Prevalence (%)	Mean intensity (range)	Site (body cavity, *bc*; liver, *l*; stomach wall, *sw*)
Bathydraconidae:					
Parachaenichthys charcoti	12	11–26	83	6 (1–15)	bc, l
Channichthyidae:					
Chaenocephalus aceratus	41	22–49	95	55 (2–194)	bc, l, sw
Chionodraco rastrospinosus	20	27–46	25	7 (1–27)	bc, l
Pseudochaenichthys georgianus	3	41–51	33	78 (78)	bc, l, sw
Gempylidae:					
Paradiplospinus gracilis	11	37–45	9	1 (1)	bc
Muraenolepididae:					
Muraenolepis microps	12	22–40	50	10 (1–26)	bc, l
Nototheniidae:					
Gobionotothen gibberifrons	12	31–43	75	2 (1–4)	bc, l
Lepidonotothen larseni	72	8–22	94	4 (1–12)	bc, l
L. nudifrons	61	6–18	43	1 (1–2)	bc, l
L. squamifrons	31	11–24	55	1 (1–3)	bc, l
Notothenia coriiceps	20	32–46	95	32 (1–121)	bc, l
Trematomus eulepidotus	27	20–26	22	1 (1–3)	bc, l
Total	322				

Discussion

Pseudoterranova decipiens was found at water depths ranging between 80 and 820 m in all examined fish species from the South Shetland Islands and in one-third of the species examined from the Weddell Sea. Together with earlier findings (Zdzitowiecki 1978; Hoogesteger and White 1981; Parukhin and Lyadov 1982; Palm et al. 1994), these results demonstrate a low degree of host specificity and a wide pattern of distribution for *P. decipiens* in Antarctic waters, as has been described for several metazoan parasites of the Antarctic rock cod *Notothenia coriiceps* by Palm et al. (1998).

The channichthyid *Chaenocephalus aceratus* from the South Shetland Islands was the most heavily infested species, reaching a prevalence of 95% and an intensity of 55 (2–194). These values, which correspond to those reported by Zdzitowiecki (1978), support the observation that bottom-dwelling *C. aceratus* (Gon and Heemstra 1990) of the size examined mainly feed on fish (Gubsch 1982) and therefore serve as paratenic hosts for *P. decipiens*. *C. aceratus* longer than 39 cm in shallow waters drastically accumulate *P. decipiens*. This demonstrates an important shift toward piscivorous feeding behavior in specimens above that body size. A similar role as a paratenic host was established for the channichthyid *Chionodraco myersi* in the Weddell Sea, for the anisakid nematodes *Contracaecum osculatum* and *C. radiatum* (Klöser et al. 1992), and for the bathy-draconid *Cygnodraco mawsoni* serving as the required intermediate host in the sense of Holmes (1979) for *P. decipiens* in the Weddell Sea (Palm et al. 1994). This also explains the light infestation found by Palm et al. (1998) in smaller *N. coriiceps* (length 20–30 cm) as compared with those of a larger size (32–46) examined in the present study.

Several other benthic or benthopelagic fish species were also found to be infested with *P. decipiens*. However, in contrast to the bathydraconids and channichthyids studied, the intensities of infestation were low and varied between only 1 and 4. Nototheniids, such as *Gobionotothen gibberifrons*, *Lepidonotothen nudifrons*, and *Trematomus* spp., mainly feed on benthic invertebrates (Gon and Heemstra 1990) and, therefore, become infested directly from benthic first intermediate hosts. This explains that even very small specimens become infested and that the infestation of *L. larseni* was not dependent on body size. Bathypelagic, pelagic, and mainly euphausid feeding fish species such as *Gerlachea australis* and *Paradiplospinus gracilis* had either no *Pseudoterranova* or only light infestations (Tables 1, 2). Kagei et al. (1978) found the euphausid *Euphausia superba* to be free of parasitic nematodes. These results clearly demonstrate that the observed pattern of infestation with *P. decipiens* provides an explanation for both the feeding ecology of the fishes and the benthic life cycle of *P. decipiens* in the Antarctic.

In fish from the Weddell Sea and the South Shetland Islands the main site of infestation was the body cavity

Table 3 Sampling sites of *P. decipiens* in the Weddell Sea

Fish species	Number examined	Fish length (cm)	ANT XIII/3[a]	Water depth (m)	*P. decipiens* (*n*)	Location
Artedidraco orianae	7	11.2–12.5	39/29	504–529	1	W of Kap Norvegia
A. skottsbergi	2	5.0–9.3	39/02	170–174	3	NW of Kap Norvegia
	3	8.3–8.8	39/06	212–215	3	W of Kap Norvegia
	3	8.7–9.9	39/16	242–246	1	Vestkapp/Halley Bay
Dolloidraco longedorsalis	50[b]	9.2–12.7	39/16	242–246	2	Vestkapp/Halley Bay
			39/17	465–468		Vestkapp/Halley Bay
	5	10.9–12.7	39/06	354–362	1	W of Kap Norvegia
	43[b]	5.6–11.7	39/29	504–529	2	W of Kap Norvegia
	7	8.7–12.4	39/09	574–604	1	W of Kap Norvegia
Chionodraco hamatus	13	27.0–34.7	39/16	242–246	3	Vestkapp/Halley Bay
C. myersi	1	30.1	39/06	354–362	1	W of Kap Norvegia
Cryodraco antarcticus	1	34.2	39/26	216–222	1	W of Kap Norvegia
	1	29.5	39/05	227–232	1	SW of Kap Norvegia
	2	34.2–35.0	39/16	242–246	4	Vestkapp/Halley Bay
	1	36.3	39/06	354–362	1	W of Kap Norvegia
Trematomus eulepidotus	12	20.8–28.5	39/11	333–338	1	Vestkapp/Halley Bay
T. hansoni	3	31.0–33.5	39/11	333–338	3	Vestkapp/Halley Bay
T. lepidorhinus	25[b]	18.2–22.8	39/16	242–246	1	Vestkapp/Halley Bay
	2	20.2–20.5	39/32	283–286	1	NW of Atka Bight
	25[b]	12.4–20.8	39/01	462–481	4	NE of Kap Norvegia
T. loennbergi	1	17.7	39/32	283–286	1	NW of Atka Bight
T. scotti	2	12.5–13.0	39/24	118–123	1	NE of Kap Norvegia
	8	9.5–14.6	39/05	227–232	3	SW of Kap Norvegia
	4	14.2–15.2	39/16	242–246	2	Vestkapp/Halley Bay
	30[b]	11.4–15.6	39/16	242–246	29	Vestkapp/Halley Bay
	1	16.6	39/21	248–253	1	Vestkapp/Halley Bay
	2	9.8–14.5	39/32	283–286	2	NW of Atka
	5	14.5–17.5	39/17	465–468	6	Vestkapp/Halley Bay
	2	16.5	39/01	462–480	2	NE of Kap Norvegia
	30[b]	11.5–15.7	39/01	462–480	27	NE of Kap Norvegia
	1	17.4	39/09	560–571	1	NW of Kap Norvegia

[a] Positions on Polarstern expedition XIII/3 are given in Arntz and Gutt (1997)
[b] examined in all organs

and the liver. Only few specimens occurred encapsulated in *Muraenolepis microps*, which does not seem to be a preferred host for *P. decipiens*. No specimen was isolated from the fish musculature (present study; Palm et al. 1994, 1998), which contrasts with the heavy flesh infestation of nototheniids in sub-Antarctic waters (Waite 1916; Johnston and Mawson 1943). An advantage of the liver might be its high concentration of antifreezing proteins, which may help the nematode to survive subzero temperatures. The liver and body cavity as the preferred site of infestation was also recorded for *C. osculatum*, in contrast to the smaller *C. radiatum*, which was mainly found in the stomach wall (Klöser et al. 1992; Palm et al. 1998). Interestingly, all worms were red-colored in fish from the Weddell Sea, whereas the color of worms in fish from the South Shetland Islands varied from white to yellow to red. This indicates differences in the concentration of pseudo-coelomic hemoglobin as observed for the Atlantic sealworm (Dixon et al. 1993) in Antarctic *P. decipiens* as well.

The comparison of different Antarctic localities reveals clear differences between the eastern Weddell Sea coast and the area around the South Shetland Islands. Whereas the sealworm burden in fish species from the sub-Antarctic Islands (Johnston and Mawson 1943) as well as around the South Shetlands is high, fish species of a similar size from the Weddell Sea have a low intensity of infestation. Des Clers and Andersen (1995) and Jensen and Idås (1992) have demonstrated that the infestation rate of invertebrates and fish inhabiting areas near large seal populations is much higher than that of fish located far away from the seal colonies. However, the main final host *Mirounga leonina* lives on the South Shetland Islands, whereas the other important final host, *Leptonychotes weddellii*, is abundant along the eastern Weddell Sea coast (Hempel 1990) and at the South Shetland Islands. Both seals similarly prey on pelagic and benthic fish species (Casaux et al. 1997). Palm et al. (1994) have suggested that the light infestation in the Weddell Sea may be due to the lack of shallow coastal waters in this region. The Weddell seal *L. weddellii* can be considered the main final host for *P. decipiens* in the Weddell Sea. As this seal lives mainly on the sea ice along the shelf ice coast, eggs of *P. decipiens* will be released either directly onto the sea ice or during diving

Fig. 1 Liver of a *Chaenocephalus aceratus* from the South Shetland Islands infested with *Pseudoterranova decipiens* (*large*, *red-colored*) and *Contracaecum* spp. (*small*, *white specimens*)

near the edge of the ice. In contrast to the South Shetlands, a shallow-water coastal zone is lacking in the Weddel Sea. The eggs must thus spend more time in the water column before they reach the ground. McConnell et al. (1997) investigated sedimentation rates of *P. decipiens* eggs and concluded that due to their high sedimentation rates, they could not be transported over great distances, even in the presence of significant oceanic currents. The authors estimated that the eggs need about 20 days to reach a 200-m water depth, whereas the time required to reach shallow waters is much shorter. Due to the lack of shallow coastal zones along the Weddell Sea shelf ice, the eggs of *P. decipiens* would need up to 20–40 days to reach the bottom in 200–400 m of water depth at the studied localities. Upwelling situations prevent the eggs from settling, enhance drift (McConnell et al. 1997), and prolong the persistence of eggs in the water column. During such a long period, eggs of *P. decipiens* might either drift to the nearby continental slope or get directly lost after drifting under the shelf ice. Both situations are unlikely in the presence of shallow coastal zones such as those found in the South Shetland Islands. Thus, the low intensity of infestation in the Weddell Sea might be explained by the

loss of egg material due to the specific coastal morphology along the eastern Weddell Sea shelf ice.

Palm et al. (1994) discussed the influence of the first intermediate hosts as the weak point in the life cycle of Antarctic *P. decipiens*. Køie and Fagerholm (1993) and Køie et al. (1995) observed that two ecdyses take place in the eggs of anisakids. The third-stage larvae emerge from *Pseudoterranova* eggs, and the further life cycle depends on the size these larvae reach in their first in-
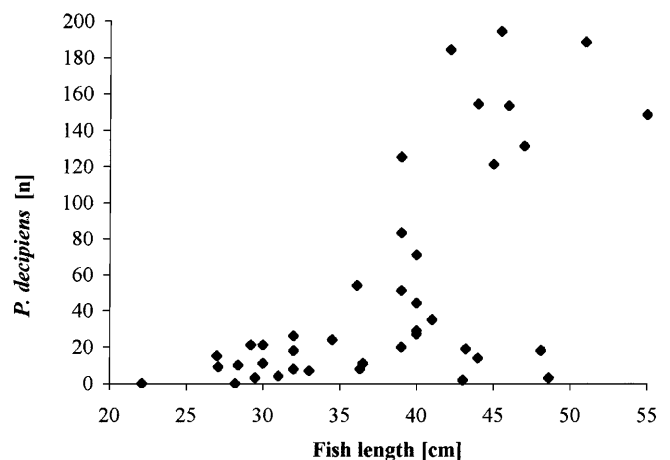

Fig. 2 Number of *P. decipiens* detected in *C. aceratus* ($n = 40$) from a water depth of 80–410 m around Elephant Island
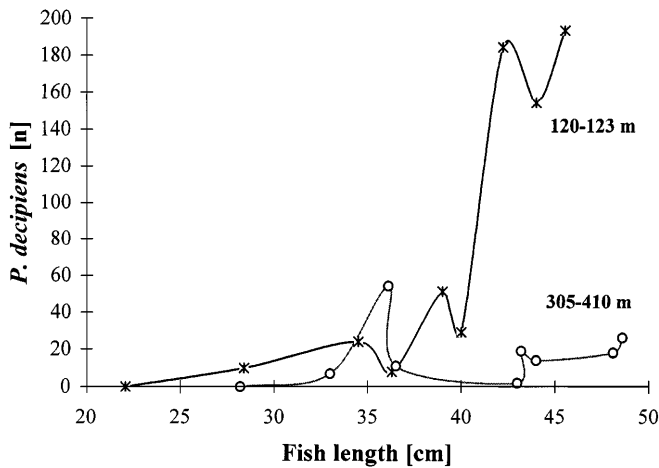
Fig. 3 Number of *P. decipiens* detected in *C. aceratus* (*n* = 18) from different water depths around Elephant Island (single position at 120–123 m and 3 positions at 305–410 m)

termediate hosts (McClelland 1995). Benthic harpacticoid or cyclopoid copepods and amphipods serve as first intermediate hosts, and unspecified benthic macroinvertebrates serve as second intermediate hosts. Measures (1996) has proposed that infective larvae ingested as soon as possible by first invertebrate hosts are more likely to be transmitted to subsequent hosts than those remaining longer in the external environment. Additionally, McClelland (1990) has demonstrated that larval amphipods are more susceptible to infection than are adults, indicating a higher level of parasite transmission when these hosts are abundant and at a susceptible age or size. Marcogliese (1996) could correlate the number of *P. decipiens* detected in sticklebacks with the total number of *P. decipiens* found in first intermediate hosts. Considering that Arctic shallow-water zones (depth 15–105 m) have a high benthic biomass in comparison with
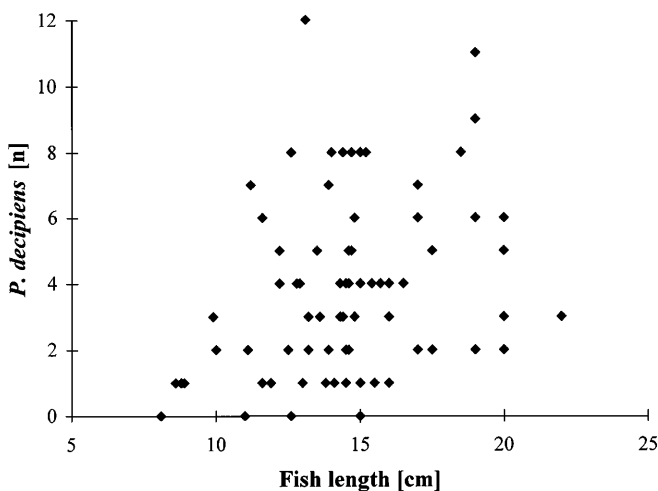

Fig. 4 Number of *P. decipiens* detected in *Lepidonotothen larseni* (*n* = 72) from a water depth of 145–353 m around Elephant Island

deep-water localities (depth 105–1088 m; Thomson 1982), the benthic first intermediate hosts for *P. decipiens* might also be more abundant in the shallow waters around the South Shetland Islands than along the eastern Weddell Sea coast. This explains the low number of *P. decipiens* detected in *Chaenocephalus aceratus* from 305–410 m of water depth in comparison with specimens from 120–123 m and might be another reason for the low infestation rates observed in the eastern Weddell Sea.

Low water temperatures might be another factor leading to lower infestation rates in the Weddell Sea (−1.6° to −2 °C) in comparison with the South Shetland Islands (−1.5° to +2 °C) (Carmack 1974; Gröhsler 1992). North Atlantic *Pseudoterranova* eggs were kept at −0.5 °C in seawater for 1–3 months, and after the temperature had been raised to 12 °C, about 72–96% of the larvae hatched (Brattey 1990). Sealworms would require more than 4 months to hatch in Labrador offshore areas (Brattey 1990), where monthly temperatures vary between −1.5° and +2 °C. Measures (1996) found no further development of *P. decipiens* eggs from Nova Scotia, Canada, which were kept at 0 °C for 1 year, and when they were placed at 18°–20 °C, very few larvae developed and hatched (0.6%). The author assumed that the inability to hatch after the prolonged period of cold may have been due to diminished larval energy reserves, which are needed for the larva to leave the egg. Transmission studies have also indicated that sealworm eggs and larvae are particularly sensitive to low water temperatures (Ronald 1960; McClelland 1982; Burt et al. 1990a). For example, copepods did not become infested when exposed to sealworm eggs stored at 0° and 5 °C for more than 120 days (McClelland 1982), and the larvae do need 135 days at 5 °C to reach an infective size for the fish intermediate hosts (McClelland 1990). Even the transfer of larval sealworms from small migratory prey fish to large predatory fish may be inhibited at low temperatures (Ronald 1960; Burt et al. 1990b). In summary, higher water temperatures reduce the time of development for *Pseudoterranova* eggs and larvae and increase the hatching success as well as the larval infectivity. However, as we found an established *P. decipiens* population in the eastern Weddell Sea, with its extremely low water temperatures, the real impact of the temperatures on the development of the Antarctic sealworm remains to be clarified. Interestingly, Bristow and Berland (1992) discussed a temperature barrier in northern waters as part of the original isolation mechanism that separated the host-specific sibling *P. decipiens* C from the other sibling species. A special adaptation to low water temperatures might be also the case for *P. decipiens* E in the Antarctic waters.

In contrast to the South Shetland waters, no difference could be observed in the occurrence of *P. decipiens* between different stations and between different water depths within the Weddell Sea. This might be related to the generally low numbers of worms found. The present data as compared with those reported by Palm et al.

(1994) indicate that the abundance of *P. decipiens* in the Weddell Sea can vary from year to year. The prevalence of infestation found for *Trematomus scotti*, *Dolloidraco longedorsalis*, and *Cryodraco antarcticus* were distinctly higher in comparison with the data reported by Palm et al. (1994) for fish sampled in 1986, and two more fish species were found infested. Both samples were taken during the Antarctic summer. However, as the fish specimens examined were not obtained from the same locality, this difference might also be a geographical variation or a matter of sampling size. The clarification of zoogeographical differences in parasite infestation within the eastern Weddell Sea will be an important question to answer in future studies.

In final summary, a combination of different factors can be seen as the reason for the infestation patterns observed at the localities studied. Besides possible differences in final host populations, the loss of eggs and larvae under the eastern Weddell Sea shelf ice and over the continental slope as well as differences in the availability of first intermediate and macroinvertebrate hosts lead to lower infestation levels. A minor role may be played by the reduced time of development and infectivity of eggs and larvae in the extremely cold waters of the Weddell Sea. *P. decipiens* is not a rare but, rather, a well-established parasite of the Antarctic fauna, which demonstrates the ability of this cosmopolitan species to establish its life cycle even under conditions of subzero temperatures. Whether this is a case of eurytherm behavior of a cosmopolitan nematode or whether this is a special adaptation of the Antarctic species *P. decipiens* E needs to be decided by future comparative experiments. A genetic isolation of Antarctic *Pseudoterranova* is unlikely, as their final hosts (*L. weddellii*, *M. leonina*) as well as some of their second intermediate hosts (*Dissostichus* spp.) regularly leave Antarctic waters (Fischer and Hureau 1985) and may thus transfer the Antarctic sibling to siblings from the South Atlantic, and vice versa.

References

Arntz W, Gutt J (1997) The expedition ANTARKTIS XIII/3 (EASIZ I) of "Polarstern" to the eastern Weddell Sea in 1996. Rep Polar Res 249: 101–103

Balguerías E, Morales-Nin B (1997) Weddell Sea fish ecology. In: Arntz W, Gutt J (eds) The expedition ANTARKTIS XIII/3 (EASIZ I) of "Polarstern" to the eastern Weddell Sea in 1996. Rep Polar Res 249: 82–97

Brattey J (1990) Effect of temperature on egg hatching in three ascaridoid nematode species from seals. In: Bowen WD (ed) Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can Bull Fish Aquat Sci 222: 27–39

Bristow GA, Berland B (1992) On the ecology and distribution of *Pseudoterranova decipiens* C (Nematoda: Anisakidae) in an intermediate host, *Hippoglossoides platessoides*, in northern Norwegian waters. Int J Parasitol 22: 203–208

Bullini L, Arduino P, Cianchi R, Nascetti G, D'Amelio S, Mattiucci S, Paggi L, Orecchia P (1992) Genetic and ecological studies on nematode endoparasites of the genera *Contracaecum* and *Pseudoterranova* in the Antarctic and Arctic-Boreal regions. Proceedings, 2nd meeting on Antarctic biology, Padova, 26–28 February, pp 131–146

Bullini L, Arduino P, Cianchi R, Nascetti G, D'Amelio S, Mattiucci S, Paggi L, Orecchia P, Plötz J, Berland B, Smith JW, Brattey J (1997) Genetic and ecological research on endoparasites of fish and marine mammals in the Antarctic and Arctic-Boreal regions. In: Battaglia B, Valencia J, Walton OWH (eds) Antarctic communities: species, structure and survival. SCAR Biol Symp Venice 6: 39–44

Burt MDB, Smith JW, Jarecka A, Pike AW, Wootten R, McClelland G (1990a) *Pseudoterranova decipiens* (Nematoda: Ascaridoidea): time of development to hatching of larvae at different temperatures and salinities. In: Bowen WD (ed) Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can Bull Fish Aquat Sci 222: 27–39

Burt MDB, Campbell JD, Likely CG, Smith JW (1990b) Serial passage of larval *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) in fish. Can J Fish Aquat Sci 47: 693–695

Camarck EC (1974) A quantitative characterization of water masses in the Weddell Sea during summer. Deep Sea Res 21: 431–443

Casaux RJ, Baroni A, Carlini A (1997) The diet of the Weddell seal *Leptonychotes weddelli* at Harmony Point, South Shetland Islands. Polar Biol 18: 371–375

Des Clers S, Andersen K (1995) Sealworm (*Pseudoterranova decipiens*) transmission to fish trawled from Hvaler, Oslofjord, Norway. J Fish Biol 46: 8–17

Dixon B, Kimmins W, Pohajdak B (1993) Variation in colour of *Pseudoterranova decipiens* (Nematoda; Anisakidae) larvae correlates with haemoglobin concentration in the pseudocoelomic fluid. Can J Fish Aquat Sci 50: 767–771

Fischer W, Hureau JC (eds) (1985) FAO species identification sheets for fishery purposes, vol 2. Southern Ocean (Fishing areas 48, 58 and 88; CCAMLR Convention Area). FAO, Rome, pp 233–470

Gon O, Heemstra PC (eds) (1990) Fishes of the Southern Ocean. Smith Institute of Ichthyology, Grahamstown

Gröhsler T (1992) Nahrungsökologische Untersuchungen an antarktischen Fischen um Elephant Island unter besonderer Berücksichtigung des Südwinters. Mitt Inst Seefisch Bundesforsch Fisch Hamburg 47

Gubsch G (1982) Zur Verbreitung und zur Biologie der Eisfische (Chaenichthyidae) im atlantischen Sektor der Antarktis. Fisch Forsch 20: 39–47

Hempel G (1990) The Weddell Sea – a high polar ecosystem. In: Sherman K, Alexander LM, Gold BO (eds) Large marine ecosystems: patterns, processes, and yields. Publication 90-305, American Association for Advanced Sciences, Washington D.C., pp 5–18

Holmes JC (1979) Parasite populations and host community structure. In: Nickel BB (ed) Host-parasite interfaces. Academic Press, New York, pp 27–46

Hoogesteger JN, White MG (1981) Notes on parasite infestation of inshore fish at Signy Island, South Orkney Islands. Br Antarct Surv Bull 54: 23–31

Hubold G (1992) Ecology of Weddell Sea fishes. Ber Polarforsch 103

Jackson CJ, Marcogliese DJ, Burt MDB (1997) Role of hyperbenthic crustaceans in the transmission of marine helminth parasites. Can J Fish Aquat Sci 54: 815–820

Jensen T, Idås K (1992) Infection with *Pseudoterranova decipiens* (Krabbe, 1878) larvae in cod (*Gadus morhua*) relative to proximity of seal colonies. Sarsia 76: 227–230

Johnston TH, Mawson PM (1943) Endoparasites from the sub-Antarctic islands. Rec S Aust Mus 7: 237–243

Kagei N, Asano K, Kihata M (1978) On the examination against the parasites of Antarctic krill, *Euphausia superba*. Sci Rep Whales Res Inst 30: 311–313

Kattner G (1998) (ed) The expedition ANTARKTIS XIV/2 of RV "Polarstern" in 1996/1997. Rep Polar Res 274

Kerstan SL (1991) Der Befall von Fischen aus dem Wattenmeer und dem Nordatlantik 1988–1990 mit Nematodenlarven und eine Bibliographie über parasitische Nematoden in Fischen und Seesäugern. Ber Inst Meereskd Kiel 219: 205

Klöser H, Plötz J, Palm HW, Bartsch A, Hubold G (1992) Adjustment of anisakid nematode life cycles to the high Antarctic food web as shown by *Contracaecum radiatum* and *C. osculatum* in the Weddell Sea. Antarct Sci 4: 171–178

Kock K-H (1998) Investigations on Antarctic fish. In: Kattner (ed) The expedition ANTARKTIS XIV/2 of RV "Polarstern" in 1996/1997. Rep Polar Res 274: 11–31

Køie M, Fagerholm H-P (1993) Third-stage larvae emerge from eggs of *Contracaecum osculatum* (Nematoda, Anisakidae). J Parasitol 79: 770–780

Køie M, Berland B, Burt MDB (1995) Development to third-stage larvae occurs in the eggs of *Anisakis simplex* and *Pseudoterranova decipiens* (Nematoda, Ascaridoidea, Anisakidae). Can J Fish Aquat Sci 52: 134–139

Marcogliese DJ (1996) Transmission of the sealworm, *Pseudoterranova decipiens* (Krabbe), from invertebrates to fish in an enclosed brackish pond. J Exp Biol Ecol 205: 205–219

McClelland G (1982) *Phocanema decipiens* (Nematoda: Anisakinae): experimental infections in marine copepods. Can J Zool 60: 502–509

McClelland G (1990) Larval sealworm (*Pseudoterranova decipiens*) infections in benthic macrofauna. Can Bull Fish Aquat Sci 222: 47–65

McClelland G (1995) Experimental infections of fish with larval sealworm, *Pseudoterranova decipiens* (Nematoda, Anisaki-

dae), transmitted by amphipods. Can J Fish Aquat Sci 52: 140–155

McConnell CJ, Marcogliese DJ, Stacey W (1997) Settling rate and dispersal of sealworm eggs (Nematoda) determined using a revised protocol for myxozoan spores. J Parasitol 83: 203–206

Measures LN (1996) Effect of temperature and salinity on development and survival of eggs and free-living larvae of sealworm (*Pseudoterranova decipiens*). Can J Fish Aquat Sci 53: 2804–2807

Paggi L, Nascett G, Cianchi R, Orecchia P, Mattiucci S, D'Amelio S, Berland B, Brattey J, Smith JW, Bullini L (1991) Genetic evidence for three species within *Pseudoterranova decipiens* (Nematoda, Ascaridida, Ascaridoidea) in the North Atlantic and Norwegian and Barent seas. Int J Parasitol 21: 195–212

Palm HW, Andersen K, Klöser H, Plötz J (1994) Occurrence of *Pseudoterranova decipiens* (Nematoda) in fish from the southeastern Weddell Sea (Antarctic). Polar Biol 14: 539–544

Palm HW, Reimann N, Spindler M, Plötz J (1998) The role of the rock cod *Notothenia coriiceps* Richardson, 1844 in the life cycle of Antarctic parasites. Polar Biol 19: 399–406

Parukhin AM, Lyadov VN (1982) [Helminthofauna of food Nototheniidae fishes from the Kerguelen subregion] (in Russian). Ekol Morja 10: 49–56.

Ronald K (1960) The effect of physical stimuli on the larval stage of *Terranova decipiens* (Krabbe, 1878) (Nematoda: Anisakidae). I. Temperature. Can J Zool 38: 623–642

Thomson DH (1982) Marine benthos in the eastern Canadian high Arctic: multivariate analyses of standing crop and community structure. Arctic 35: 61–74

Waite ER (1916) Fishes. In: Australasian Antarctic expedition 1911–1914 under the leadership of Sir Douglas Mawson. Zool Bot Ser C 3: 1–92

Zdzitowiecki K (1978) Wstepne badania nad pasozytami ryb okolic Poludniowych Szetlandow i Poludniowej Georgii (Antarktyka). Kosmos 6: 651–659

Zdzitowiecki K (1997) Faunistic analysis of fish parasites. In: Arntz W, Gutt J (eds) The expedition ANTARKTIS XIII/3 (EASIZ I) of "Polarstern" to the eastern Weddell Sea in 1996. Rep Polar Res 249: 101–103