

UDC 595.1:597.5(1-13:411.2:1-15:9)

HELMINTH DIVERSITY IN TELEOST FISHES FROM THE SOUTH ORKNEY ISLANDS REGION, WEST ANTARCTICA

T. A. Kuzmina^{1*}, O. O. Salganskiy², K. O. Vishnyakova^{2,3}, J. Ivanchikova^{1,2,3},
O. I. Lisitsyna¹, E. M. Korol⁴, Yu. I. Kuzmin^{1,5}

¹Schmalhausen Institute of Zoology, NAS of Ukraine, vul. B. Khmelnytskogo, 15, Kyiv, 01030 Ukraine

²State Institution National Antarctic Scientific Center; Taras Shevchenko Blvd, 16, Kyiv, 02000 Ukraine

³Scientific Research Institution Ukrainian Scientific Centre of Ecology of the Sea,
Ministry of Ecology and Natural Resources of Ukraine, 89, Frantsuzsky Blvd, Odesa, 65062, Ukraine

⁴National Museum of Natural History NAS of Ukraine; 15, Bogdan Khmelnytskyi Street, Kyiv, 01030 Ukraine

⁵African Amphibian Conservation Research Group, Unit for Environmental Sciences and Management,
North-West University, Potchefstroom Campus; Private Bag X6001, Potchefstroom 20520, South Africa

*Corresponding author

E-mail: taniak@izan.kiev.ua

T. A. Kuzmina (<https://orcid.org/0000-0002-5054-4757>)

O.O. Salganskiy (<https://orcid.org/0000-0002-7063-1807>)

K. O. Vishnyakova (<https://orcid.org/0000-0002-6455-6601>)

J. Ivanchikova (<https://orcid.org/0000-0001-8194-6989>)

O. I. Lisitsyna (<https://orcid.org/0000-0002-2975-3300>)

E. M. Korol (<https://orcid.org/0000-0002-4061-5179>)

Yu. I. Kuzmin (<https://orcid.org/0000-0002-1723-1265>)

Helminth Diversity in Teleost Fishes from the South Orkney Islands Region, West Antarctica. Kuzmina, T. A., Salganskiy, O. O., Vishnyakova, K. O., Ivanchikova, J., Olga, O. I., Lisitsyna, O. I., Korol, E. M., Kuzmin, Yu. I. — Helminths of 12 fish species collected near the South Orkney Islands, West Antarctica were studied. In the whole sample of 115 fish specimens, we identified one species of Monogenea, 5 species of Trematoda, 4 species of Cestoda, 5 species of Nematoda, and 7 species of Acanthocephala. All cestode species, 3 species of nematodes, and 5 species of acanthocephalans were represented only by larval stages; fish are definitive hosts for the remaining 10 helminth species. Details of composition and structure of helminth communities were studied in 3 fish species: *Chaenocephalus aceratus* (Lönnerberg, 1906), *Champscephalus gunnari* Lönnerberg, 1905, and *Pseudochaenichthys georgianus* Norman, 1937, each represented by more than 20 specimens in a sample. In these hosts, 19, 8, and 16 helminth species were found, correspondingly. In the helminth communities of *C. aceratus* and *P. georgianus*, the highest values of the infection prevalence and abundance were recorded for larval cestodes (*Diphyllobothrium* sp., Tetrabothriidea), nematodes (*Pseudoterranova* sp., *Contraecum* sp.), acanthocephalans (*Corynosoma* spp.), as well as adults of the trematode *Neolebouria georgiensis* Gibson, 1976. The same trematode species and larval cestodes predominated in the helminth community of *C. gunnari*. All recorded species of parasites are generalists, each known from a range of fish hosts in Antarctica.

Key words: Helminths, Acanthocephala, Nematoda, Cestoda, Trematoda, teleost fishes, Antarctica.

Introduction

Rapid modifications caused by climatic changes and anthropogenic influence are taking place nowadays in terrestrial and marine ecosystems. Special attention of researchers worldwide is paid to the exploration of the changes in ecosystems, as well as to the study of different groups of organisms as indicators of these changes. Metazoan parasites are considered as one of the most sensitive indicators of the state of marine ecosystems (Hudson et al., 2006; Poulin, 2006; Poulin and Mouritsen, 2006; Hechinger et al., 2007). Most marine parasites are included in the food chains of their definitive, intermediate and paratenic hosts (Marcogliese, 2002, 2016; Thompson et al., 2004). Changes in the composition and structure of parasite communities of marine animals were recorded in various regions of the world (Sala and Knowlton, 2006; Blonar et al., 2009; Byers, 2021; Kuzmina et al., 2020, 2022). Due to the complexity of the functioning of host-parasite systems in marine ecosystems, assessment of the changes in communities of different groups of parasites may reveal general trends in the changes in the ecosystems even faster than it can be observed using geological or oceanographic monitoring data.

The structure of polar ecosystems in the Arctic and Antarctic is much more complex and ecologically diverse than it was previously thought (Chown et al., 2015). Besides, marine ecosystems in Antarctica and the Southern Ocean are highly endemic. Recent surveys suggest that 50 % to 97 % of the Southern Ocean species of such groups as sponges, tube worms, amphipods, molluscs, isopods, sea spiders and notothenioid fish are endemic (Eastman, 2000, 2005; De Broyer et al., 2014; Chown et al., 2015). Organisms inhabiting the extreme conditions of Antarctic marine ecosystems have developed particular physiological and behavioural mechanisms to adapt to survival, growth, and reproduction. Moreover, the isolation of the Southern Ocean ecosystems by the circular Antarctic Polar Front increases ecological diversification of the Antarctic shelf; therefore, ecosystems of the Antarctic shelf areas can be considered as evolutionary hot spots (Eastman, 2005).

The fish fauna in the Southern Ocean around Antarctica, as known today, consists of 322 species from 50 families (Eastman, 2005); the dominant group of fishes belongs to the perciform suborder Notothenioidei, which comprises about 77 % of Antarctic fish species diversity (Kock, 2005; Near, 2009; Near et al., 2012). The suborder includes more than 130 species in eight families (Artedidraconidae, Bovichtidae, Pseudaphritidae, Eleginopsidae, Nototheniidae, Harpagiferidae, Bathydraconidae, Channichthyidae) which are endemic of Southern Ocean (Near et al., 2012). This group includes the species of high economic importance to fisheries (Gon and Heemstra, 1990; Kock 1992; Collins et al. 2010), as well as the species that represent critical links in the Antarctic food webs, especially for higher-level consumers such as seals, whales, and marine birds (Targett 1981; Smith et al., 2007; Parker et al., 2020). In recent years, there has been an increase in the interest in the study of Antarctic fish parasites (Oğuz et al., 2012, 2015; Shendrik et al., 2014; Gordeev and Sokolov, 2016; Sokolov et al., 2016, 2019; Münster et al., 2016, 2017; Kuhn et al., 2018; Kvach and Kuzmina, 2020; Kuzmina et al., 2020, 2021a,b, 2022). The collection and publication of new data have broadened the understanding of the diversity in parasite fauna of teleost fish. However, the lack or insufficient baseline data for Antarctic parasite communities do not allow integrating these organisms in any forecasts of the changes in Southern Ocean biodiversity (Bielecki et al., 2008; Muñoz and Cartes, 2020).

In previous decades, the majority of the studies on fish parasites has been carried out either on economically important fish species such as *Dissostichus mawsoni* Norman, 1937, *D. eleginoides* Smitt, 1898, *Gobionotothen gibberifrons* Lönnberg, 1905, etc. (Parukhin and Lyadov, 1982; Parukhin, 1986; Brickle et al., 2005; Gordeev and Sokolov, 2016), or on demersal fishes *Notothenia coriiceps* Richardson, 1844, *Trematomus newnesi* Boulenger, 1902, *T. bernacchii* Boulenger, 1902, etc., which could be easily caught using simple fishing gear (Wojciechowska, 1993; Zdzitowiecki, 1979, 1983, 1987, 1996; Zdzitowiecki and White, 1996; Zdzitowiecki and Laskowski, 2004; Laskowski and Zdzitowiecki, 2005; Laskowski et al., 2007; Kuzmina et al., 2020, 2021 a, 2022). Very few publications were devoted to the study of parasites of pelagic fish species in deep-sea areas (Palm, 2007; Münster et al., 2017; Kuhn et al., 2018; Sokolov et al., 2016, 2019; Muñoz and Cartes, 2020). On the other hand, the wide distribution and long-distance migrations of pelagic fish might enable collecting the information on the role of teleost fishes in the life cycles of different groups of metazoan parasites as well as their role in the food webs of marine mammals and birds of Antarctica.

In the present study, we examined the helminth diversity in 12 species of teleost fishes from three families of the suborder Notothenioidei from the South Orkney Islands region, West Antarctica and analysed the helminth community structure in three most abundant fish species, namely *Champscephalus gunnari* Lönnberg, 1905, *Pseudochaenichthys georgianus* Norman, 1937, and *Chaenocephalus aceratus* (Lönnberg, 1906). Comparative analysis of the parasite communities of shallow-water (10–30 m depth) and deep-water (> 60–800 m) fish species was performed to obtain new information on the influence of shallow- or deep-water habitats on helminth fauna in Antarctic fish.

Material and methods

Field studies and the material collection were carried out from December 2020 till March 2021 in waters around South Orkney Islands (60°40'54" S; 45°11'09" W) during the research trip on the Ukrainian krill fishing

trawler “More Sodruzhestva” (CCAMLR statistical subarea 48.2). Totally, 115 fish specimens of 12 species were collected as by-catch from the depth of 60 m to more than 800 m (table 1). All fishes collected were transported to the laboratory, measured, weighed and examined using the standard parasitological techniques (see Zdzitowiecki and Laskowski, 2004; Weber and Govett, 2009). The fishes were examined on the same day they were caught; all precautions were followed to prevent confusion of the parasites between fish specimens.

Parasites were collected manually from the fish body cavity, stomach, intestine, liver and mesentery; all ectoparasites were carefully gathered from the fish body surface and gills; only monogenean helminths were examined and identified in the present study. All helminths were washed in saline and fixed in 70 % ethanol. Acanthocephalans were kept in tap water for 30 min to 3 hours for proboscis evagination prior to their fixation in ethanol. Helminths belonging to main taxonomic groups (monogeneans, nematodes, cestodes, trematodes and acanthocephalans) were counted, fixed and stored separately. Identification of the parasites was performed in the laboratory of the Department of Parasitology, I. I. Schmalhausen Institute of Zoology NAS of Ukraine in Kyiv, Ukraine, using the Zeiss Axio Imager M1 compound microscope equipped with DIC optics and a digital imaging system. Prior to identification, all nematodes, cestodes and trematodes were clarified in lactophenol (25 % lactic acid, 25 % phenol, 25 % glycerin, and 25 % distilled water); acanthocephalans were studied on temporary total mounts in the Berlese medium (Swan, 1936).

Identification of nematodes was performed according to Mozgovoy (1951) and Rocka (1999, 2004, 2017); cestodes were identified according to Wojciechowska (1993) and Rocka (2003, 2017); trematodes were identified according to Zdzitowiecki (1996), Zdzitowiecki and Cielecka (1997 a, b), Gibson et al. (2002), and Jones et al. (2005). Identification of acanthocephalans was performed according to Zdzitowiecki (1983, 1984 a, b, 1987, 1996) and Laskowski and Zdzitowiecki (2017). The helminth specimens were deposited in the Parasitological collection of the Department of Parasitology of the I. I. Schmalhausen Institute of Zoology NAS of Ukraine (Kyiv, Ukraine).

Data summaries and descriptive analyses were performed using Microsoft Excel and Paleontological Statistics Software (PAST v. 3.0) (Hammer et al., 2001). The prevalence (P), mean abundance (MA), mean and median intensity (I) of infection were calculated for each helminth species following the definitions of Bush et al. (1997). The species richness in the helminth communities estimated using Chao1 and bootstrap methods was calculated using the PRIMER 6 software (Clarke and Gorley, 2006). For comparative analysis of the helminth communities of shell-water (10–30 m depth) and deep-water (60 – > 800 m) fish species, previously collected and partially published (see Kuzmina et al., 2021 a) data from the area of the Ukrainian Antarctic Station “Akademik Vernadsky” in 2019–2021 were used. Information on the helminth communities of three fish species: *N. coriiceps* (n = 78; 15,451 helminth specimens), *P. charcoti* (n = 18; 5,298 helminth specimens) and *C. aceratus* (n = 6; 4,830 helminth specimens) was included in the analysis. The similarity between helminth faunas in shallow- and deep-water fishes was analyzed using the Sørensen index, the Bray-Curtis index, and SIMPER (similarity percentage) routine.

Table 1. Parameters of the samples and number of helminths collected from 12 species of teleost fishes in waters around the South Orkney Islands in 2020–2021

Fish species	No.	Weight, g (min–max)	TBL*, cm (min–max)	No. of helminths collected
Family Channichthyidae Gill, 1861				
1. <i>Chaenocephalus aceratus</i> (Lönnerberg, 1906)	22	177–1347	336.0–58.0	5,789
2. <i>Champocephalus gunnari</i> Lönnerberg, 1905	34	260–900	37.0–49.0	1,267
3. <i>Pseudochaenichthys georgianus</i> Norman, 1937	33	797–1910	41.0–56.0	7,645
4. <i>Neopagetopsis ionah</i> Nybelin, 1947	6	95–1005	25.0–53.5	90
5. <i>Chionodraco rastrospinosus</i> DeWitt et Hureau, 1979	4	368–580	35.5–40.0	192
6. <i>Chaenodraco wilsoni</i> Regan, 1914	1	120	24.5	11
Family Nototheniidae Günther, 1861				
7. <i>Notothenia coriiceps</i> Richardson, 1844	2	1047–1110	39.0–48.0	440
8. <i>N. rossii</i> Richardson, 1844	1	3400	64.0	193
9. <i>Gobionotothen gibberifrons</i> (Lönnerberg, 1905)	5	286–675	33.5–39.5	214
10. <i>Nototheniops larseni</i> (Lönnerberg, 1905)	1	52.9	19.5	80
Family Bathylaconidae Regan, 1913				
11. <i>Parachaenichtys charcoti</i> (Vaillant, 1906)	2	330–350	38.5–40.0	557
12. <i>Gymnodraco acuticeps</i> Boulenger, 1902	4	75–166	24.0–29.5	1,683

* Total body length.

Results

All 12 fish specimens examined were found to be infected with helminths; each host individual harboured from 1 to 13 helminth species and from 2 to 955 helminth specimens. In total, 18,159 helminth specimens were collected and assigned to 22 species belonging to five taxonomic groups: Monogenea (1 species), Trematoda (5), Nematoda (5), Cestoda (4), and Acanthocephala (7) (table 2). Trilocular metacestodes (unidentified species of the order Tetrabothriidea) were found in all host species except *N. larseni*. Larval nematodes *Contracaecum* sp., as well as bilocular metacestodes and metacestodes of *Diphyllobothrium* sp. were found each in 10 fish host species. More than a half of examined host species were infected with the nematode *Pseudoterranova* sp. (9 hosts), with acanthocephalan species of the genus *Corynosoma*, namely *C. bullosum* (8 hosts), *C. hamanni* (7 hosts), and *C. evae* (7 hosts), and the trematode *N. georgiensis* (8 hosts). The acanthocephalan *C. shackletoni* was found only in *C. aceratus*, while the monogenean *P. nototheniae* was found in two species of *Notothenia*, and the trematode *L. garrardi* was found in *N. larseni* and *P. charcoti*.

In the present study, the detailed analysis of the helminth communities was performed for three fish species, for which we had samples of more than 20 specimens, namely *Chaenocephalus aceratus* (n = 22), *Champscephalus gunnari* (n = 34), and *Pseudochaenichthys georgianus* (n = 33). For each of the other fish species, we present only the information on helminth species found and the predominant group of parasites.

Neopagetopsis ionah

Six examined specimens of Jonah's icefish harboured a total of 4 helminth species (from 1 to 4 species per host): larval nematodes *Contracaecum* sp. were found in three host individuals, metacestodes of *Diphyllobothrium* sp. (in one host), bilocular metacestodes (in three hosts), and trilocular metacestodes (in three hosts). Cestodes predominated in the sample comprising 93.3 % of the total helminth number (table 2).

Chionodraco rastrospinosus

Four examined specimens of the ocellated icefish harboured 8 helminth species (from 4 to 7 species per host). Nematodes were represented by larval stages of *Pseudoterranova* sp. found in two hosts and *Contracaecum* sp. (in one host), and adults of *A. nototheniae* (in two hosts). Trematodes were represented by a single specimen of *N. georgiensis*. Cestodes at the metacestode stage predominated by their diversity (4 species) and occurrence. Bilocular and trilocular metacestodes were found in all hosts examined, *Diphyllobothrium* sp. was found in 3 hosts, one monolocular metacestode was found in one host. Cestodes comprised 88.5 % of all helminth specimens collected.

Chaenodraco wilsoni

One examined specimen of the spiny icefish harboured only bilocular (3 specimens) and trilocular (8 specimens) metacestodes; no other helminth species were recorded (table 2).

Notothenia coriiceps

Two specimens of the black rockcod harboured 13 helminth species (from 7 to 12 species per host) (table 2). A single specimen of the monogenean *P. nototheniae* was found on one host. Cestodes *Diphyllobothrium* sp. were found in both hosts; bilocular and trilocular metacestodes were found each in one black rockcod. Three trematode species infected one of two hosts examined. Acanthocephalans were represented by adults of *A. megarhynchus* in one host and larval *Corynosoma* spp., 4 species, each infecting both host specimens (table 2). Acanthocephalans composed the largest part of helminths in *N. coriiceps*; they comprised 72.0 % of the total number of helminths collected. Nematodes,

Table 2. Abundance of helminth species found in 12 species of teleost fishes off the South Orkney Islands area, West Antarctica, in 2020–2021

Helminth species	Number of helminth specimens collected in fish species											
	CG (n=34)	PG (n=33)	CA (n=22)	NI (n=6)	CR (n=4)	CW (n=1)	NC (n=2)	NR (n=1)	GG (n=5)	NL (n=1)	PC (n=2)	GA (n=1)
PLATYHELMINTHES: MONOGENEA												
1. <i>Pseudobenedenia nototheniae</i> Johnston, 1931	—	—	—	—	—	—	1	1	—	—	—	—
PLATYHELMINTHES: TREMATODA												
2. <i>Macvicaria pennelli</i> (Leiper & Atkinson, 1914)	—	1	2	—	—	—	1	—	—	1	—	—
3. <i>Genolinea bowersi</i> (Leiper et Atkinson, 1914)	—	1	8	—	—	—	—	—	—	—	—	6
4. <i>Neolebouria georgiensis</i> Gibson, 1976	88	319	594	—	1	—	6	—	—	2	24	4
5. <i>Lectithaster macrocotyle</i> Szidat et Graefe, 1967	—	—	—	—	—	—	1	—	—	—	29	10
6. <i>Lepidapedon garrardi</i> (Leiper et Atkinson, 1914)	—	—	—	—	—	—	—	—	—	1	2	—
PLATYHELMINTHES: CESTODA												
7. <i>Diphyllobothrium</i> sp.	277	629	1391	4	23	—	19	5	49	4	19	271
8. Monolocular metacestode	7	47	31	—	1	—	—	—	—	—	—	1
9. Bilocular metacestode	262	1241	101	41	71	3	5	—	—	3	355	1231
10. Trilocular metacestode	608	3699	264	39	75	8	3	5	1	—	28	51
NEMATODA: CHROMADOREA												
11. <i>Ascarophis nototheniae</i> Johnston et Mawson, 1945	5	3	2	—	2	—	—	—	—	—	—	—
12. <i>Dichelyne fraseri</i> (Baylis, 1929)	—	208	118	—	—	—	—	3	107	11	—	—
13. <i>Anisakis</i> sp.	—	11	4	—	—	—	—	1	—	—	—	—
14. <i>Contracaecum</i> sp.	16	341	337	6	8	—	2	53	6	—	7	103
15. <i>Pseudoterranova</i> sp.	3	666	2144	—	11	—	85	72	4	5	68	—
ACANTHOCEPHALA: PALAEACANTHOCEPHALA												
16. <i>Aspersentis megarhynchus</i> (Linstow, 1892)	—	—	5	—	—	—	20	—	2	—	2	—
17. <i>Corynosoma bullosum</i> (Linstow, 1892)	—	59	83	—	—	—	2	43	2	43	7	2
18. <i>C. evae</i> Zdzitowiecki, 1984	—	11	340	—	—	—	224	4	3	4	4	—
19. <i>C. hamanni</i> (Linstow, 1892)	—	7	320	—	—	—	46	2	40	4	8	—
20. <i>C. pseudohamanni</i> Zdzitowiecki, 1983	—	—	26	—	—	—	25	2	—	2	—	—
21. <i>C. shackletoni</i> Zdzitowiecki, 1978	—	—	5	—	—	—	—	—	—	—	—	—
22. <i>Metacanthocephalus rennicki</i> (Leiper & Atkinson, 1914)	—	2	8	—	—	—	—	—	—	—	4	4
Total number of species:	8	16	20	4	8	2	14	11	9	11	13	10
Number of species per host, average (min–max)	4.2 (1–6)	6.8 (3–12)	8 (3–13)	2.5 (1–4)	2 (1–4)	9.5 (7–12)	10 (7–12)	11 (2–6)	4.2 (2–6)	4.2 (2–6)	11 (10–12)	6.3 (4–8)

Note. Fish species: CA — *Chaenocephalus aceratus*, CG — *Chamsocephalus gunnari*, CR — *Chionodraco rastrospinosus*, CW — *Chaenodraco wilsoni*, GA — *Gymnodraco acuticeps*, GG — *Gobionotothen gibberifrons*, NC — *Notothenia coriiceps*, NI — *Neopagetopsis tonah*, NL — *Nototheniopsis larseni*, NR — *N. rossii*, PC — *Parachaenichthys charcoti*, PG — *Pseudochaenichthys georgianus*.

cestodes, and trematodes were less abundant and comprised 19.8 %, 6.1 %, and 1.8 % of the total helminth number, correspondingly.

Notothenia rossii

One examined specimen of the marbled rockcod appeared to be infected with 11 species of helminths: the monogenean *P. nototheniae*, 4 species of nematodes (larval *Pseudoterranova* sp., *Contracaecum* sp. and *Anisakis* sp., adult *D. fraseri*), trilocular metacestodes and *Diphyllobothrium* sp., and 4 species of larval acanthocephalans of the genus *Corynosoma* (table 2). In this host, nematodes were the most abundant group comprising 66.8 % of all helminths collected.

Gobionotothen gibberifrons

Five examined species of the humped rockcod harboured 9 helminth species (from 2 to 6 species per host). The nematode *D. fraseri* was found in all 5 host specimens, while *Pseudoterranova* sp. and *Contracaecum* sp. each infected one fish. Similarly, cestode *Diphyllobothrium* sp. was found in all hosts, while a single trilocular metacestode was in one host. Two host specimens appeared to be infected with the acanthocephalan *A. megarhynchus*. *Corynosoma bullosum* was found in one host, *C. evae* in two hosts, and *C. hammani* in three hosts. Nematodes predominated among helminths of humped rockcod, they comprised 54.7 % of all helminths collected. Cestodes and acanthocephalans comprised 23.4 % and 22.0 % of all helminths, correspondingly.

Nototheniops larseni

One examined specimen of the painted notothen harboured 11 helminth species. Nematodes were represented by the larvae of *Pseudoterranova* sp. and the adults of *D. fraseri*, cestodes by *Diphyllobothrium* sp. and bilocular metacestodes. Trematodes were not abundant (table 2) and belonged to three species: *M. pennelli*, *N. georgiensis*, and *L. garrardi*. Four acanthocephalan species of the genus *Corynosoma* were found; in total, they comprised 66.2 % of all helminths collected.

Parachaenichthys charcoti

Both of the two examined specimens of the Antarctic dragonfish appeared to be infected with the larvae of two nematode species (*Pseudoterranova* sp. and *Contracaecum* sp.) and three species of cestodes: bilocular and trilocular metacestodes, and *Diphyllobothrium* sp.; from 10 to 12 helminth species parasitized one fish. The trematodes *N. georgiensis* and *L. macrocotyle* were found in both host specimens, while *L. garrardi* was in one fish. Acanthocephalans were represented by adults of *A. megarhynchus* and *M. rennicki* (both in one host), and cystacanths of three species of the genus *Corynosoma*: *C. hammani* and *C. evae* in both hosts, and *C. bullosum* in one host. Among 13 helminth species collected from Antarctic dragonfish, bilocular metacestodes were the most abundant (table 2), and due to this cestodes predominated the community comprising 72.2 % of all helminths collected.

Gymnodraco acuticeps

Four examined specimens of the ploughfish harboured 10 helminth species (from 4 to 8 species per host). Nematodes were represented only by *Contracaecum* sp. found in all host individuals. *Diphyllobothrium* sp., bilocular and trilocular metacestodes were also found in all 4 hosts, while a single monolocular metacestode was found in one fish. Trematodes were not abundant (table 2); *N. georgiensis* and *L. macrocotyle* were found each in two host specimens, *G. bowersi* was found in one. Two hosts were infected each with 2 specimens of adult acanthocephalan *M. rennicki*; two cystacanths of *C. bullosum* were found in one fish. Cestodes strongly predominated in the ploughfish comprising 95.9 % of all helminths collected.

Chaenocephalus aceratus

In the blackfin icefish, 19 helminth species were recorded (from 3 to 13 species per host), including 3 species of trematodes, 4 species of cestodes, 5 species of nematodes and 7 species of acanthocephalans (table 3). Estimated species richness was 20 (Chao1), 24 (jackknife), or 22 (bootstrap) species. The diversity indices equalled 1.88 (Shannon), 0.78 (Simpson), and 0.63 (Pielou's evenness).

All the cestode species, as well as nematodes of the genera *Anisakis*, *Contracaecum* and *Pseudoterranova* and acanthocephalans of the genus *Corynosoma* parasitized this fish host on the immature stages. Thus, *C. aceratus* is considered to be a definitive host for 7 out of 19 helminth species recorded. Nematodes predominated in the helminth community of blackfin icefish, they comprised 44.99 % of the total helminth number. The proportion of other groups of helminths was lower: 30.96 % for cestodes, 13.61 % for acanthocephalans, and 10.43 % for trematodes (fig. 1).

According to the prevalence, three species predominated in the helminth community in *C. aceratus*: the cestode *Diphyllobothrium* sp. (P = 100 %), the trematode *N. georgiensis* (P = 95.5 %), and the nematode *Pseudoterranova* sp. (P = 95.5 %) (table 3). Five other helminth species had an infection prevalence higher than 50 % and may be considered as subdominant species: bilocular and trilocular metacestodes, the nematode *Contracaecum* sp., and the acanthocephalans *C. bullosum* and *C. hamanni*. The nematode *D. fraseri* and the acanthocephalan *C. evae* were common, with an infection prevalence of 45.5 %. Other 10 species of helminths were found in less than 30 % of examined *C. aceratus*.

Champscephalus gunnari

In the mackerel icefish, only 8 helminth species were recorded (from 1 to 6 species per host): 1 species of trematodes, 4 species of cestodes and 3 species of nematodes (table 3). Species richness estimated using Chao1, jackknife, and bootstrap methods equalled 8 species. The diversity indices were 1.32 (Shannon), 0.67 (Simpson), and 0.63 (Pielou's evenness).

Only two helminth species, a digenean trematode *N. georgiensis* and a nematode *A. notheniae* parasitized *C. gunnari* on the adult stage; all other parasites were found on im-

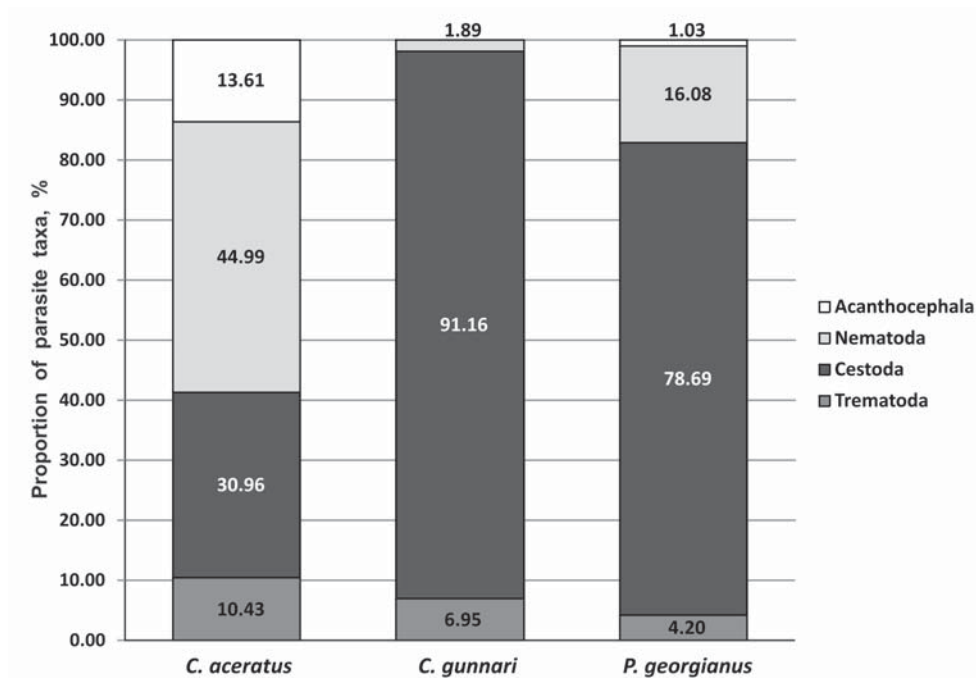


Fig. 1. Proportion (%) of four parasite taxa in three fish species from the South Orkney Islands area, West Antarctica.

mature stages. Therefore, *C. gunnari* is considered to be a definitive host for 2 out of 8 helminth species recorded. Cestodes predominated in the helminth community of mackerel icefish; together they comprised 91.16 % of the total helminth number (fig. 1).

According to the prevalence (table 3), helminths of *C. gunnari* might be separated into two groups. Four species, namely *Diphyllbothrium* sp., bilocular and trilocular metacestodes, and the trematode *N. georgiensis* reached the prevalence of 79–94 %; thus, these species predominated in the helminth community. Other species occurred rarely, with the highest prevalence of 35.3 % in *Contraecaecum* sp.

Pseudochaenichthys georgianus

In the South Georgia icefish, 16 helminth species were recorded (from 3 to 12 species per host), including 3 species of trematodes, 4 species of cestodes, 5 species of nematodes and 4 species of acanthocephalans (table 3). Estimated species richness was 18 (Chao1), 19 (jackknife) or 17 (bootstrap) species. The diversity indices equalled 1.54 (Shannon), 0.68 (Simpson), and 0.55 (Pielou's evenness).

All the cestode species, as well as the nematodes *Anisakis* sp., *Contraecaecum* sp. and *Pseudoterranova* sp. and acanthocephalans *Corynosoma* spp. parasitize *P. georgianus* on larval stages. Thus, *P. georgianus* is considered to be a definitive host for 6 out of 16 helminth species recorded. As in the mackerel icefish, cestodes predominated in the helminth community of *P. georgianus*; together they comprised 78.7 % of the total helminth number (fig. 1).

According to the prevalence of infection, 8 species predominated in the helminth community in *P. georgianus* (table 3). Bilocular and trilocular metacestodes had an infection prevalence higher than 95 %. The cestode *Diphyllbothrium* sp., the trematodes *M. pennelli* and *N. georgiensis*, the nematodes *Contraecaecum* sp. and *Pseudoterranova* sp. had an infection prevalence of 70–95 %. The nematode *D. fraseri* and monolocular metacestodes were common, with the infection prevalence of 36.4 % and 45.5 %, correspondingly. Other 8 species of helminth occurred in less than 30 % of examined *P. georgianus*.

In all three latter fish species, the proportion of helminth species found on larval stages was larger (62.5–75 %) than that of the species represented by adult parasites (25–37.5 %) (fig. 2).

The helminth species richness appeared to be much higher in fishes from shallow-water (10–30 m deep) habitats than in deep-water (60–800 m) habitats (table 4).

Analysis of similarity between helminth faunas in studied samples of shallow- and deep-water fishes (table 5) revealed the highest similarity of helminth faunas in two shallow-water species from the Ukrainian Antarctic Station area: *P. charcoti* and *N. coriiceps* (Sørensen index 90.6 %) and *C. aceratus* with *N. coriiceps* and *P. charcoti* (88.0 % and 89.8 %, respectively). Also, helminth faunas of deep-water populations of *C. aceratus* and *P. georgianus* were similar (Sørensen index 88.9 %). The lowest similarity was recorded for the helminth fauna of the deep-water population of *C. gunnari*; the similarity between *N. coriiceps* and *C. gunnari* was minimal (20.0 %).

Visualization of the helminth faunal similarities according to the Bray-Curtis index using the cluster analysis (fig. 3) showed a clear division of groups of shallow- and deep-water fish species.

According to the results of the SIMPER analysis, the overall dissimilarity between the helminth communities of shallow- and deep-water fishes was 80.1 %. Four helminth species had the largest contribution to the dissimilarity: the acanthocephalan *Corynosoma pseudohamanni* (19.4 % contribution), anisakid nematodes *Contraecaecum* sp. (17.4 % contribution) and *Pseudoterranova* sp. (14.4 % contribution), and trilocular metacestodes (11.4 % contribution). Infection of shallow-water fishes with *C. pseudohamanni* and anisakid nematodes was more than 10–15 times higher, while deep-water fishes had 168 times higher infection with trilocular metacestodes.

Table 3. Helminth species found in three teleost fish species off the South Orkney Islands area

Helminth species	<i>Chaenocephalus aceratus</i> (n = 22)			<i>Champsoccephalus gunnari</i> (n = 34)			<i>Pseudochaenichthys georgianus</i> (n = 22)		
	P, %	I	MA	P, %	I	MA	P, %	I	MA
PLATYHELMINTHES: TREMATODA									
1. <i>Macvicaria pennelli</i>	4.6	2.0	0.09	0	0	0	3.0	1.0	0.03
2. <i>Genolinea bowersi</i>	9.1	4.0 (1-7)	0.36	0	0	0	3.0	1.0	0.03
3. <i>Neolebouria georgianus</i>	95.5	28.3 (2-107)	27.00	79.4	3.3 (1-10)	2.59	72.7	13.3 (1-44)	9.67
PLATYHELMINTHES: CESTODA									
4. <i>Diphyllobothrium</i> sp.	100.0	63.5 (5-291)	63.45	88.2	9.2 (1-33)	8.15	93.4	21.7 (1-99)	20.39
5. Monolocular metacestode	22.7	6.2 (1-18)	1.41	14.7	1.6 (1-3)	0.24	45.5	3.5 (1-12)	1.58
6. Bilocular metacestode	63.6	7.3 (1-24)	4.64	91.2	8.5 (1-27)	7.71	96.9	39.8 (6-343)	38.64
7. Trilocular metacestode	68.2	17.6 (1-79)	12.00	94.1	19.0 (2-101)	17.88	100.0	1.5 (9-418)	121.70
NEMATODA: CHROMADOREA									
8. <i>Ascarophis nototheniae</i>	9.1	1.0 (1)	0.09	8.8	1.7 (1-2)	0.15	6.1	1.5 (1-2)	0.09
9. <i>Dichelyne fraseri</i>	45.5	11.8 (1-37)	5.36	0	0	0	36.7	17.3 (1-141)	6.30
10. <i>Anisakis</i> sp.	13.6	1.3 (1-2)	0.18	0	0	0	9.1	3.4 (2-7)	0.33
11. <i>Contracaecum</i> sp.	72.7	21.1 (1-86)	15.32	35.3	1.3 (1-2)	0.47	84.9	12.2 (1-72)	10.33
12. <i>Pseudoterranova</i> sp.	95.5	102.1 (2-394)	97.45	8.8	1.0	0.09	78.8	25.6 (1-101)	20.18
ACANTHOCEPHALA: PALAEACANTHOCEPHALA									
13. <i>Aspersentis megarhynchus</i>	4.6	5 (5)	0.23	0	0	0	0	0	0
14. <i>Corynosoma bullosum</i>	59.1	6.4 (2-21)	3.77	0	0	0	24.2	7.4 (1-42)	1.79
15. <i>C. evae</i>	45.5	34.0 (1-294)	15.45	0	0	0	12.1	2.8 (1-6)	0.33
16. <i>C. hamanni</i>	54.6	26.7 (1-124)	14.55	0	0	0	9.1	2.3 (1-5)	0.21
17. <i>C. pseudohamanni</i>	13.6	8.7 (2-186)	1.18	0	0	0	0	0	0
18. <i>C. shackletoni</i>	13.6	1.7 (1-3)	0.23	0	0	0	0	0	0
19. <i>Metacanthocephalus rennicki</i>	4.6	8.0 (8)	0.36	0	0	0	3.0	2.0	0.06

Note. Parameters of fish infection; P — prevalence, I — intensity (mean and range in parentheses), MA — mean abundance.

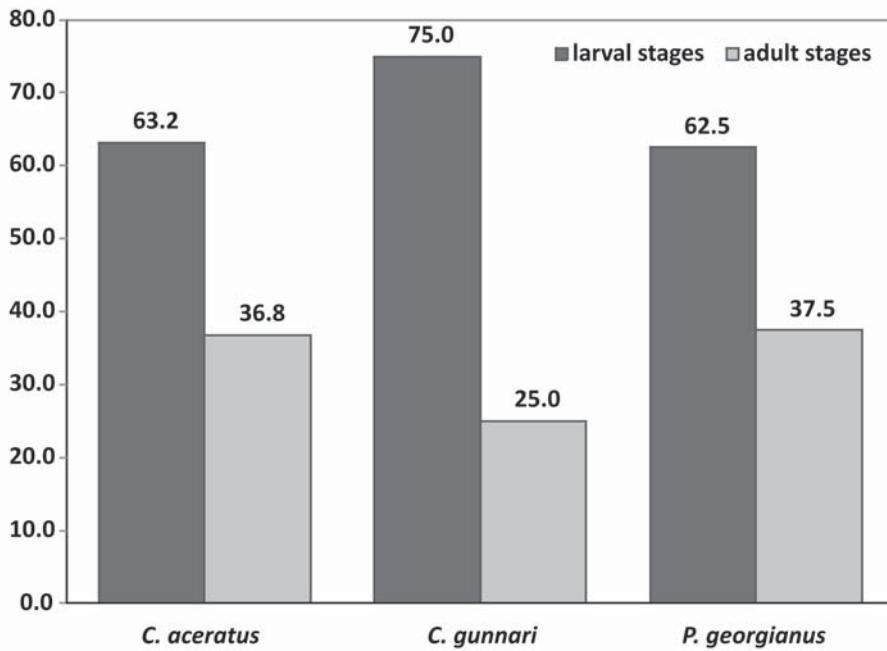


Fig. 2. Proportion (%) of helminth species parasitizing three teleost fishes from the South Orkney Islands area, West Antarctica on larval and adult stages.

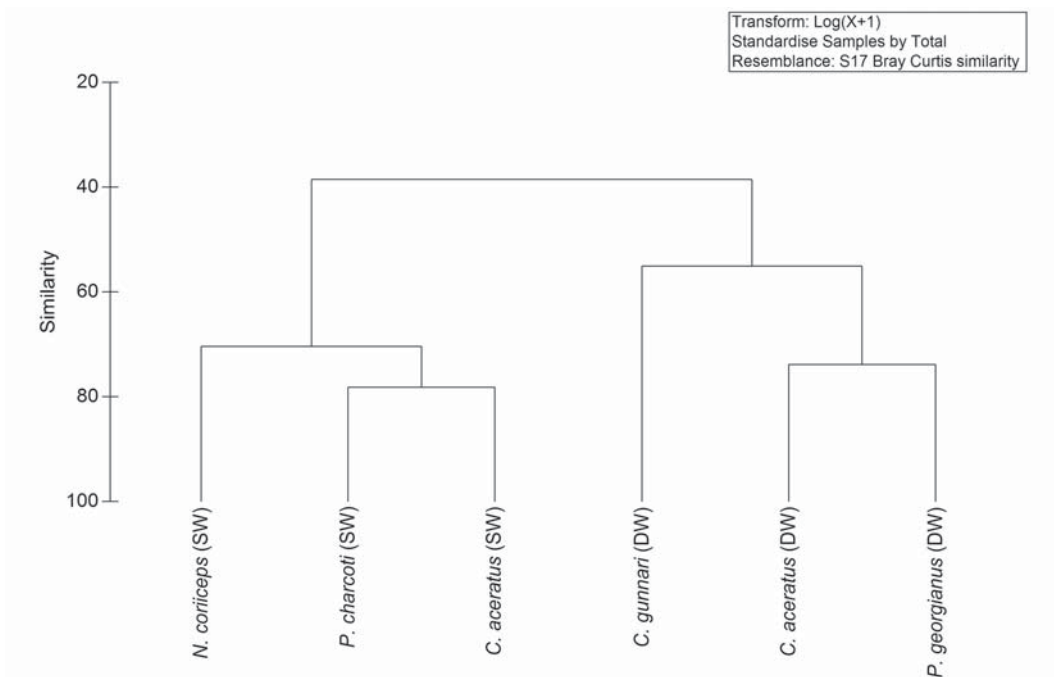


Fig 3. Cluster analysis of the similarity between the helminth communities of the shallow-water (SW) and deep-water (DW) populations of fish species determined by the Bray-Curtis index.

Discussion

The results obtained in our study expand the knowledge on the species composition of the fauna of teleost fish parasites in the South Orkney Islands region. These data indicate a significant role of teleost fishes in food webs in the region as well as their key role in the life cycles of metazoan parasites of marine mammals and birds in West Antarctica.

Table 4. Species richness and abundance of helminths collected from teleost fishes in shallow- or deep-water habitats in West Antarctica

Fish species	Number of specimens	Depth of fish collection	Number of helminths collected	
			specimens	species
1. <i>Champscephalus gunnari</i>	34	107–665 m	1 267	8
2. <i>Pseudochaenichthys georgianus</i>	33	107–581 m	7 645	16
3. <i>Chaenocephalus aceratus</i> *	22	104–270 m	5 789	19
4. <i>Notothenia coriiceps</i>	78	10–30 m	15 451	27
5. <i>Parachaenichtys charcoti</i>	18	10–30 m	5 298	26
6. <i>Chaenocephalus aceratus</i> **	6	10–30 m	4 830	23

* Specimens of *C. aceratus* from the area of Orkney Islands; ** Specimens of *C. aceratus* from the Ukrainian Antarctic station (UAS) area.

Table 5. Similarity of helminth faunas between the shallow-water (SW) and deep-water (DW) fish populations based on the Sørensen index (% below the diagonal) and the Bray-Curtis index (% above the diagonal)

Species	<i>N. coriiceps</i> (SW)	<i>P. charcoti</i> (SW)	<i>C. aceratus</i> (SW)	<i>C. aceratus</i> (DW)	<i>C. gunnari</i> (DW)	<i>P. georgianus</i> (DW)
<i>N. coriiceps</i> (SW)	–	72.2	68.6	46.9	20.0	33.3
<i>P. charcoti</i> (SW)	90.6	–	78.2	50.7	27.3	44.2
<i>C. aceratus</i> (SW)	88.0	89.8	–	55.6	24.6	43.9
<i>C. aceratus</i> (DW)	80.9	69.6	69.8	–	45.3	73.8
<i>C. gunnari</i> (DW)	45.7	47.1	45.2	57.1	–	64.8
<i>P. georgianus</i> (DW)	74.4	71.4	66.7	88.9	66.7	–

All parasite species found were not specific to their fish hosts; all of them infected from two to 11 different fish species. The high species richness of the parasite fauna of teleost fishes was reported in different regions of Antarctica (Palm et al., 2007; Zdzitowiecki, 2001 a; Zdzitowiecki and Laskowski, 2004; Laskowski and Zdzitowiecki, 2005; Shendryk et al., 2014; Oğuz et al., 2015; Münster et al., 2016, 2017; Kuhn et al., 2018; Alt et al., 2021; Kuzmina et al., 2022 a, b). Moreover, most of these studies reported the absence of host-specificity in the helminths of Antarctic fish (Palm et al. 2007; Rohde and Heap, 1998; Zdzitowiecki, 2001 a; Laskowski and Zdzitowiecki, 2005; Oğuz et al., 2015; Kuhn et al., 2018; Kuzmina et al., 2022 a, b).

The species richness in the helminth infracommunities varied from 2 to 13 species. The highest number of helminth species was recorded in *C. aceratus* (up to 13 species per one fish host), and in *P. georgianus*, *P. charcoti*, and *N. coriiceps* (up to 12 species per host). Generally, the species composition and richness of the parasite communities in marine fishes is determined by their feeding ecology, the depth of fish habitats and migrations (Klimpel et al. 2003, 2006 a, b; Rocka, 2006; Palm et al., 2007; Kuhn et al., 2018; Alt et al., 2021). In *C. aceratus*, *P. georgianus*, *P. charcoti*, *N. larseni*, and two *Notothenia* species, the high parasite species richness is connected with their less specialized feeding behaviour and reflects their migrations from shallow coastal waters to the deep-sea habitats (Siegel, 1980 a, b; Gon and Heemstra 1990; Palm et al., 2007; Zdzitowiecki, 2001 a; Barrera-Oro, 2002; Laskowski and Zdzitowiecki, 2010; Kuhn et al., 2018; Alt et al., 2021). At the same time, fish species feeding mainly on Antarctic krill, such as *C. gunnari*, *C. wilsoni*, or *N. ionah*, have less rich parasite fauna (Hoogesteger and White, 1981; Kuhn et al., 2018).

All twelve fish species examined were infected with both larval and adult helminths. The cestodes, anisakid nematodes, and acanthocephalans from the genus *Corynosoma* were found in fishes on the larval stages; they used the teleosts as their intermediate or paratenic hosts. Moreover, in the largest samples of fish species (*C. aceratus*, *C. gunnari*, and *P. geor-*

gianus), the proportion of larvae in the parasite communities was from 62.5 % to 75 %. We did not calculate the exact proportion of larval stages in the helminth communities of the other nine fish species; however, larvae comprised more than 50 % of the total helminth number collected from every examined fish.

In the present study, cestodes were found to be the dominant group of parasites; they were found in all 12 fish species. Moreover, the intensity of fish infection with cestodes might reach more than 400 specimens per host; especially highly infected was the deep-sea species *P. georgianus* with bilocular and trilocular metacestodes, as well as *C. aceratus* with *Diphyllobothrium* sp. (see table 3). For the tetrabothriid cestodes, Antarctic elasmobranchs and birds are the final hosts; while the diphyllobothriid cestodes are the parasites of marine mammals (Rocka, 2006, 2017). In our study, the deep-sea fish species, such as *C. wilsoni*, *G. acuticeps*, *P. charcoti*, *C. rastrospinosus*, *N. ionah*, and *C. gunnari* were mainly infected with tetrabothriid metacestodes; the proportion of other taxonomic groups in the samples was much lower.

Nematodes, especially Anisakidae were found to predominate in the helminth communities of demersal omnivorous fish species (*C. aceratus*, *N. larseni*, and *Notothenia* spp.); the same was observed in previous researches (Zdzitowiecki and Laskowski, 2004; Laskowski and Zdzitowiecki, 2005; Palm et al., 2007; Alt et al., 2021; Kuzmina et al., 2021 b). In pelagic and deep-water fish species (*C. gunnari*, *P. georgianus*, *N. ionah*, *C. rastrospinosus*, *C. wilsoni*, etc.), the proportion of nematodes in helminth communities was much lower in our study as well as in the data published by other researchers (e. g., Kuhn et al., 2018). We believe that this is primarily due to the peculiarities of the diet of the demersal fish species, in which, according to literature data, krill, mysids, amphipods, copepods, and fish prevail (McKenna, 1991; Flores et al., 2004; Kock et al., 2013; Alt et al., 2021). At the same time, the deep-water fish species feed primarily on Antarctic krill (*Euphausia superba*) and, to a much lesser degree, on other euphausiids, mysids, and the hyperiids (Kock et al., 1994, 2013; Flores et al., 2004; Kock, 2005; Kuhn et al., 2018). Also, the infection of teleost fishes with anisakid nematodes largely depends on the presence and density of marine mammals, mostly seals, which are the definitive hosts of these nematodes in the region (Klöser et al., 1992; Palm, 1999; McClelland, 2002; Palm et al., 2007; Rocka, 2004, 2006, 2017; Alt et al., 2021).

The infection of teleost fishes with digenean trematodes in our study was moderate; in four out of 12 fish species, trematodes were not found at all. Six species of trematodes were recorded, and *Neolebouria georgiensis* was the most prevalent; the rest of the species were found sporadically in single specimens (see table 3). All digenean species found were not host-specific; previously, all of them were reported in several teleost fish species in West Antarctica (Zdzitowiecki, 1991, 1998; Oğuz et al., 2015; Faltýnková et al., 2017). Most known species of Antarctic digeneans infecting fish hosts are associated with benthic habitats (Zdzitowiecki, 1988; 1998; Faltýnková et al., 2017; Alt et al., 2021); while pelagic fishes are usually not infected with digeneans (Zdzitowiecki, 1991). The most probable intermediate hosts of the digeneans are copepods, amphipods, benthic gastropods or bivalves and annelids (Zdzitowiecki, 1988); thus, infection of demersal omnivorous fishes with these trematodes is usually high. The absence of trematodes in three demersal fish species (*C. wilsoni*, *N. rossii*, and *G. gibberifrons*) in our study is probably due to the small number of fish specimens examined and is connected with the feeding of these fish species mainly on Antarctic krill, which has been reported as not infected with helminths (Kagei et al., 1978; Zdzitowiecki, 1991). The infection of most fish species with the trematode *N. georgiensis* is apparently connected with the feeding of these fish on crustaceans of the family Mysidae, which are known as intermediate hosts of this digenean (Gaevskaya, 1982).

The infection of studied fish with acanthocephalans varied widely; four fish species (*C. gunnari*, *N. ionah*, *C. rastrospinosus*, and *C. wilsoni*) were not found to harbour acan-

thocephalans at all, while *C. aceratus* was found to be infected with 7 species (with the intensity of up to 294 specimens for *Corynosoma evae*); *N. coriiceps* and *P. charcoti* were infected each with 5 acanthocephalan species. All Acanthocephala parasitic in Antarctic fish have two or three hosts in their life cycles (Rocka, 2006; Laskowski and Zdzitowiecki, 2017); the intermediate hosts for all acanthocephalans are crustaceans of the order Amphipoda (Hoberg, 1986; Zdzitowiecki, 2001 b; Zdzitowiecki and Presler, 2001) which are an essential component of the diet of demersal fish. Therefore, in Antarctica, acanthocephalans frequently parasitize demersal bottom-feeding fish hosts and are almost absent in fishes with a pelagic lifestyle (Rocka, 2006; Laskowski and Zdzitowiecki, 2017; Alt et al., 2021; Kuzmina et al., 2021 a). In our study, two acanthocephalans specific for Antarctic teleost fishes (*A. megarhynchus* and *M. rennicki*) were found in 4 fish hosts each; the intensity of fish infection with these species was low, from one to 8 specimens. Acanthocephalans from the genus *Corynosoma* predominated in all fishes infected with this group of helminths. The definitive hosts of *Corynosoma* spp. are marine mammals and birds; moreover, *Corynosoma* spp. are known to be specific to their definitive hosts (Hoberg, 1986; Zdzitowiecki, 1984, 1996; Zdzitowiecki and White, 1996; Laskowski and Zdzitowiecki, 2017). Thus, the high level of fish infection recorded in our study indicated the presence of certain marine mammals: *Mirounga leonina*, *Lobodon carcinophaga*, *Leptonychotes weddellii*, and *Hydrurga leptonyx* in the examined marine habitats.

Only two specimens of one Monogenea species, *Pseudobenedenia nototheniae*, were found in our study in two hosts: *N. coriiceps* and *N. rossii*; other ten fish species were not infected with monogeneans. Despite *P. nototheniae* being reported to have a rather wide range of fish hosts (see Klapper et al., 2017), here and in our previous studies performed at Argentine Islands area, this species was not found in any other fish except *Notothenia* spp. (Kuzmina et al., 2020, 2021 a).

All fish species examined in the South Orkney Islands area were caught at depths from 60 m to more than 800 m (average fishing/trawling depths varied from 104 m to 665 m); therefore, all 12 fish species studied in this work can be classified as deep-sea species, compared to shallow-water fish species caught and examined near to the UAS “Akademik Vernadsky” at the depth of 10–30 m. Comparative analysis of differences in helminth communities of three deep-water and three shallow-water fish populations showed that the species richness of the helminth fauna in shallow-water fishes is much higher, especially considering fish infection with digenean trematodes, acanthocephalans and anisakid nematodes. In the helminth fauna of deep-sea fish, larval stages of tetrabotriid cestodes — parasites of elasmobranchs were dominant groups of parasites. We agree with the opinion (see Campbell, 1983; Zdzitowiecki, 1990, 1998; Zdzitowiecki and Presler, 2001; Laskowski and Zdzitowiecki, 2005, 2010; Rocka, 2004, 2006; Palm et al., 1998, 2007; Shendryk et al., 2014; Alt et al., 2021) that the rich helminth fauna of shallow-water fish species is associated with the presence of a large number of helminth intermediate hosts (molluscs, small crustaceans) in shallow waters compared to deep-sea habitats. It is evident from our data that despite a much smaller number of studied specimens of the shallow-water population of *C. aceratus* ($n = 6$), the number of helminth species in this sample was higher compared to the sample from the deep-water population: 23 species versus 19 (see Kuzmina et al., 2021 a). Besides, the deep-sea fishes *C. gunnari* and *P. georgianus* feed mainly on Antarctic krill (*E. superba*) which is not an intermediate host of helminths (Kagei et al., 1978; Zdzitowiecki, 1991).

The results of the SIMPER analysis revealed four helminth species mostly influencing the difference between the helminth fauna of shallow- and deep-sea fish: nematodes *Contracaecum* sp. and *Pseudoterranova* sp., the acanthocephalan *C. pseudohamanni*, and trilocular metacestodes. We suppose that the high level of shallow-water fish infection with anisakids and *C. pseudohamanni* is a result of the presence and high density of definitive hosts of these helminths, Weddell seals (*L. weddellii*), leopard seals

(*H. leptonyx*), and crabeater seal (*L. carcinophaga*) in coastal waters of the Argentine Islands near the UAS “Akademik Vernadsky” (Dykyy and Peklo, 2012). In the deep waters near the South Orkney Islands, the density of these mammals is lower, therefore, the deep-sea fish species were 10–15 times less infected with anisakid nematodes and *Corynosoma* spp. At the same time, the high infection rates of tetrabotriid cestodes observed in deep-sea fish species indicate the important role of deep-sea teleosts in the life cycles of parasites of elasmobranchs in the West Antarctic. Our results confirm the previously suggested indicator role of helminths for teleost fish population studies (Siegel, 1980 a, b; Kuhn et al., 2018; Kvach and Kuzmina, 2020; Kuzmina et al., 2022). More information on the parasite communities of fish populations is necessary for a reliable analysis of these data. Nevertheless, the results obtained in our study might be considered as the “basic point” for long-term monitoring parasitological studies in West Antarctica in future and the analysis of the changes in the Antarctic marine ecosystems caused by climatic and anthropogenic factors.

This study was partially supported by the National Research Foundation of Ukraine (project number 2020.02/0074) and by the National Antarctic Scientific Center, Ministry of Education and Science of Ukraine (project number H/03-2021).

References

- Alt, K. G., Cunze, S., Kochmann, J., Klimpel, S. 2021. Parasites of three closely related Antarctic fish species (Teleostei: Nototheniinae) from Elephant Island. *Acta Parasitologica*, <https://doi.org/10.1007/s11686-021-00455-8>.
- Barrera-Oro, E. 2002. The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. *Antarctic Science*, **14** (4), 293–309.
- Bielecki, A., Rokicka, M., Ropelewska, E., Dziekońska-Rynko, J. 2008. Leeches (Hirudinida: Piscicolidae) parasites of Antarctic fish from Channichthyidae family. *Wiadomości Parazytologiczne*, **54**, 345–348.
- Blanar, C. A., Munkittrick, K. R., Houlahan, J., Maclatchy, D. L., Marcogliese, D. J. 2009. Pollution and parasitism in aquatic animals: a meta-analysis of effect size. *Aquatic Toxicology*, **93** (1), 18–28.
- Brickle, P., MacKenzie, K., Pike, A. 2005. Parasites of the Patagonian toothfish, *Dissostichus eleginoides* Smitt 1898, in different parts of the Subantarctic. *Polar Biology*, **28** (9), 663–671.
- Bush, A. O., Lafferty, K. D., Lotz, J. M., Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, **83** (4), 575–583.
- Byers, J. E. 2021. Marine parasites and disease in the era of global climate change. *Annual Review of Marine Science*, **13**, 397–420.
- Campbell, R. A. 1983. Parasitism in the deep sea. In: Rowe, G., ed. *The Sea. Deep-sea biology*. Wiley, New York, 473–552.
- Chown, S. L., Clarke, A., Fraser, C. I., Cary, S. C., Moon, K. L., McGeoch, M. A. 2015. The changing form of Antarctic biodiversity. *Nature*, **522** (7557), 431–438.
- Clarke, K. R., Gorley, R. N. 2006. *PRIMER v6: User Manual/Tutorial* (Plymouth Routines in Multivariate Ecological Research). PRIMER-E, Plymouth.
- Collins, M. A., Brickle, P., Brown, J., Belchier, M. 2010. The Patagonian toothfish: biology, ecology and fishery. *Advances in Marine Biology*, **58**, 227–300.
- De Broyer, C., Koubbi, P., Griffiths, H. J., Raymond, B., Udekem d’Acoz, C. d’, Van de Putte, A. P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A., Ropert-Coudert, Y., eds. 2014. *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, 1–498.
- Dykyy, I. V., Peklo, A. M. 2012. Seals of the Argentine Islands (Antarctica). *Zbirnyk Prats Zoologichnogo Muzeju*, **43**, 104–116 [In Russian].
- Eastman, J. T. 2000. Antarctic notothenioid fishes as subjects for research in evolutionary biology. *Antarctic Science*, **12** (3), 276–287.
- Eastman, J. T. 2005. The nature of the diversity of Antarctic fishes. *Polar Biology*, **28**, 93–107.
- Faltýnková, A., Georgieva, S., Kostadinova, A., Bray, R. A. 2017. Biodiversity and Evolution of Digeneans of Fishes in the Southern Ocean. In: Klimpel, S., Kuhn, T., Mehlhorn, H., eds. *Biodiversity and Evolution of Parasitic Life in the Southern Ocean*. Parasitology Research Monographs, vol. 9. Springer, Cham, 49–75.
- Flores, H., Kock, K.-H., Wilhelms, S., Jones, C. D. 2004. Diet of two icefish species from the South Shetland Islands and Elephant Island, *Champsocephalus gunnari* and *Chaenocephalus aceratus*. *Polar Biology*, **27** (2), 119–129.

- Gaevskaya, A. V. 1982. The discovery of the trematode metacercariae in mysids of the South Georgia Island. *Nauchnye doklady vysshe shkoly. Biologicheskie nauki*, 8, 27–29 [In Russian].
- Gibson, D. I., Jones, A., Bray, R. A. 2002. *Keys to the Trematoda*. Volume 1. CABI & Natural History Museum, Wallingford, UK, 1–544.
- Gon, O., Heemstra, P. C. 1990. *Fishes of the Southern Ocean*, 1st edn. J. L. B. Smith Institute of Ichthyology, Grahamstown.
- Gordeev, I. I., Sokolov, S. G. 2016. Parasites of the Antarctic toothfish (*Dissostichus mawsoni* Norman, 1937) (Perciformes, Nototheniidae) in the Pacific sector of the Antarctic. *Polar Research*, 35, 29364.
- Hammer, Ø., Harper, D. A. T., Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4, 9.
- Hechinger, R., Lafferty, K., Huspeni, T., Brooks, A., Kuris, A. 2007. Can parasites be indicators of free-living diversity? Relationships between species richness and the abundance of larval trematodes and local benthos and fishes. *Oecologia*. 151, 82–92.
- Hoberg, E. P. 1986. Aspects of ecology and biogeography of Acanthocephala in Antarctic seabirds. *Annales de parasitologie humaine et compare*, 61, 199–214.
- Hoogesteger, J. N., White, M. G. 1981. Notes on parasite infestation of inshore fish at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, 54, 23–31.
- Hudson, P. J., Dobson, A. P., Lafferty, K. D. 2006. Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology and Evolution*, 21 (7), 381–385.
- Jones, A., Bray, R. A., Gibson, D. I. 2005. *Keys to the Trematoda*. Volume 2. CABI & Natural History Museum, Wallingford, UK, 1–768.
- Kagei, N., Asano, K., Kihata, M. 1978. On the examination against the parasites of Antarctic krill, *Euphausia superba*. *The Scientific Reports of the Whales Research Institute*, 30, 311–313.
- Klapper, R., Münster, J., Kochmann, J., Klimpel, S., Kuhn, T. 2017. Biodiversity and Host Specificity of Monogenea in Antarctic Fish Species. In: Klimpel, S. et al., eds. *Biodiversity and Evolution of Parasitic Life in the Southern Ocean*. Parasitology Research Monographs, vol. 9, 33–47.
- Klimpel, S., Seehagen, A., Palm H. W. 2003. Metazoan parasites and feeding behaviour of four small-sized fish species from the central North Sea. *Parasitology Research*, 91, 290–297.
- Klimpel, S., Rückert, S., Piatkowski, U., Palm, H. W., Hanel, R. 2006a. Diet and metazoan parasites of silver scabbard fish *Lepidopus caudatus* from the Great Meteor Seamount (North Atlantic). *Marine Ecology Progress Series*, 315, 249–257.
- Klimpel, S., Palm, H. W., Busch, M. W., Kellermanns, E., Rückert, S. 2006b. Fish parasites in the Arctic deep-sea: Poor diversity in meso-bathypelagial vs. heavy parasite load in a demersal fish. *Deep-Sea Research Part I*, 53, 1167–1181.
- Klöser, H., Plötz, J., Palm, H. W., 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. *Antarctic Sciences*, 4, 171–178.
- Kock, K.-H. 1992. *Antarctic fish and fisheries*. Cambridge University Press, 1–359.
- Kock, K.-H. 2005. Antarctic icefishes (Channichthyidae): a unique family of fishes. A review, Part I. *Polar Biology*, 28 (12), 862–895.
- Kock, K.-H., Wilhelms, S., Everson, I., Groger, J. 1994. Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). *Marine Ecology Progress Series*, 108, 43–58.
- Kock, K.-H., Gröger, J., Jones, C. D. 2013. Interannual variability in the feeding of ice fish (Notothenioidei, Channichthyidae) in the southern Scotia Arc and the Antarctic Peninsula region (CCAMLR Subareas 48.1 and 48.2). *Polar Biology*, 36 (10), 1451–1462.
- Kuhn, T., Zizka, V. M. A., Münster, J., Klapper, R., Mattiucci, S., Kochmann, J., Klimpel, S. 2018. Lighten up the dark: metazoan parasites as indicators for the ecology of Antarctic crocodile icefish (Channichthyidae) from the north-west Antarctic Peninsula. *PeerJ*. 6: e4638.
- Kuzmina, T. A., Salganskij, O. O., Lisitsyna, O. I., Korol, E. M. 2020. Helminths of Antarctic rockcod *Notothenia coriiceps* (Perciformes, Nototheniidae) from the Akademik Vernadsky Station area (Argentine Islands, West Antarctica): new data on the parasite community. *Zoodiversity*, 54 (2), 99–110.
- Kuzmina, T. A., Laskowski, Z., Salganskij, O. O., Zdzitowiecki, K., Lisitsyna, O. I., Kuzmin, Y. 2022. Helminth assemblages of the Antarctic black rockcod, *Notothenia coriiceps* (Actinopterygii: Nototheniidae) in coastal waters near Galindez Island (Argentine Islands, West Antarctica): temporal changes in the endoparasite community. *Acta Parasitologica*, 67(1):207–217.
- Kuzmina, T. A., Dykyy, I. V., Salganskij, O. O., Lisitsyna, O. I., Korol, E. M., Kuzmin, Yu. I. 2021 a. Helminth diversity in teleost fishes from the area of the Ukrainian Antarctic station “Akademik Vernadsky”, Argentine Islands, West Antarctica. *Zoodiversity*, 55 (3), 251–264.
- Kuzmina, T. A., Salganskij, O. O., Dykyy, I. V., Lisitsyna, O. I., Korol, E. M., Faltýnková, A., Kuzmin, Y. I. 2021 b. Helminths of the Antarctic dragonfish, *Parachaenichthys charcoti* (Perciformes, Notothenioidei, Bathydraconidae) Studied near Galindez Island (Argentine Islands, West Antarctica). *Acta Parasitologica*, 66 (4), 1424–1430.

- Kvach, Y., Kuzmina, T. 2020. Parasitological research in Antarctica: review of the issues and future prospects. *Ukrainian Antarctic Journal*, 1, 102–110 [In Ukrainian].
- Laskowski, Z., Zdzitowiecki, K. 2005. The helminth fauna of some notothenioid fishes collected from the shelf of Argentine Islands, West Antarctica. *Polish Polar Research*, 26 (4), 315–324.
- Laskowski, Z., Zdzitowiecki, K. 2010. Contribution to the knowledge of the infection with Acanthocephala of a predatory Antarctic ice-fish *Chaenocephalus aceratus*. *Polish Polar Research*, 31, 303–308.
- Laskowski, Z., Zdzitowiecki, K. 2017. Acanthocephalans in Sub-Antarctic and Antarctic. In: Klimpel S., Kuhn T., Mehlhorn H., eds. *Biodiversity and Evolution of Parasitic Life in the Southern Ocean*. Parasitology Research Monographs, vol. 9. Springer, Cham, 141–182.
- Laskowski, Z., Rocka, A., Zdzitowiecki, K., Ozouf-Costaz, C. 2007. Occurrence of endoparasitic worms in dusky notothen, *Trematomus newnesi* (Actinopterygii Nototheniidae), at Adelie Land, Antarctica. *Polish Polar Research*, 28 (1), 37–42.
- Marcogliese, D. J. 2002. Food webs and the transmission of parasites to marine fish. *Parasitology*, 124 Suppl., S83–99.
- Marcogliese, D. J. 2016. The Distribution and abundance of parasites in aquatic ecosystems in a changing climate: more than just temperature. *Integrative and Comparative Biology*, 56 (4), 611–619.
- McClelland, G. 2002. The trouble with sealworms (*Pseudoterranova decipiens* species complex, Nematoda): a review. *Parasitology*, 124, 183–203.
- McKenna, Jr., J. E., 1991. Trophic relationships within the Antarctic demersal fish community of South Georgia Island. *Fishery Bulletin*, 89, 643e654.
- Mozgovoy, A. A. 1951. *Ascariadata of animals and man, and the diseases caused by them*. Osnovy nematodologii. Vol. II. Izd-vo AN SSSR, Moskva, 1–616 [In Russian].
- Muñoz, G., Cartes, F. D. 2020. Endoparasitic diversity from the Southern Ocean: is it really low in Antarctic fish? *Journal of Helminthology*, 94, e180, 1–10.
- Münster, J., Kochmann, J., Klimpel, S., Klapper, R., Kuhn, T. 2016. Parasite fauna of Antarctic *Macrourus whitsoni* (Gadiformes: Macrouridae) in comparison with closely related macrourids. *Parasites & Vectors*, 9, 403.
- Münster, J., Kochmann, J., Grigat, J., Klimpel, S., Kuhn T. 2017. Parasite fauna of the Antarctic dragonfish *Parachaenichthys charcoti* (Perciformes: Bathydraconidae) and closely related Bathydraconidae from the Antarctic Peninsula, Southern Ocean. *Parasites & Vectors*, 10, 235.
- Near, T. J. 2009. Notothenioid fishes (Notothenioidei). In: Hedges, S. B., Kumar, S., eds. *The Timetree of Life*. Oxford University Press, 339–343.
- Near, T. J., Dornburg, A., Kuhn, K. L., Eastman, J. T., Pennington, J. N., Patarnello, T., Zane, L., Fernández, D. A., Jones, C. D. 2012. Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proceedings of the National Academy of Sciences of the United States of America*, 109 (9), 3434–3439.
- Oğuz, M. C., Heckmann, R. A., Cheng, C. H. C., El-Naggar, A., Tepe, Y. 2012. Ecto and endoparasites of some fishes from the Antarctic Region. *Scientia Parasitologica*, 13 (3), 119–128.
- Oğuz, M. C., Tepe, Y., Belk, M. C., Heckmann, R. A., Aslan, B., Gürgen, M., Bray, R. A., Akgül, Ü. 2015. Metazoan parasites of Antarctic fishes. *Türkiye Parazitoloji Derneği*, 39, 174–178.
- Palm, H. W. 1999. Ecology of *Pseudoterranova decipiens* (Krabbe, 1878) (Nematoda: Anisakidae) from Antarctic waters. *Parasitology Research*, 85, 638–646.
- Palm, H. W., 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 Biology*, 19 (6), 399–406.
- Palm, H. W., Klimpe, S., Walter, T. 2007. Demersal fish parasite fauna around the South Shetland Islands; high species richness and low host specificity in deep Antarctic waters. *Polar Biology*, 30 (12), 1513–1522.
- Parker, E., Jones, C. D., Arana, P. M., Alegría, N. A., Sarralde, R., Gallardo, F., Phillips, A. J., Williams, B. W., Dornburg, A. 2020. Infestation dynamics between parasitic Antarctic fish leeches (Piscicolidae) and their crocodile icefish hosts (Channichthyidae). *Polar Biology*, 43, 665–677.
- Parukhin, A. M. 1986. Helminthofauna peculiarities of commercial Notothenioides from the SubAntarctic region of the Indian Ocean. *Vestnik Zoologii*, 3, 6–10 [In Russian].
- Parukhin, A. M., Lyadov, V. N. 1982. Helminth fauna of food Nototheniidae fishes from Kerguelen subregion. *Ekologija Morya*, Kiev, 10, 49–57 [In Russian].
- Poulin, R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology*, 132 (1), 143–151.
- Poulin, R., Mouritsen, K. N. 2006. Climate change, parasitism and the structure of intertidal ecosystems. *Journal of Helminthology*, 80 (2), 183–191.
- Rocka, A. 1999. Biometrical variability and occurrence of *Ascarophis nototheniae* (Nematoda, Cystidicolidae), a parasitic nematode of Antarctic and subantarctic fishes. *Acta Parasitologica*, 44 (4), 188–192.
- Rocka, A. 2003. Cestodes of the Antarctic Fishes. *Polish Polar Research*, 24 (4), 261–276.
- Rocka, A. 2004. Nematodes of the Antarctic fishes. *Polish Polar Research*, 25 (2), 135–152.
- Rocka, A. 2006. Helminths of Antarctic fishes: Life cycle biology, specificity and geographical distribution. *Acta Parasitologica*, 51, 26–35.

- Rocka, A. 2017. Cestodes and Nematodes of Antarctic Fishes and Birds. In: Klimpel, S., Kuhn, T., Mehlhorn, H., eds. *Biodiversity and Evolution of Parasitic Life in the Southern Ocean*. Parasitology Research Monographs, vol 9. Springer, Cham, 77–107.
- Rohde, K., Heap, M. 1998. Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasites of marine teleost fish. *International Journal for Parasitology*, 28, 461–474.
- Sala, E., Knowlton, N. 2006. Global Marine Biodiversity Trends. *Annual Review of Environment and Resources*, 31, 93–122.
- Shendrik, T. V., Giginyak, Y. G., Borodin, O. I. 2014. Helminthofauna *Trematomus newnesi* (Actinopterygii; Nototheniidae), obtained from the Bay of Azure, Antarctica. *Trudy BGU*, 9 (2), 32–38.
- Siegel, V. 1980 a. Parasite tags for some Antarctic channichthyid fish. *Archiv für Fischereiwissenschaft*, 31, 97–103.
- Siegel, V. 1980 b. Quantitative investigations on parasites of Antarctic channichthyid and nototheniid fishes. *Meeresforschung – Reports on Marine Research*, 28, 146–156.
- Smith, W. O. Jr., Ainley, D. G., Cattaneo-Vietti, R. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 95–111.
- Sokolov, S. G., Gordeev, I. I., Atopkin, D. M. 2016. Redescription of trematode *Gonocerca muraenolepisi* Parukhin et Lyadov 1979 (Hemiuroidea, Derogenidae), a body cavity parasite of Antarctic fishes, with a discussion of its phylogenetic position. *Invertebrate Zoology*, 13 (2), 191–202.
- Sokolov, S. G., Lebedeva, D. I., Gordeev, I. I., Khasanov, F. K. 2019. *Zdzitowieckitrema incognita* gen. et sp. nov. (Trematoda, Xiphidiata) from the Antarctic fish *Muraenolepis marmorata* Günther, 1880 (Gadiformes: Muraenolepidae): ordinary morphology but unclear family affiliation. *Marine Biodiversity*, 49, 451–462.
- Swan, D. C. 1936. Berlese's Fluid: Remarks upon its Preparation and use as a Mounting Medium. *Bulletin of Entomological Research*, 27 (3), 389–391.
- Targett, T. E. 1981. Trophic Ecology and Structure of Coastal Antarctic Fish Communities. *Marine Ecology Progress Series*, 4, 243–263.
- Thompson, R. M., Mouritsen, K. N., Poulin, R. 2004. Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *Journal of Animal Ecology*, 74, 77–85.
- Weber, E. P. 3rd, Govett, P. 2009. Parasitology and necropsy of fish. *Compendium on Continuing Education for the Practising Veterinarian*, 31 (2). E12.
- Wojciechowska, A. 1993. The tetraphyllidean and tetrabothriid cercoids from Antarctic bony fishes. I. Morphology. Identification with adult forms. *Acta Parasitologica*, 38 (1), 15–22.
- Zdzitowiecki, K. 1979. Digenetic trematodes in alimentary tracts of fishes of South Georgia and South Shetland Islands (Antarctica). *Acta Ichthyologica et Piscatoria*, 9 (1), 15–30.
- Zdzitowiecki, K. 1983. Antarctic acanthocephalans of the genus *Metacanthocephalus*. *Acta Parasitologica Polonica*, 28 (4), 417–437.
- Zdzitowiecki, K. 1984 a. Some Antarctic acanthocephalans of the genus *Corynosoma* parasitizing Pinnipedia, with descriptions of three new species. *Acta Parasitologica Polonica*, 29 (4), 359–377.
- Zdzitowiecki, K. 1984 b. Redescription of *Corynosoma hamanni* (Linstow, 1892) and description of *C. pseudo-hamanni* sp. n. (Acanthocephala) from the environs of the South Shetlands (Antarctic). *Acta Parasitologica Polonica*, 29 (4), 379–393.
- Zdzitowiecki, K. 1987. Acanthocephalans of marine fishes in the regions of South Georgia and South Orkneys (Antarctic). *Acta Parasitologica Polonica*, 31 (4), 211–217.
- Zdzitowiecki, K. 1988. Occurrence of digenetic trematodes in fishes off South Shetlands (Antarctic). *Acta Parasitologica Polonica*, 33, 155–167.
- Zdzitowiecki, K. 1990. Occurrence of acanthocephalans in fishes of the open sea off the South Shetlands and South Georgia (Antarctic). *Acta Parasitologica Polonica*, 35, 131–141.
- Zdzitowiecki, K. 1991. Occurrence of digeneans in open sea fishes off the South Shetland Islands and South Georgia, and a list of fish digeneans in the Antarctic. *Polish Polar Research*, 12 (1), 55–72.
- Zdzitowiecki, K. 1996. Acanthocephala in fish in the Weddell Sea (Antarctica). *Acta Parasitologica Antarctic*, 41 (3), 199–203.
- Zdzitowiecki, K. 1998. Diversity of Digenea, parasites of fishes in various areas of the Arctic. In: Di Prisco, G., Pisano, E., Clarke, A., eds. *Fishes of Antarctica*. Milano, Springer, 87–94.
- Zdzitowiecki, K. 2001 a. Occurrence of endoparasitic worms in fish, *Parachaenichthys charcoti* (Bathydraconidae), off the South Shetland Islands (Antarctica). *Acta Parasitologica*, 46 (1), 18–23.
- Zdzitowiecki, K. 2001 b. Acanthocephala occurring in intermediate hosts, amphipods, in Admiralty Bay (South Shetland Islands, Antarctica). *Acta Parasitologica*, 46 (3), 202–207.
- Zdzitowiecki, K., Cielecka, D. 1997 a. Digenea of fishes of the Weddell Sea. II. The Genus *Macvicaria* (Opecoelidae). *Acta Parasitologica*, 42 (2), 77–83.
- Zdzitowiecki, K., Cielecka, D. 1997 b. Digenea of fishes of the Weddell Sea. III. The Lepocreadiidae (genera *Neolepidapedon* and *Lepidapedon*), parasites of Notothenioidea, *Acta Parasitologica*, 42 (2), 84–91.
- Zdzitowiecki, K., Laskowski, Z. 2004. Helminths of an Antarctic fish, *Notothenia coriiceps*, from the Vernadsky Station (Western Antarctica) in comparison with Admiralty Bay (South Shetland Islands). *Helminthologia*, 41 (4), 201–207.

- Zdzitowiecki, K., Presler, P. 2001. Occurrence of, Acanthocephala in intermediate hosts Amphipoda, in Admiralty Bay, South Shetland Islands, Antarctica. *Polish Polar Research*, 22, 205–212.
- Zdzitowiecki, K., White, M. G. 1992. Digenean Trematoda infection of inshore fish at South Georgia. *Antarctic Science*, 4 (1), 51–55.

Received 11 January 2022

Accepted 30 March 2022