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REVIEW ARTICLE

Helminths of Antarctic fishes: Life cycle biology, specificity and geographical distribution

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Abstract

Bony fishes (Teleostei) play an important role in the completion of life cycles of helminth parasites in the Antarctica. These fishes may be definitive, second intermediate or paratenic hosts of the helminths. The most species-rich taxon is Digenea. Virtually all of these digeneans use teleosts as definitive hosts. Only one species, *Otodistomum cestoides*, occurs as the adult stage in skates (Chondrichthyes), with teleosts as its second intermediate host. Among 14 cestode species maturing in fishes only one, *Parabothriocephalus johnstoni*, occurs in a bony fish, *Macrourus whitsoni*, whereas the others are parasites of Chondrichthyes (cartilaginous fishes). Antarctic Chondrichthyes are not infected with nematode and acanthocephalan species. Specificity to the intermediate and/or paratenic hosts of the majority of Antarctic helminths is wide, whereas that for definitive hosts is often narrower, restricted to one order or sometimes even to one or two host species. Almost all of 73 helminth species maturing in Antarctic fishes are endemics. Only 4 digenean and one nematode species are cosmopolitan or bipolar.

Key words

Helminths, fish, biology, specificity, distribution, Antarctica

Introduction

Geographically the Antarctica comprises a continent, a vast expanse of ocean, and a scattering of small archipelagos and islands, with a total area of about 45 million square kilometres. The northern boundary of the Antarctica is the Antarctic convergence line which runs about 60°S in the Pacific and about 50°S in the Atlantic and the Indian Ocean. North of this line extends the Subantarctica reaching to the subtropical convergence line which runs about 40°S. South of the Antarctic convergence line there are three subregions or provinces – East Antarctica, West Antarctica and South Georgia. The latter province is considered by some authors as a part of Subantarctica. Many of the islands and sea mounts of the Indian and Pacific Oceans as well as those near to the southern tip of South America belong to Subantarctica.

Often the terms "high Antarctica" and "low Antarctica" are used. The Antarctic Polar Circle is at 66°33´S latitude; areas inside the Polar Circle are named high Antarctica whereas those outside the Polar Circle – low Antarctica.

Antarctic vertebrates are definitive hosts of internal parasitic worms belonging to four helminth taxa: Digenea, Cestoda, Nematoda and Acanthocephala. The most species-rich group of Antarctic vertebrates is the bony fishes. According to Eastman and Clarke (1998), 274 species from 49 families occur in the Antarctic and Subantarctic waters and over 120 species belong to the endemic superfamily Notothenioidei. Chondrichthyes are represented by sharks and skates (Fischer and Hureau 1985, Gon and Heemstra 1990). Sharks are rare in Antarctica but 3 species have been caught off South Georgia. All Antarctic skates belong to the family Rajidae with about 10 species from two genera: *Raja* Linnaeus, 1758 and *Bathyraja* Ishiyama, 1958.

Antarctic bony fishes play an important role in the completion of life cycles of many helminth species. Teleosts serve as either definitive or intermediate and paratenic hosts. By contrast, skates and sharks are definitive hosts only.

There are four major reviews describing the occurrence of fish helminths in Antarctica. Zdzitowiecki (1997a) produced a monograph on digeneans, but within a short time 10 addi-

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tional species from the Weddell Sea and one off Adelie Land were described (Zdzitowiecki 1997b, c, d; 1998a, b; Zdzitowiecki and Cielecka 1997a, b, c). Zdzitowiecki (1991a) also reviewed Antarctic acanthocephalans: So far, no additional species have been described. Two papers provide data on Antarctic fish cestodes and nematodes (Rocka 2003, 2004).

The purpose of the present communication is to summarize the information on fish helminths occurring in Antarctic waters. Particular emphasis is given to their biology, specificity and geographical distribution in order to evaluate the necessity for and direction of future research on fish in Antarctic waters.

Life cycles of Antarctic parasites

Digenea

Overall life cycles of Antarctic parasites are poorly known. Zdzitowiecki (1997a) suggested that probably all digeneans maturing in Antarctic bony fishes use molluscs as hosts of parthenogenetic generations (the first intermediate hosts in traditional nomenclature) and various marine invertebrates as intermediate hosts (or the second intermediate hosts). Up to now, only metacercariae of *Neolebouria antarctica* (Szidat et Graefe, 1967) have been found in Antarctic crustaceans (Gaevskaya 1982). One species maturing in skates, *Otodistomum cestoides* (Beneden, 1871), has been found in final hosts in Antarctica (Zdzitowiecki 1991b) and Subantarctica (Gibson 1976, Zdzitowiecki and Pisano 1996). Metacercariae of this species were found in the body cavity of teleosts in the Weddell Sea (Zdzitowiecki 1997d).

Rediae, cercariae and metacercariae of two bird parasites, *Paramonostomum antarcticum* Graefe, 1968 and *Gymnophallus delicious* (Olsson, 1893), have been recorded in Antarctic marine snails (Graefe 1968, Feiler 1986).

Cestoda

Only one complete life cycle of a cestode is known in Antarctica. *Hymenolepis arctowskii* Jarecka et Ostas, 1984 (Cyclophyllidea), maturing in *Larus dominicanus* (Dominican gull), uses *Branchinecta gaini* (Branchiopoda) as its intermediate host (Jarecka 1984). As elsewhere life cycles of the Cyclophyllidea (parasites of birds) and the Bothriocephalidae and Echinophallidae (Pseudophyllidea, parasites of bony fishes) probably are realized with two hosts.

Life cycles of species from the Tetraphyllidea (parasites of skates) and the families Diphyllobothriidae and Tetrabothriidae (parasites of birds and mammals) are more complex. Outside Antarctica these groups have crustaceans as first intermediate hosts while second intermediate and/or paratenic hosts are bony fishes. Larvae of Tetraphyllidea as well as plerocercoids of Diphyllobothriidae occur commonly in the Antarctic and Subantarctic bony fishes (Table V).

The occurrence of larval forms in bony fishes that are permanently resident in Antarctica suggests that these life cycles are completed in the region. Five morphological forms of tetraphyllidean cercoids have been reported from Antarctica (Wojciechowska 1993a, b, c; Wojciechowska *et al*. 1994; Rocka 2003). There were cercoids with subdivided bothridia (one, two and three loculi), bothridia undivided with hook-like projections, and subcylindrical bothridia. Cercoids with monolocular bothridia are regarded as representatives of *Anthocephalum* spp., those with bilocular bothridia are larvae of *Pseudanthobothrium*, *Notomegarhynchus* and *Anthobothrium*. Cercoids with trilocular bothridia are recognized as larvae of the family Oncobothriidae; only one species of this family, *Oncobothrium antarcticum* Wojciechowska, 1990, has been described in Antarctica. Cercoids with undivided bothridia and hook-like projections probably belong to the species *Dinobothrium septaria* Beneden, 1889, a parasite of a pelagic shark, *Lamna nasus* (Bonnaterre, 1788), occurring on the shelves around of South Georgia and the Kerguelen Islands. Cercoids with subcylindrical bothridia are determined as *Marsupiobothrium* spp. Two species of this genus have been described from Antarctica (Wojciechowska 1991, Rocka and Zdzitowiecki 1998).

The other common cestode larval forms occurring in bony fishes are plerocercoids of the Diphyllobothriidae (Table V), that as adults occur in seals and birds (see Rocka 2003). Unfortunately, matching of larval with adult cestodes has not proved possible so far. However, Prudhoe (1969) identified plerocercoids from nine teleost species of the superfamily Notothenioidei as belonging to *Glandicephalus perfoliatus* (Railliet et Henry, 1912), a parasite of seals.

Cercoids lacking bothridia were found in fishes caught off South Georgia. Hoberg (1987) regarded similar larvae as belonging to the family Tetrabothriidae. Representatives of this family are common parasites of Antarctic birds and mammals (Table V).

Nematoda

Life cycles of nematodes parasitising Antarctic bony fishes are unknown. Various anisakid genera *Anisakis* Dujardin, 1845, *Contracaecum* Railliet et Henry, 1912, *Hysterothylacium* Ward et Magath, 1917 and *Pseudoterranova* Mozgovoy, 1950 whose adults infect marine mammals, birds and fishes, occur commonly in Antarctic teleosts as larvae (Table V). Anisakid nematodes of mammals use various marine invertebrates, mainly crustaceans, as first intermediate hosts; Antarctic bony fishes are second intermediate and paratenic hosts (Palm *et al*. 1994, 1998; Palm 1999; Walter *et al*. 2002).

According to Johnston and Mawson (1945), Klöser and Plötz (1992) and Klöser *et al*. (1992) two species, *Contracaecum osculatum* (Rudolphi, 1802) and the endemic *C. radiatum* (Linstow, 1907), were obtained from pinnipeds in high Antarctic waters. A third species *C. mirounga* has been recorded from Subantarctica (Nikolskiy 1974). Orecchia *et al*. (1994) reported two distinct reproductively isolated species, *C. osculatum* D and E, from Antarctica. Johnston and Mawson (1945) and Mozgovoy (1953) found *Anisakis similis* Baylis, 1920 and *A. physeteris* Baylis, 1923 in Antarctic marine mam-

mals. However, the status of *A. similis* is doubtful as Anderson (2000) stated that three valid species represented the genus *Anisakis*: *A. simplex* (Rudolphi, 1802), *A. typica* (Diesing, 1860) and *A. physeteris*. Mattiucci *et al*. (1997) regarded *A. simplex* as a complex consisting of three sibling species, *A. simplex* A occurring in the Austral region, between 35°S and 55°S, as well as in the Mediterranean Sea; the name *A. pegreffii* was proposed for this species. *A. simplex* B is widespread between 30°N and the Arctic Polar Circle. *A. simplex* C has a discontinuous range, including Pacific Canada and regions south of 35°S latitude. So, it is possible that *A. similis* is a synonym of *A. simplex*, possibly *A. pegreffii*.

Palm (1999) stated that one sibling species, *Pseudoterranova decipiens* E, occurred in Antarctic waters. The genetic distance of this species from other species within the *Pseudoterranova decipiens* complex was described by Zhu *et al*. (2002). A frequent parasite of bony fishes, *Hysterothylacium aduncum* (Rudolphi, 1802) was recorded from two notothenioid species from environs of the South Shetland Islands and off South Georgia (Gaevskaya *et al*. 1990, Rokicki unpubl.).

Acanthocephala

According to Zdzitowiecki (1991a) all acanthocephalans that mature in Antarctic fishes have two hosts in their life cycles, whereas species adult in Antarctic birds and pinnipeds (*Corynosoma* spp. and *Andracantha* spp.) have in addition a third paratenic host, a teleost (Table V). Whale acanthocephalans (*Bolbosoma* spp.) probably have either two or three hosts. Antarctic Amphipoda are recorded as the intermediate hosts of four acanthocephalan species (Hoberg 1986, Zdzitowiecki 2001, Zdzitowiecki and Presler 2001).

Zdzitowiecki (1991a) reported that acanthocephalans are common in bottom-living fishes, but absent from pelagic ones. This is most probably due to the role of benthic (not pelagic) crustaceans as intermediate hosts of most Antarctic species occurring in fishes. Some *Corynosoma* and *Andracantha* species have been found in Antarctica in both definitive and paratenic hosts. Zdzitowiecki (1991a) reported cystacanths of seven acanthocephalan species (parasites of birds and seals) in teleosts as paratenic hosts (Table V). Some species of *Corynosoma* and all *Bolbosoma* spp. are known from Antarctica exclusively in their definitive hosts. Possibly their intermediate hosts do not occur in Antarctica, the infections originating from Subantarctica and temperate zones. *Bolbosoma* spp. are associated with pelagic rather than benthic environments; their cystacanths have been found outside Antarctica in pelagic euphasiid crustaceans (Zdzitowiecki 1991a).

Geographical distribution and host specificity of Antarctic fish parasites

Digenea (Table I; data according to Zdzitowiecki 1997a, 1998a, b, 1999). Adult Antarctic fish digeneans from the superfamily Hemiuroidea occur in the stomach and in the intestine, and only a parasite of skates, *Otodistomum cestoides*, occurs in an immature stage in the body cavity of teleosts. Apart from *O. cestoides*, only *Lecithochirium whitei* Zdzitowiecki, 1994 and probably *Lecithophyllum champsocephali* Zdzitowiecki, 1989, have a narrow specificity to final hosts. As only a single specimen of *Aphanurus* sp. was found nothing can be said about its specificity. The remaining hemiuroid species occur in fishes belonging to 2–7 orders.

Four species, *O. cestoides*, *Derogenes varicus* (Müller, 1784), *Gonocerca phycidis* Manter, 1925 and *Glomericirrus macrouri* (Gaevskaya, 1975), are cosmopolitan or bipolar. Probably three of them occur in all areas of Antarctica; the fourth species, *D. varicus*, the most abundant digenean species in the World Ocean, is replaced in the high Antarctica by *Derogenes johnstoni* Prudhoe et Bray, 1973 (Zdzitowiecki *et al*. 1993). The second pair of closely related species are *Lecithaster macrocotyle* Szidat et Graefe, 1967 and *L. micropsi* Zdzitowiecki, 1992. Their distribution is restricted to the southern hemisphere. The former occurs in the low Antarctica, in the Subantarctica and rarely in the Ross Sea, the latter occurs in the Subantarctica and off South Georgia. Specimens of both pairs of parasites occur partly in the same fish species, for example *Derogenes* spp. in *Trematomus hansoni* Boulenger, 1902 and *Lecithaster* spp. in *Chaenocephalus aceratus* Lönnberg, 1906. It suggests that their presence or absence is not associated with the distribution of definitive hosts, but rather with the presence or absence of the molluscan hosts for the parthenogenetic generations.

Nine species from the family Opecoelidae occur in the Eastern Antarctica, but only two of them also off the South Shetland Islands. Two other species occur off South Georgia and in Subantarctica. The specificity to definitive hosts is narrower than that of Hemiuroidea.

Two species, *Macvicaria georgiana* (Kovaljova et Gaevskaya, 1974) and *M. microtestis* Zdzitowiecki et Cielecka, 1997, occur entirely in Notothenioidei. Two other species, *M. antarctica* (Kovaljova et Gaevskaya, 1974) and *Helicometra pisanoae* Zdzitowiecki, 1998, were found in Nototheniidae [the former occurs in *Notothenia kempi* Norman, 1937 and *Nototheniops nudifrons* (Lönnberg, 1905), the latter in *Trematomus hansoni* (Boulenger, 1902)]. Three species, *Discoverytrema markowskii* Gibson, 1976, *D. gibsoni* Zdzitowiecki, 1990 and *Macvicaria muraenolepidis* Zdzitowiecki, 1990, appear to be specific to the Muraenolepididae. One species, *Macvicaria longibursata* Zdzitowiecki et Cielecka, 1997, is specific to Zoarcidae. Two species, *Macvicaria ophthalmolyci* Zdzitowiecki, 1990 and *Helicometra antarcticae* Holloway et Bier, 1968, occur in both Nototheniidae and Zoarcidae. Three species, *Stenakron glacialis* Zdzitowiecki, 1989, *Neolebouria antarctica* and *N. terranovaensis* Zdzitowiecki, Pisano et Vaccchi, 1993, normally occurring in Notothenioidei, also rarely occur in Liparididae and another one, *Macvicaria pennelli* (Leiper et Atkinson, 1914), in Zoarcidae. Some closely related but distinct species occur in different areas. For example, *M. pennelli* occurs in the Ross Sea and the southern part of the Indian Ocean, *M. antarctica* in Subantarctica and rarely off South Georgia; *Neolebouria antarctica* occurs in the Western Antarctica and off South

Georgia, whereas *N. terranovaensis* in the Eastern Antarctica. In contrast, two species of the genus *Discoverytrema* occur in the same host (*Muraenolepis microps* Lönnberg, 1905), habitat (posterior part of the small intestine) and locality (off South Georgia). None of the opecoelid species occurring in subcontinental waters of Antarctica was recorded in Subantarctica.

The South Georgia represents an intermediate position, as both Antarctic and Subantarctic opecoelids occur there.

Table I. A list of Digenea found in Antarctic fishes as definitive hosts (data according to Zdzitowiecki 1997a, 1998a, b, 1999)

Digenea	Hosts	West Antarctica	East Antarctica	South Georgia	Subant-arctica	Cosmo-politan or bipo-lar
Hemiuroidea						
*Otodistomum cestoides**	Chondrichthyes	+			+	+
Genolinea bowersi	Notothenioidei	+	+	+	+	
Aphanurus sp.	*Ophthalmolycus amberensis* (Zoarcidae)		+			
Derogenes johnstoni	Notothenioidei		+			
D. varicus	various teleosts	+			+	+
Gonocerca phycidis	Notothenioidei, Gadiformes	+	+	+	+	+
Elytrophalloides oatesi	various teleosts	+	+	+	+	
Glomericirrus macrouri	Notothenioidei, Gadiformes	+	+		+	+
Lecithochirium whitei	*Bathylagus antarcticus* (Bathylagidae)		+?	+		
Lecithaster macrocotyle	Notothenioidei	+	+	+	+	
L. micropsi	Notothenioidei, Muraenolepididae			+	+	
Lecithophyllum champsocephali	Channichthyidae	+				
Opecoelidae						
Discoverytrema markowskii	Muraenolepididae			+	+	
D. gibsoni	*Muraenolepis microps* (Muraenolepididae)			+		
Macvicaria pennelli	Notothenioidei, ?Zoarcidae		+			
M. georgiana	Notothenioidei	+	+	+		
M. antarctica	Nototheniidae			+	+	
M. microtestis	Notothenioidei		+			
M. ophthalmolyci	Nototheniidae, Zoarcidae	+				
M. longibursata	Zoarcidae		+			
M. muraenolepidis	*Muraenolepis microps* (Muraenolepididae)			+		
Neolebouria terranovaensis	Notothenioidei		+			
N. antarctica	Notothenioidei	+		+		
Helicometra antarcticae	Nototheniidae, Zoarcidae		+			
H. pisanoae	*Trematomus hansoni* (Nototheniidae)		+			
H. rakusai	*T. loennbergi* (Nototheniidae)		+			
Stenakron glacialis	Notothenioidei	+	+			
Lepocreadiidae						
Lepidapedon garrardi	Notothenioidei	+	+	+	+	
L. balgueriasi	Nototheniidae		+			
L. notogeorgianus	Nototheniidae	+?		+		
L. tertius	*Ophthalmolycus amberensis* (Zoarcidae)	+				
L. paralebouri	*Muraenolepis microps* (Muraenolepididae)			+		
L. brayi	*Macrourus whitsoni* (Macrouridae)		+			
L. ninae	*Macrourus whitsoni* (Macrouridae)		+			
Neolepidapedon magnatestis	Nototheniidae			+	+	
N. trematomi	Notothenioidei	+	+	+		
N. macquariensis	Notothenioidei		+		+	
Paralepidapedon antarcticum	*Macrourus whitsoni* (Macrouridae)		+			
P. dubium	*Macrourus whitsoni* (Macrouridae)		+			
P. awii	*Macrourus whitsoni* (Macrouridae)		+			
Muraenolepitrema magnatestis	*Muraenolepis microps* (Muraenolepididae)			+		
Postlepidapedon opisthobifurcatus	Muraenolepididae, Macrouridae		+	+		
Monorchiidae						
Postmonorchis variabilis	Nototheniidae, Harpagiferidae			+	+	
Fellodistomidae						
Steringophorus arntzi	Bathydraconidae, Artedidraconidae		+			
S. liparidis	*Paraliparis antarcticus* (Liparididae)		+			

*Parasite of skates found in teleosts as intermediate hosts in the Weddell Sea and adult in *Bathyraja eatonii* off the South Shetland Islands.

Most of species of the family Lepocreadiidae are specific either to Notothenioidei or even only to Nototheniidae (five specific species and one additionally recorded in a zoarcid) or to Gadiformes – families Muraenolepididae and/or Macrouridae. Only one species, *Lepidapedon tertius* Zdzitowiecki, 1990, is specific to Zoarcidae. Distribution is usually restricted either to exclusively subcontinental waters (7 species) or to subcontinental waters and shelves around South Georgia area (3 species). Two species, *Lepidapedon paralebouri* Zdzitowiecki, 1990 and *Muraenolepitrema magnatestis* Gaevskaya et Rodjuk, 1988, have been recorded only off South Georgia. Three species, *Lepidapedon garrardi* (Leiper et Atkinson, 1914), *Neolepidapedon magnatestis* (Gaevskaya et Kovaljova, 1976) and *N. macquariensis* Zdzitowiecki, 1993, occur in both Antarctic and Subantarctic regions. *L. garrardi* is common in all areas investigated. The only representative of Monorchiidae, *Postmonorchis variabilis* Prudhoe et Bray, 1973, is common in Notothenioidei that are its principal hosts off South Georgia and in Subantarctica, and is absent in subcontinental waters.

Two fellodistomid species were described from the Weddell Sea and each is specific to one higher taxon of fishes: *Steringophorus arntzi* Zdzitowiecki, 1997 to Notothenioidei, and *S. liparidis* Zdzitowiecki, 1997 to Liparididae.

Cestoda (Table II)

The 13 cestode species parasitising Antarctic Chondrichthyes are endemics and each infects one or rarely two host species. If two hosts, these belong to the same genus (Rocka 2003). Only skates from environs of the South Shetland Islands, South Georgia, and several specimens from the Weddell Sea have been examined so that it is not possible to comment about the geographical distribution of these cestodes. Only one Antarctic cestode, *Parabothriocephalus johnstoni* Prudhoe, 1969, has been recorded from a gadid host, *Macrourus whitsoni* Regan, 1913, caught in the Eastern Antarctica (Prudhoe 1969, Rocka and Zdzitowiecki 1998). Up to now, adult cestodes have not been found in Antarctic species of Notothenioidei, although two species, *Bothriocephalus kerguelensis* Prudhoe, 1969 and *B. antarcticus* Wojciechowska, Pisano et Zdzitowiecki, 1995, occur in Subantarctic fishes from this superfamily (*Notothenia cyanobrancha* Richardson, 1844, *N. rossii* Richardson, 1844, *Champsocephalus gunnari* Lönnberg, 1905 and *Channichthys rhinoceratus* Richardson, 1844) (Prudhoe 1969, Wojciechowska *et al*. 1995).

Nematoda (Table III)

Only six nematode species have been found as adults in Antarctic teleosts (Rocka 2004). Common species, *Ascarophis nototheniae* Johnston et Mawson, 1945, a parasite of Notothenioidei and rarely Congiopodidae and Zoarcidae, occurs in various localities of Antarctica and Subantarctica. Two other species, *Paranisakiopsis weddelliensis* Rocka, 2002 and *Capillaria* (*Procapillaria*) sp. (see Rocka 2002), were found only in *Macrourus whitsoni* from the Weddell Sea. *Cystidicola beatriceinsleyae* (Holloway et Klewer, 1969) was described from two species of Zoarcidae, *Lycodichthys dearborni* (DeWitt, 1962) and *L. antarcticus* Pappenheim, 1911, caught in Eastern Antarctica. *Hysterothylacium aduncum* (Rudolphi, 1802), has been reported from two species of Nototheniidae (*Dissostichus mawsoni* Norman, 1937 and *D. eleginoides* Smitt, 1898) in the environs of the South Shetlands and off South Georgia. Contrary to other nematode species it is cosmopolitan and has wide specificity. *Dichelyne fraseri* (Baylis, 1929) is a common parasite of various notothenioid fishes occurring circumpolarly on both sides of the Antarctic con-

Table II. A list of Cestoda found in Antarctic fishes as definitive hosts (data according to Rocka 2003)

Cestoda	Hosts	West Antarctica	East Antarctica	South Georgia
Parasites of skates and sharks				
Tetraphyllidea				
Phyllobothrium dentatum	unidentified shark			+
Anthocephalum georgiense	*Raja georgiana*			+
A. rakusai	*Bathyraja maccaini*	+		
A. siedleckii	*B. maccaini, B. eatonii*	+	+	
A. arctowskii	*Bathyraja* sp. 2	+	+	
Marsupiobothrium antarcticum	*B. maccaini, B. eatonii*	+		
M. awii	*B. maccaini*		+	
Anthobothrium sp.	*Bathyraja* sp. 2	+		
Pseudanthobothrium notogeorgianum	*R. georgiana*			+
P. minutum	*B. eatonii*	+		
Notomegarhynchus shetlandicum	*B. maccaini, B. eatonii*	+		
Oncobothrium antarcticum	*B. maccaini, B. eatonii*	+	+	
Diphyllidea				
Echinobothrium acanthocolle	*R. georgiana*			+
Parasites of bony fishes				
Pseudophyllidea				
Parabothriocephalus johnstoni	*Macrourus whitsoni* (Macrouridae)		+	

Table III. A list of Nematoda found in Antarctic bony fishes as definitive hosts (data according to Rocka 2004)

Nematoda	Hosts	West Antarctica	East Antarctica	South Georgia	Subant-arctica	Cosmo-politan or bipolar
Spirurida						
Ascarophis nototheniae	Notothenioidei, Congiopodidae, Zoarcidae	+	+	+	+	
Cystidicola beatriceinsleyae	*Lycodichthys dearborni*, *L. antarcticus* (Zoarcidae)		+			
Ascaridida						
Hysterothylacium aduncum	*Dissostichus mawsoni*, *D. eleginoides* (Nototheniidae)	+		+		+
Paranisakiopsis weddelliensis	*Macrourus whitsoni* (Macrouridae)		+			
Dichelyne fraseri	Notothenioidei, Muraenolepididae	+		+	+	
Enoplida						
Capillaria (*Procapillaria*) sp.	*Macrourus whitsoni* (Macrouridae)		+			

vergence line – in the Kerguelen and Magellanic subregions of Subantarctica and in Western Antarctica at open sea islands situated up to 62°S (Zdzitowiecki and Cielecka 1996). This parasite is absent in fishes from subcontinental waters. The infection seems to be associated with a benthic environment. It should be noted that Antarctic Chondrichthyes are not infected with adult nematodes. However, representatives of the families Anisakidae, Cystidicolidae and Camallanidae occur in Chondrichthyes in other geographical regions of the World (Mozgovoy 1953; Hartwich 1974; Chabaud 1975a, b; Anderson 2000; Knoff *et al*. 2001a).

Acanthocephala (Tables IV and V)

Zdzitowiecki (1991a) reported that eight acanthocephalan species mature in teleosts and each of these species has a wide range of definitive hosts. The occurrence of mature females of *Aspersentis megarhynchus* (Linstow, 1892), *Metacanthocephalus johnstoni* Zdzitowiecki, 1983, *M. dalmori* Zdzitowiecki, 1983 and *M. rennicki* (Leiper et Atkinson, 1914), were usually found in fishes belonging to two or three families grouped in the superfamily Notothenioidei. According to Holloway and Spence (1974, 1980) *Metacanthocephalus campbelli* (Leiper et Atkinson, 1914), was additionally found in representatives of Zoarcidae, systematically far from Notothenioidei. Two further species, *Echinorhynchus petrotschenkoi* (Rodjuk, 1984) and *E. muraenolepisi* (Rodjuk, 1984), appear to be parasites of gadiform fishes.

Echinorhynchus muraenolepisi has been found exclusively in *Muraenolepis microps* Lönnberg, 1905 in the environs of the South Shetland Islands and South Georgia (Rodjuk 1984). *E. petrotschenkoi* was abundant in *M. microps* off South Georgia (Zdzitowiecki 1989, 1990) and *Macrourus whitsoni* in the Weddell Sea (Zdzitowiecki 1996). Additionally, this species was reported from various nototheniids at the Enderby Land (Kagei and Watanuki 1975), South Shetland Islands (Rodjuk 1984; Zdzitowiecki 1986a, b, 1989, 1990) and South Georgia (Rodjuk 1986; Zdzitowiecki 1989, 1990; Gaevskaya *et al*. 1990; Zdzitowiecki and White 1992). Gravid females of *Heterosentis heteracanthus* (Linstow, 1896) have not so far been found. According to Zdzitowiecki (1985, 1991a) two species, *Corynosoma shackletoni* Zdzitowiecki, 1978 and *Andracantha baylisi* (Zdzitowiecki, 1986), mature in Antarctic

Table IV. A list of Acanthocephala found in Antarctic bony fishes as definitive hosts (data according to Zdzitowiecki 1991a, 1996)

Acanthocephalan species	Hosts	West Antarctica	East Antarctica	South Georgia	Subantarctica
Echinorhynchida					
Aspersentis megarhynchus	Notothenioidei	+		+	+
Heterosentis heteracanthus	Notothenioidei	+		+	+
Echinorhynchus petrotschenkoi	Notothenioidei, *Macrourus whitsoni* (Macrouridae), *Muraenolepis microps* (Muraenolepididae)	+	+	+	
E. muraenolepisi	*M. microps* (Muraenolepididae)	+		+	
Metacanthocephalus campbelli	Notothenioidei, Zoarcidae	+	+		
M. dalmori	Notothenioidei	+	+	+	
M. rennicki	Notothenioidei		+		+?
M. johnstoni	Notothenioidei	+	+	+	

Table V. A list of parasites found in Antarctic bony fishes as intermediate or paratenic hosts

Parasites	Kind of host	Definitive host	West Antarctica	East Antarctica	South Georgia	Subantarctica	Cosmopolitan or bipolar
Digenea							
Otodistomum cestoides[*]	2nd interm.	skate	+			+	+
Cestoda[**]							
Tetraphyllidea	2nd interm., paratenic						
Cercoid monolocular		skate	+	+	+	+	
Cercoid bilocular		skate	+	+	+	+	
Cercoid trilocular		skate	+	+			
Cercoid with projections		shark			+	+	+?
Cercoid subcylindrical		skate		+			
Diphyllobothriidae	2nd interm., paratenic						
Plerocercoid		mammal, bird	+	+	+	+	+
Tetrabothriidae	2nd interm., paratenic						
Cercoid lacking acetabula		bird or mammal			+		
Nematoda[***]	2nd interm., paratenic						
Contracaecum radiatum		seal	+	+	+	+?	
C. osculatum D, E		seal	+	+	+		
Contracaecum spp.		seal, bird	+	+	+	+	
Anisakis spp.		whale	+		+	+	
Pseudoterranova decipiens E		seal	+	+	+	+	
Acanthocephala[****]	paratenic						
Corynosoma arctocephali		seal, fur seal	+	+	+		
C. bullosum		seal	+	+	+	+	+?
C. evae		seal, fur seal	+		+	+	
C. hamanni		seal	+	+	+		
C. pseudohamanni		seal	+	+			
C. shackletoni		bird	+		+		
Andracantha baylisi		bird	+		+	+	

[*]Data according to Zdzitowiecki (1997a); [**]data according to Rocka (2003); [***]data according to Rocka (2004); [****]data according to Zdzitowiecki (1991a).

birds. Also, seven species of the genus *Corynosoma* and five species of the genus *Bolbosoma* occur in seals, fur seals and whales (Zdzitowiecki 1991a).

The Antarctic Chondrichthyes are not infected with Acanthocephala. According to Petrotschenko (1971a, b) and Knoff *et al*. (2001b) acanthocephalan species have been found in Chondrichthyes outside Antarctica. Adult acanthocephalan species usually occur in mammals, birds or teleosts so that Chondrichthyes are probably accidental hosts.

Analysis of the occurrence of all acanthocephalan species in various latitudes permits the division of the species recorded in Antarctica into three groups. The first group comprises three species found mainly inside the Polar Circle, but also occurring outside the Polar Circle. These are: *Metacanthocephalus campbelli*, *M. rennicki* and *Corynosoma pseudohamanni* Zdzitowiecki, 1984. The second group comprises common species characteristic mainly for the environs of the continent's coasts outside the Polar Circle and subcontinental archipelagos such as the South Shetland Islands and the South Orkneys. Most of these species (except *Metacanthocephalus dalmori*) also occur, often particularly, in the environs of the islands situated in close proximity to the Antarctic convergence line and in Subantarctica. This group includes 9 species: *Metacanthocephalus johnstoni*, *M. dalmori*, *Aspersentis megarhynchus*, *Echinorhynchus petrotschenkoi*, *E. muraenolepisi*, *Corynosoma bullosum* (Linstow, 1892), *C. arctocephali* Zdzitowiecki, 1984, *C. hamanni* (Linstow, 1892) and *C. shackletoni*. However, *M. dalmori*, *E. petrotschenkoi* and *C. bullosum* were found in fish in the Weddell Sea (Zdzitowiecki 1996). The relative high abundance of the latter species is perplexing because the definitive host, elephant seals, only occasionally visit high Antarctica. According to Zdzitowiecki and Laskowski (2004) for *A. megarhynchus* and *C. hamanni* the southern boundary of their distribution is probably near 65°S off the Argentine Islands.

The representatives of the third group of Acanthocephala normally do not occur in Antarctic fishes but are usually found in definitive hosts on both sides of the Antarctic convergence line and also outside Antarctica. The representatives of this group penetrate far into Antarctica, but do not occur commonly there. This group includes species of the genus *Bolbosoma* (parasites of whales) and *Profilicollis antarcticus* Zdzitowiecki, 1985 (parasite of birds found at the South Shetland Islands). Unquestionable representatives of the third group are three further species: *Corynosoma australe* Johnston, 1937, *C. hannae* Zdzitowiecki, 1984 and *C. evae* Zdzitowiecki, 1984 (one cystacanth found at South Georgia).

Two species, *Heterosentis heteracanthus* and *Andracantha baylisi*, occur mainly in Subantarctica and rarely in low Antarctica. Recently, these species have been found in notothenioid fishes in the Beagle Channel, Magellanic subregion of Subantarctica (Zdzitowiecki, pers. comm.).

The vast majority of Antarctic acanthocephalans do not occur in the northern hemisphere. The exceptions to this rule seemed to be the cosmopolitan representatives of the genus *Bolbosoma*, whale parasites. Skryabin (1972) observed morphological differences between specimens belonging to the same species, but originating from different hemispheres. Schmidt and Dailey (1971) stated that *C. bullosum*, a parasite of southern elephant seal, *Mirounga leonina*, also occurred in a Californian host, *Mirounga angustirostris*. Taking into account the geographical separation of the two hosts, the occurrence of *C. bullosum* in the northern hemisphere is considered uncertain. Such a view is supported by the fact that two closely related pairs of species of the genus *Corynosoma* are known in mammals, with one species in the northern, and a second in the southern hemisphere. These are *C. obtuscens* with *C. australe* and *C. semerme* with *C. hannae*.

Conclusions

Antarctic helminth parasites are diverse, with a total of 91 different species recorded so far. Fishes may be definitive, second intermediate or paratenic hosts of these helminths. Seventy-three species are parasites in the adult stage (Digenea 45, Cestoda 14, Nematoda 6, Acanthocephala 8). In addition, 11 larval stages of Cestoda (7) and Nematoda (4) are known, together with 7 species of Acanthocephala in the cystacanth stage.

The most species-rich group is Digenea. Almost all of these digeneans use teleosts as definitive hosts. Only one species, *O. cestoides*, occurs as the adult stage in skates; teleosts are intermediate hosts for this species.

Among 14 cestode species parasitising Antarctic fishes, only one, *P. johnstoni*, occurs in the deep-water gadiform bony fish, *Macrourus whitsoni*. The other species are parasites of Chondrichthyes (12 species of Tetraphyllidea and one of Diphyllidea).

The majority of parasites maturing in fishes are Antarctic or Antarctic/Subantarctic endemics. Only 4 digeneans and one nematode species, *H. aduncum*, are cosmopolitan or bipolar.

All acanthocephalans, almost all digeneans (except of one species), the majority of cestodes and some nematodes occur mainly or exclusively in benthic fishes.

Specificity of the majority of parasites that utilize teleosts as intermediate and/or paratenic hosts is low. Among parasites using fishes as definitive hosts, all Cestoda, most species of Digenea (other than Hemiuroidea) and Nematoda, and almost all Acanthocephala have a range of hosts restricted to one order or even to 1–2 host species.

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