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RESEARCH

Infection patterns of helminth community in black rockcod *Notothenia coriiceps* in West Antarctica over a 6-year term

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Abstract

Patterns of the rockcod *Notothenia coriiceps* infection with helminths were analysed to understand the dynamics of parasite communities in this Antarctic fish and to test their stability over time. The study was performed using helminth samples collected from 183 *N. coriiceps* in 2014–2015 and 2020–2021 in the vicinity of the Ukrainian Antarctic station (UAS) "Akademik Vernadsky", Galindez Island, Argentine Islands, West Antarctica. Overall, 25 helminth taxonomical categories (nine trematodes, four cestodes, five nematodes, and seven acanthocephalans) were subjected to analysis. A direct comparison of the helminth population characteristics showed that nine species significantly changed their infection parameters during the 6 years between the samples. Seven of them (*Pseudoterranova* sp., *Contracaecum* sp., *Ascarophis nototheniae*, monolocular metacestodes, bilocular metacestodes, *Metacanthocephalus rennicki*, and *Diphyllobothrium* sp.) were found to have a significant impact on the differences between helminth infracommunities in 2014–2015 and 2020–2021. Most studied patterns of helminth component community appeared to show a stable tendency, and observed fluctuations were close to the steady trend. Slight but significant changes in the infection patterns observed in this study might have been caused by changes in the populations of intermediate, paratenic, and definitive hosts of helminths (marine invertebrates, mammals, and birds), which participate in helminth transmission in Antarctic ecosystems.

Keywords Antarctic black rockcod · Helminths · Component community · Infracommunity · Ukrainian Antarctic station

Introduction

Ecological changes caused by global warming and anthropogenic influences can be observed in terrestrial and marine ecosystems on a global scale (Walther et al. 2002; Hoegh-Guldberg and Bruno 2010; Doney et al. 2012; Chen 2021). In the polar regions of the Arctic and Antarctic, these changes are especially pronounced and are apparent as rapid reductions in ice cover and the ozone layer and in changes of the biodiversity of marine and terrestrial ecosystems (Laws et al. 1992; Clarke and Harris 2003; Convey and Peck 2019; Post et al. 2019). A high level of endemicity in marine fishes and invertebrates was recently reported in Antarctica. Between 50 and 97% of Southern Ocean species from various taxonomic groups, including sponges, polychaetes, amphipods, molluscs, isopods, pantopods, and notothenioid fish, are endemic (De Broyer et al. 2014). Thus, it is reasonable to consider Antarctica as a model region for investigating global ecological and evolutionary processes

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(Clarke et al. 2007; Barnes and Peck 2008; Klimpel et al. 2017).

Parasitic organisms from various taxonomic groups are known as some of the most sensitive indicators of the state of ecosystems, especially in the marine environment (Mouritsen and Poulin 2002; Hudson et al. 2006; Poulin 2006; Poulin and Mouritsen 2006), which is associated with the complex life cycles of separate groups of parasites, including various invertebrate and vertebrate animals as definitive, intermediate, and paratenic hosts (Poulin 2011). Because of the complexity of host-parasite systems, changes in the composition of parasite communities reflect the changes in the ecosystem state even more rapidly than they could be documented by monitoring geological or oceanographic parameters (Poulin and Mouritsen 2006; Poulin 2011; Kvach and Kuzmina 2020). Most Antarctic animals such as birds and mammals are strictly protected (Shirihai 2008), while the populations of most teleost fishes in the Southern Ocean are still abundant and, consequently, are available for extensive parasitological examinations.

The fish fauna in the Southern Ocean around Antarctica is dominated by the perciform suborder Notothenioidei, which comprises up to 90% of the fish biomass and about 77% of fish species diversity (Near 2009; Near et al. 2012). Notothenioidei is uniquely adapted to the cold environment and is endemic to the Antarctic and sub-Antarctic regions (Eastman 1991; Near 2009). Notothenioidei is a food source for various mammals and birds in the Antarctic ecosystem food chains (La Mesa et al. 2004) and is involved in the complex life cycles of different groups of parasites of predatory fish, fish-eating birds, and marine mammals as their intermediate and/or paratenic hosts (Palm et al. 1998; Rocka 2006). Therefore, the parasite fauna of this group of bony fish has high species diversity in all ecoregions of the Southern Ocean (Oguz et al. 2015; Klimpel et al. 2017; Münster et al. 2017; Kuzmina et al. 2020, 2021a, b, 2022a, b). Several notothenioid fish species, such as Antarctic black rockcod, *Notothenia coriiceps* Richardson, 1844, are promising objects for long-term monitoring studies of parasite communities because they are abundant in different parts of the Southern Ocean including West Antarctica and during the last decades did not demonstrate steady population dynamics (Barrera-Oro et al. 2000; Barrera-Oro and Marschoff 2007; Near 2009). Moreover, in the coastal water area of the Ukrainian Antarctic station (UAS) "Akademik Vernadsky", *N. coriiceps* compose 76–90% of fishes in ichthyological catches (Manilo 2006; Veselskyy and Khoetskyy 2018). Such *N. coriiceps* is a good model organism to study the dynamics of helminth populations in the West Antarctic marine ecosystems (Kvach and Kuzmina 2020).

The present study was performed as a part of the project exploring helminth fauna of Antarctic fish. *N. coriiceps* appeared to be the most convenient fish host species for testing within the project's scope due to the large samples collected in 2014–2015 and 2020–2021 demonstrating its rich helminth fauna. The similarity analysis of helminth infracommunities (Kuzmina et al. 2022c) revealed that although the species richness of helminths was similar in the samples from 2014–2015 to 2020–2021, the helminth abundance in the infracommunities was significantly higher in the sample collected in 2020–2021 compared to that collected in 2014–2015 due to higher intensity of rockcod infection with larval stages of nematodes (*Pseudoterranova* sp., *Contracaecum* sp.), diphyllobothriid metacestodes, and the acanthocephalans *Corynosoma* spp.

This study aimed to characterise the patterns of helminth community of *N. coriiceps* and test how stable helminth communities were over a middle-time scale by comparison the community patterns and infection parameters of separate helminth species in 2014–2015 and 2020–2021.

Materials and methods

Fish sampling

One hundred eighty-three specimens of black rockcod, *Notothenia coriiceps*, were collected from April 2014 to January 2015 and from February 2020 to January 2021 in the vicinity of the Ukrainian Antarctic station (UAS) "Akademik Vernadsky", Galindez Island, Argentine Islands Archipelago (65°15′ S, 64°16′ W). The fishes were caught using a fishing rod off the shore at depths of 10–30 m. All fish collected were immediately transported to the laboratory, measured, dissected, and examined using standard parasitological techniques (see Zdzitowiecki and Laskowski 2004; Weber and Govett 2009). For each fish, information on the total length was collected and analysed. Sampled fish were processed on the same day they were caught; precautions were taken to meticulously label vials with specimens to prevent confusion about the parasites between fish specimens.

Parasite collection and identification

Parasites were collected manually from the skin, body cavity, stomach, intestine, liver, and mesentery. In total, 30,951 individual specimens of 25 taxonomic categories (nine trematodes, four cestodes, five nematodes, and seven acanthocephalans) were collected and analysed (see Kuzmina et al. 2022c for details). All collected parasites were washed in saline and fixed in 70% ethanol. Acanthocephalans were kept in tap water for 30 min to 3 h for proboscis evagination prior to their fixation in ethanol. Parasite identification based on morphological characters was performed at the Institute of Zoology in Kyiv, Ukraine, using dissecting and compound microscopes. Due to complications of the excystation technique, all encysted stages of *Corynosoma* spp. collected in 2014–2015 were identified only to the genus level. In the present analysis, we combined all specimens of *Corynosoma* spp. Therefore, we use the term “taxonomic categories” in the results, referring to the identified helminth species and the taxa, including several species. All helminth specimens were deposited in the parasitological collections of the I. I. Schmalhausen Institute of Zoology in Kyiv, Ukraine.

Meteorological data

All meteorological data (air temperature, water temperature, and water salinity) used in our analysis were obtained from the Meteorological Archive of the State Institution National Antarctic Scientific Centre of Ukraine (NASC of Ukraine at http://meteodata.uac.gov.ua/).

Data analysis

We used the suggested terminology (Bush et al. 1997) for describing parasite communities. The parasitological dataset analysed in this study was the same as that reported by Kuzmina et al. (2022a,c). We analysed the dataset at the levels of component community and infracommunity using relevant approaches to determine whether infection patterns in black rockcod differed between the 2014–2015 and 2020–2021 seasons. Most analyses were performed in R 4.2.0 (R core Team 2022). We used the package *tidyverse* (Wickham et al. 2019) for data manipulation and visualisation.

For each helminth species, we calculated the mean intensity and prevalence of infection. Confidence intervals (95%) for infection prevalence were calculated using Sterne’s method with the function *epi.prev* from the package *epiR* (Stevenson et al. 2018; Rózsa et al. 2000). Statistical differences in infection prevalence and mean intensity of each species in the two samples were estimated using the unconditional exact test and the bootstrap *t*-test, respectively, in the Quantitative Parasitology 3.0 software (Rózsa et al. 2000).

To estimate the probability of whether each species is common or rare, we used a fuzzy clustering algorithm implemented in the *FuzzyQ package* (Balbuena et al. 2021). It simultaneously evaluates the dissimilarities in occupancy and abundance among species in a community and applies fuzzy clustering to allocate them into two clusters of rare and common species.

To reveal direct and indirect associations between helminth species of the community, we visualised a multispecies generalised linear model by a copula graphical model using the *ecoCopula* package (Popovic et al. 2019). Before that, we fitted the negative binomial regression models, using the year as a predictor and the matrix with raw data on intensity as a response. Also, we used the same models for testing whether the year significantly drives community composition and which species contribute significantly to that. The models were fitted with the function *manyglm* from the package *mvabund* (Wang et al. 2012). To visualise the similarity across infracommunities, we used nonmetric multidimensional scaling (nMDS). For this, we utilised the function *metaMDS* from the package *vegan* (Oksanen et al. 2022) to visualise community composition based on the Bray–Curtis dissimilarities matrix of untransformed abundance data. Then, we used the functions *iNEXT* and *ggiNEXT* from the package *iNEXT* (Hsieh et al. 2016) to plot rarefaction curves. Furthermore, we statistically compared these curves with the function *EcoTest.sample* from the package *rareNMtests* (Cayuela et al. 2015). To fit the model and plot nMDS, we excluded the helminth species that infected less than ten hosts from the dataset.

Additionally, to test whether fish body length affects the intensity of infection, we fitted a negative binomial generalised linear mixed model (GLMM). In the model, we included the intensity of infection as a response, fish body length as a predictor, and the years as a random factor. We tested the fitted model for overdispersion and singularity. We used the packages *lme4* (Bates et al. 2015) and *performance* (Lüdecke et al. 2021) to fit and test the model.

We used the Student’s *t*-test to reveal differences in the means between seasons for the climate variables (air temperature, water temperature, and salinity of water) and fish body length. Before this test, we checked the normality of the samples with the Shapiro–Wilk test.

Results

Comparison of climate variables

Analysis of meteorological data revealed a significant difference in the mean air and water temperature and water salinity between 2014–2015 and 2020–2021. The mean air temperature (Fig. 1A) in 2014–2015 was -2.6 °C and ranged from -19.8 °C in August to +5.1 °C in May. In 2020–2021, the mean air temperature was -2 °C and ranged from -13.3 °C in August to +4.5 °C in May. The mean water temperature (Fig. 1B) in 2014 was -1 °C and ranged from -2.1 °C in May to +2.8 °C in February. In 2020–2021, the mean water temperature was -0.8 °C and ranged from -1.9 °C in May to +2.4 °C in February. The mean water salinity (Fig. 1C) in 2014–2015 was 33.7‰ and ranged from 29.1‰ in July to 35‰ in August. In 2020–2021, the mean water salinity was 32.2‰ and ranged from 24.5‰ in July to 34‰ in August.

The *t*-test comparison showed a significant difference in the mean water temperature ($t = -2.2$, $p = 0.03$), salinity ($t = 16.17$, $p = 1.9e^{-50}$), and air temperature ($t = -2.38$, $p = 0.018$) between 2014–2015 and 2020–2021.

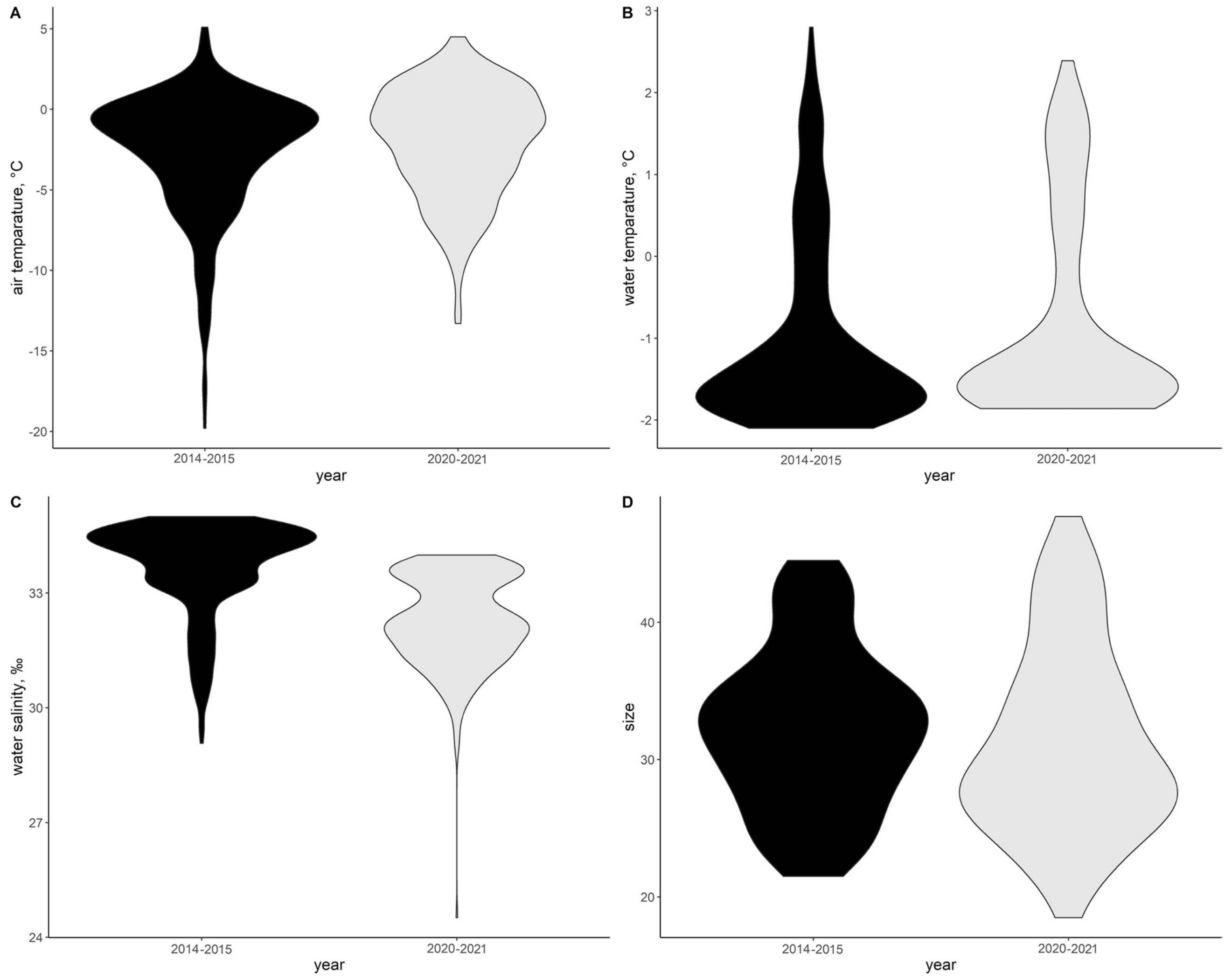


Fig. 1 Comparison of kernel probability density (the width of the filled area represents the proportion of the data located there) between 2014–2015 and 2020–2020 for climate variables (**A**, **B**, **C**) and fish size (total body length) (**D**)

Analysis of helminth component community patterns

The copula graphical model (Fig. 2) revealed 11 positive and one negative association between taxonomic categories in the community. Bilocular metacestodes and the nematode *Pseudoterranova* sp. had the largest number of associations. One negative association was observed between the acanthocephalan *Metacanthocephalus rennicki* and bilocular metacestodes, probably indicating a mutual competitive relationship.

A comparison of the rarefaction curves showed a high similarity between 2014–2015 and 2020–2021 (Fig. 3). The observed species richness was almost identical, and the estimated species richness was slightly higher for 2020–2021; confidence intervals for each year overlapped for observed and estimated species richness. The result of the EcoTest for comparing rarefaction curves was insignificant ($p = 0.465$) (Fig. 3). Hence, the unrejected null hypothesis suggests that the parasite communities did not differ between 2014–2015 and 2020–2021 in the species richness.

In a comparison (Fig. 4, Table 1), the helminth community in 2014–2015 included almost the same number (24) of helminth taxonomic categories as the community in 2020–2021 (23). In 2014–2015, 17 helminth taxonomic categories were rare, and seven were common. *Caudotestis kerguelensis* and *Macvicaria microtestis* were unique for 2014–2015 and *Echinorhynchus petrotschenkoi* was unique for 2020–2021. Meanwhile, in 2020–2021, 13 helminth taxonomic categories were rare and ten were common. Three helminth taxonomic categories changed from rare to common between 2014–2015 and 2020–2021: the nematode *Contracaecum* sp., bilocular metacestode, and trematode *E. oatesi*. However, the change in *E. oatesi*'s status is doubtful as the negative silhouette width value of the species suggests a poor fit for the cluster of common species in 2020–2021.

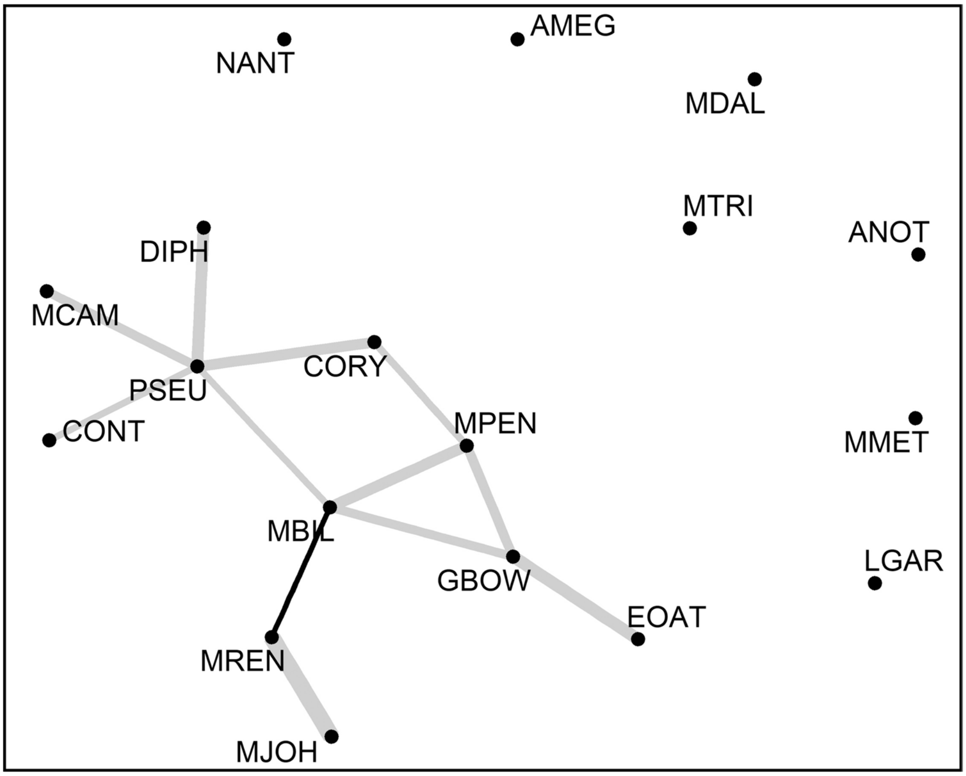


Fig. 2 Map of associations between helminth taxonomical categories plotted by copula graphical model (the direct positive associations are shown in grey, and the negative associations are in black; the thickness of the lines indicates the relative intensity of associations)

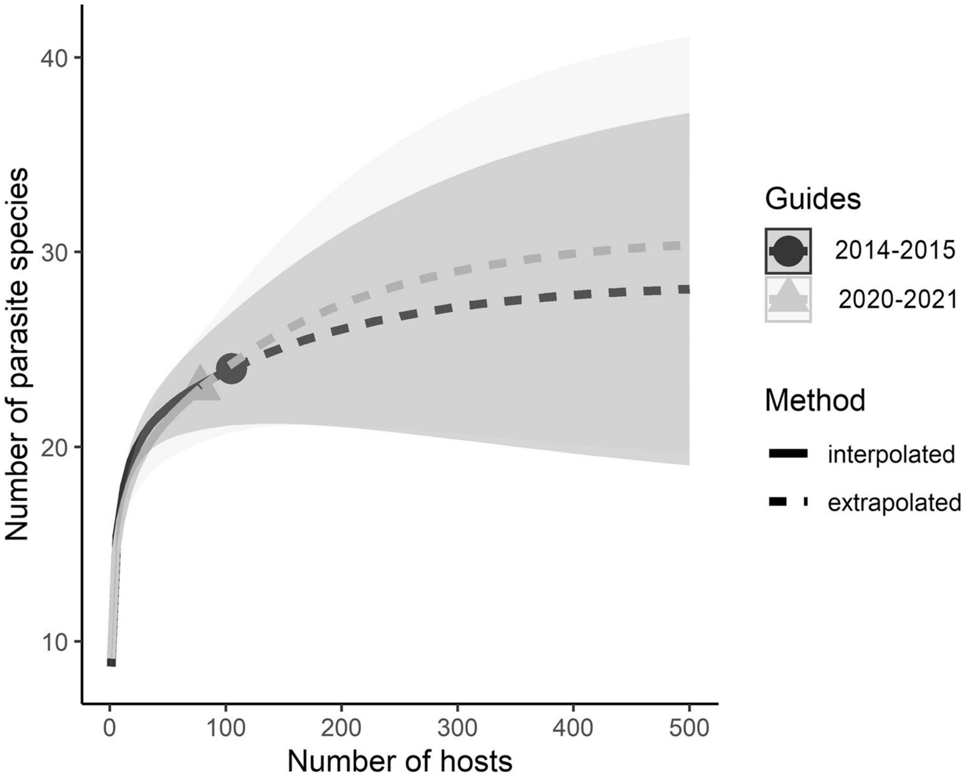


Fig. 3 Sample-based (hosts) rarefaction curves (with 95% confidence intervals) for *N. coriiceps* helminth communities

Twenty-two helminth taxonomic categories were present in both samples. Most of them (16) had similar values of infection prevalence in 2014–2015 and 2020–2021 (Table 1). Moreover, the prevalence of black rockcod infection with the nematodes *Pseudoterranova* sp. and *D. fraseri*, the trematodes *E. oatesi*, *L. garrardi*, *N. antarctica*, and *D. johnstoni*, and the acanthocephalans *M. campbelli* and *A. megarhynchus* was statistically not

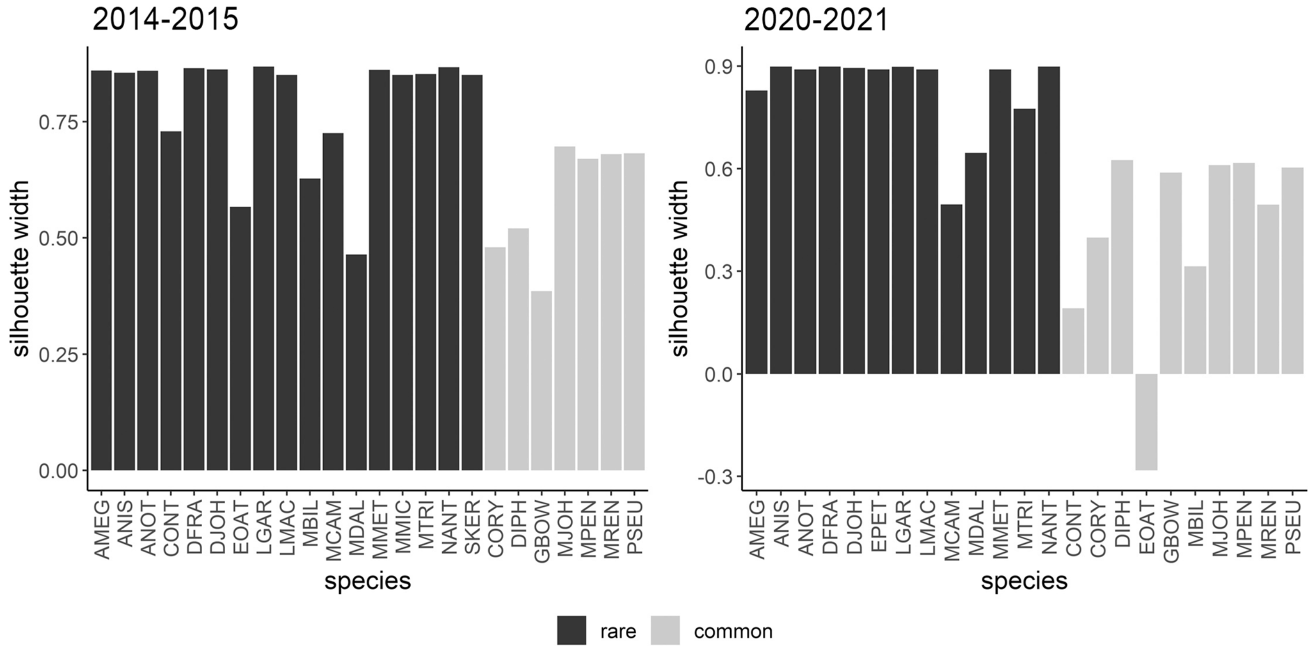


Fig. 4 Fuzzy quantification of common and rare species in *N. coriiceps* helminth communities of 2014–2015 and 2020–2021

different ($p = 1$) in 2014–2015 and 2020–2021. Significant changes in the prevalence of infection were found for six helminth taxonomic categories. The occurrence of *Contracaecum* sp. and bilocular metacestodes in *N. coriiceps* increased significantly in 2020–2021 compared to 2014–2015. The prevalence of infection confidence intervals in these two species did not overlap (Fig. 5), which demonstrated the strict differences between samples. The infection prevalence in 2020–2021 was significantly lower than in 2014–2015 for the nematode *A. nototheniae*, monolocular metacestodes, and the acanthocephalans *M. rennicki* and *M. dalmori*. Despite the confidence intervals of the infection prevalence of these species slightly overlapping in the two samples (Fig. 5), the differences were statistically significant ($p < 0.05$).

The intensity of black rockcod infection significantly increased in 2020–2021 compared to 2014–2015 in three helminth taxonomic categories parasitising *N. coriiceps* in immature (larval) stages: *Pseudoterranova* sp., bilocular metacestodes, and *Corynosoma* spp. In *Diphyllobothrium* sp., the increase in the intensity of infection was evident, though not statistically significant ($p = 0.09$) (Table 1). In two acanthocephalan species, *M. rennicki* and *M. johnstoni*, the intensity of infection was significantly lower in 2020–2021 than in 2014–2015.

Comparison helminth infracommunity patterns

Nonmetric multidimensional scaling (Fig. 6) did not detect any apparent clustering of the helminth infracommunities related to the year's factor. On the other hand, the multivariate analysis showed that the factor year did have a significant multiplicative effect ($p = 0.0009$) on the mean abundance in the infracommunities. The following helminth taxonomical categories were affected by the factor year: *Pseudoterranova* sp. ($p = 0.001$), *Contracaecum* sp. ($p = 0.042$), *Ascarophis nototheniae* ($p = 0.034$), *Diphyllobothrium* sp. ($p = 0.022$), monolocular metacestode ($p = 0.022$), bilocular metacestode ($p = 0.001$), and *Metacanthocephalus rennicki* ($p = 0.017$).

Influence of fish body size on fish infection

The mean total body length of the fish (Fig. 1D) in 2014–2015 was 32.2 cm and ranged from 21.5 to 44.5 cm; the mean fish total body length in 2020–2021 was 31.4 cm and ranged from 18.5 to 47.7 cm. The difference between means was statistically insignificant ($t = 0.88$, $p = 0.379$). There was a significant positive effect of fish body size on the intensity of infection (coefficient = 0.037, z-value = 6.038, $p = 1.6e^{-09}$) (Fig. 7).

Table 1 Comparison of infection prevalence (shown with 95% confidence intervals in parentheses) and intensity (shown as mean and range in parentheses) of helminth taxa in two samples of *Notothenia coriiceps* collected in 2014–2015 and 2020–2021; significant differences are marked in bold

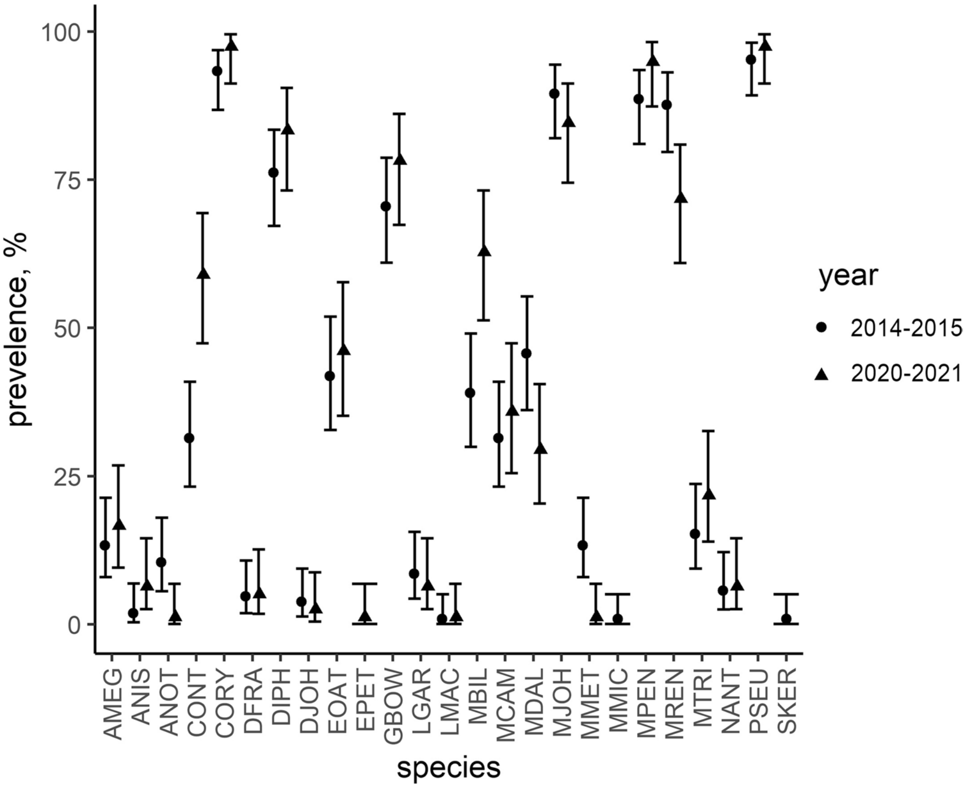
Species	Abbreviation	Prevalence, %		Intensity	
		2014–2015	2020–2021	2014–2015	2020–2021
Nematoda: Chromadorea					
Pseudoterranova sp.	PSEU	95.2 (89.2–98.1)	97.4 (91.2–99.5)	**12.7** **(1–47)**	**22.9** **(1–91)**
Contracaecum sp.	CONT	**31.4** **(23.2–40.9)**	**59.0** **(47.4–69.3)**	2.8 (1–17)	3.4 (1–13)
Anisakis sp.	ANIS	1.9 (0.3–6.9)	6.4 (2.6–14.5)	2 (2–2)	1.8 (1–3)
Ascarophis nototheniae Johnston et Mawson, 1945	ANOT	**10.5** **(5.6–18.0)**	**1.3** **(0.1–6.8)**	12.6 (1–49)	1*
Dichelyne fraseri (Baylis, 1929)	DFRA	4.8 (1.9–10.8)	5.1 (1.8–12.6)	1.4 (1–3)	1.25 (1–2)
Platyhelminthes: Cestoda					
Diphyllobothrium sp.	DIPH	76.2 (67.2–83.4)	83.3 (73.2–90.4)	9.4 (1–49)	17.4 (1–209)
Monolocular metacestode	MMET	**13.3** **(8.0–21.3)**	**1.3** **(0.1–6.8)**	1.5 (1–4)	1*
Bilocular metacestode	MBIL	**39.0** **(29.9–49.0)**	**62.8** **(51.3–73.2)**	**2.2** **(1–8)**	**4.4** **(1–18)**
Trilocular metacestode	MTRI	15.2 (9.4–23.7)	21.8 (13.9–32.6)	1.4 (1–3)	1.5 (1–4)
Platyhelminthes: Trematoda					
Macvicaria microtestis Zdzitowiecki et Cielecka, 1997	MMIC	**1.0** **(0.05–5.1)**	**0**	1*	0
Macvicaria pennelli (Leiper et Atkinson, 1914)	MPEN	88.6 (81.0–93.5)	94.9 (87.4–98.2)	26.7 (1–122)	20.6 (1–127)
Genolinea bowersi (Leiper et Atkinson, 1914)	GBOW	70.5 (61.0–78.7)	78.2 (67.4–86.1)	9.4 (1–37)	10.8 (1–82)
Elytrophalloides oatesi (Leiper et Atkinson, 1914)	EOAT	41.9 (32.8–51.9)	46.2 (35.2–57.7)	3.4 (1–19)	4.3 (1–31)
Lepidapedon garrardi (Leiper et Atkinson, 1914)	LGAR	8.6 (4.4–15.6)	6.4 (2.6–14.5)	1.4 (1–3)	3.2 (1–6)
Neolebouria antarctica (Szidat et Graefe, 1967)	NANT	5.7 (2.5–12.2)	6.4 (2.6–14.5)	2.8 (1–7)	1.4 (1–2)
Derogenes johnstoni Prudhoe et Bray, 1973	DJOH	3.8 (1.3–9.4)	2.6 (0.5–8.8)	1 (1–1)	1.5 (1–2)
Caudotestis kerguelensis (Prudhoe et Bray, 1973)	SKER	**1.0** **(0.05–5.1)**	**0**	1*	0
Lecithaster macrocotyle Szidat et Graefe, 1967	LMAC	1.0 (0.05–5.1)	1.3 (0.1–6.8)	1*	2*
Acanthocephala: Palaeacanthocephala					
Metacanthocephalus rennicki (Leiper et Atkinson, 1914)	MREN	**87.6** **(79.6–93.1)**	**71.8** **(60.9–80.9)**	**9.9** **(1–79)**	**6.0** **(1–38)**
Metacanthocephalus johnstoni Zdzitowiecki, 1983	MJOH	89.5 (82.0–94.4)	84.6 (74.5–91.2)	**11.2** **(1–62)**	**8.0** **(1–28)**
Metacanthocephalus campbelli (Leiper et Atkinson, 1914)	MCAM	31.4 (23.2–40.9)	35.9 (25.5–47.4)	3.7 (1–14)	4.6 (1–25)
Metacanthocephalus dalmori Zdzitowiecki, 1983	MDAL	**45.7** **(36.1–55.3)**	**29.5** **(20.4–40.5)**	4.7 (1–33)	4.1 (1–19)
Aspersentis megarhynchus (von Linstow, 1892)	AMEG	13.3 (8.0–21.3)	16.7 (9.5–26.8)	4 (1–17)	2.2 (1–8)

Table 1 (continued)

Species	Abbreviation	Prevalence, %		Intensity	
		2014–2015	2020–2021	2014–2015	2020–2021
Echinorhynchus petrotschenkoi (Rodjuk, 1984)	EPET	**0**	**1.0 (0.05–5.1)**	0	1*
Corynosoma spp.	CORY	93.3 (86.8–96.8)	97.4 (91.2–99.5)	**78.2 (1–274)**	**110.2 (1–414)**

*One host specimen was infected

Fig. 5 Comparison of prevalence of separate helminth species in *N. coriiceps* between samples of 2014–2015 and 2020–2021 (error bars indicate the 95% confidence intervals)



Discussion

The present analysis of the time scale changes in helminth communities in *N. coriiceps* demonstrates that community structure patterns almost did not change during the 6-year term, although the climate variables differed. The analysis of meteorological data in the UAS water area revealed a slight but significant increase in water and air temperature and a decrease in water salinity, which is consistent with the results of long-term observations in various regions of West Antarctica (Vaughan et al. 2003; Turner et al. 2014; Gutt et al. 2015). However, the range of these changes was apparently insufficient to significantly impact the helminth community patterns. Most community patterns did not change between 2014–2015 and 2020–2021; however, few statistical changes are observed on different community levels. The differences in the species compositions of communities are very slight. On the other hand, the essential differences in component community patterns were caused by the differences in prevalence and intensity of *N. coriiceps* infection by separate helminth species.

The direct comparison of prevalence and intensity of the helminth taxonomic categories between the samples collected in 2014–2015 and 2020–2021 showed that nine of these categories significantly changed the infection parameters during the 6 years between them (see Table 1). According to comparison with model approach, only six species (*Pseudoterranova* sp., *Contracaecum* sp., *A. nototheniae*, monolocular metacestodes, bilocular metacestodes, *Metacanthocephalus rennicki*) and *Diphyllobothrium* sp. were also found to have a significant impact on the differences between helminth infracommunities in 2014–2015 and 2020–2021. Not all of those taxonomical categories were

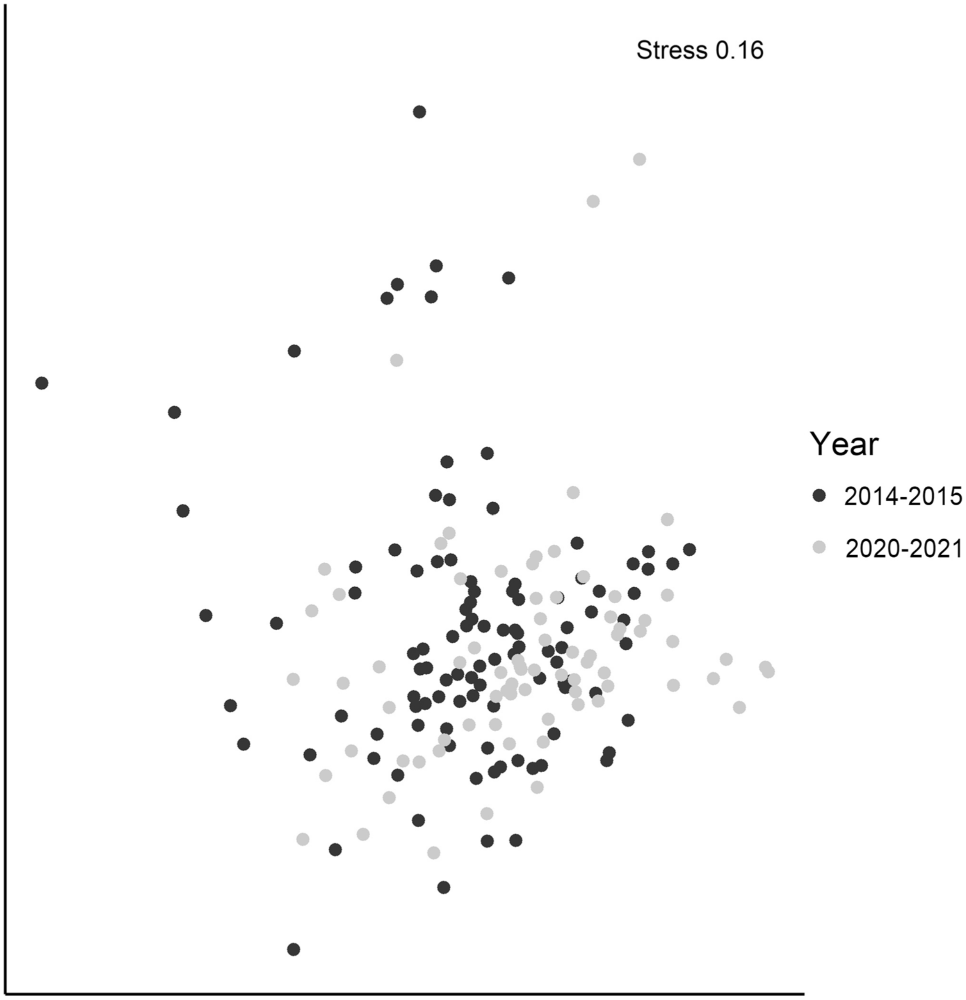


Fig. 6 Nonmetric multidimensional scaling plot of helminth infracommunity (each dot represents an intracommunity of a host specimen; the less the distance between two dots, the higher the level of similarity between two infracommunities)

classified in the cluster of "common" species (see Fig. 4). Namely, *A. nototheniae* and monolocular metacestode are in a "rare" category cluster; the status of bilocular metacestodes and *Contracaecum* sp. is unstable. It can be supposed that the changes are not significant because they did not affect the majority of the "core" species in the community.

Three taxonomic categories, the acanthocephalan *M. rennicki*, bilocular metacestodes, and the nematode *Pseudoterranova* sp., are central nodes for species associations (Fig. 2), indicating their essential role in the formation of the community patterns. In the two latter species, the infection intensity increased significantly in 2020–2021 compared with 2014–2015, while both infection prevalence and intensity decreased in *M. rennicki*. In our opinion, these changes may indicate a particular direction in changes in the helminth community of the studied *N. coriiceps* population. Further studies on the transmission peculiarities of the species in the marine ecosystem near Galindez Island may reveal the exact reasons for such changes. A similar increase in infection parameters of larval helminths in *Parachaenichthys charcoti* were reported previously from the same area (Kuzmina et al. 2021b) as well as in other Antarctic fish species (Rokicki et al. 2009; Kuhn et al. 2018; Muñoz and Cartes 2020); while in other cases, researchers observed a decrease in the abundance of larval stages of acanthocephalans or some ascaroid nematodes (Laskowski et al. 2012; Rokicki et al. 2009). Presumably, increasing infection rates of various fishes with helminth larvae are caused by the increase in the abundance and density of populations of their definitive hosts, which are marine mammals and fish-eating birds in Antarctica.

The associations between helminth taxonomical categories revealed in our study using the copula graphical model, in our opinion, are related to the biology and routes of transmission of these individual parasite species. The high intensity of associations of two acanthocephalan species *M. rennicki* (MREN) and *M. johnstoni* (MJOH) or trematodes *G. bowersi* (GBOW) and *E. oatesi* (EOAT) is undoubtedly due to the similarity of their transmission routes using the same species of intermediate and/or paratenic hosts (Rocka 2006; Faltynkova et al. 2017, 2022). Presumably, the high intensity of association

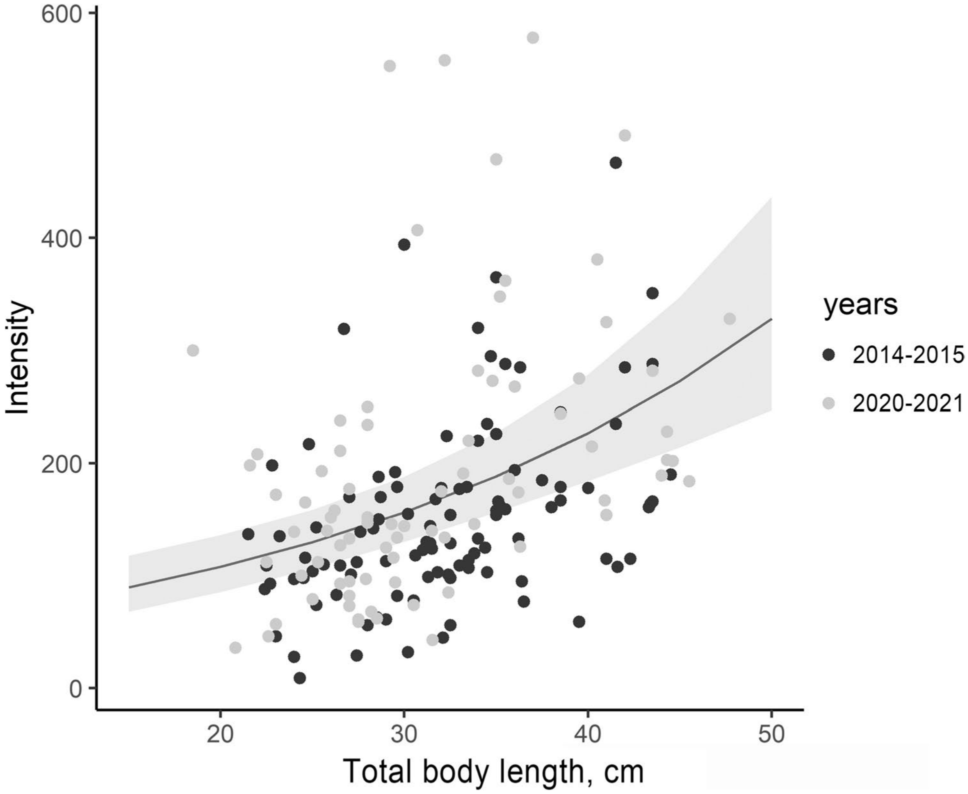


Fig. 7 Relationship between total body length of fish and total intensity of infection. Solid line: the effect estimated by the applied GLMM (confidence intervals are marked by grey colour). Circles: observed data points (host specimens)

between trematodes and bilocular metacestodes is also related to their transmission using the same intermediate/paratenic hosts (Rocka 2017).

Three taxonomically distant helminth species, the nematode *Pseudoterranova* sp. (PSEU), cestode *Diphyllobothrium* sp. (DIPH), and acanthocephalans *Corynosoma* spp. (CORY), have the same definitive hosts, namely the Antarctic seals (Rocka 2004, 2006, 2017; Laskowski and Zdzitowiecki 2017). For polymorphic acanthocephalans (Order Polymorphida) such as *Corynosoma* spp., crustaceans of the order Amphipoda are known as intermediate hosts in Antarctic waters (Hoberg 1986; Zdzitowiecki 2001; Zdzitowiecki and Presler 2001). Intermediate hosts of diphyllobothriid cestodes and anisakid nematodes in Antarctic waters remain unknown (Rocka 2003, 2017). We suppose that the solid associations of these helminth species revealed in our study may suggest that the same species of Amphipoda serve as the intermediate hosts for all these helminths, which promotes simultaneous fish infection. An increase in the populations of Weddell seals, *Leptonychotes weddellii*, and other pinnipeds observed in the waters of Galindez Island in recent decades (Dykyy and Peklo 2012) increased helminth infection of teleost fishes with these helminths (Kuzmina et al. 2022b).

The negative association between the acanthocephalan *Metacanthocephalus rennicki* (MREN) and bilocular metacestodes (MBIL) may indicate a mutual competitive relationship. However, direct competition is hardly possible in the two species with different niches (site of infection) within the host. Presumably, factors other than direct competition might cause a negative association between these species. Investigation of those factors may be the subject of a separate study.

The positive correlation between fish size and intensity of infection found in our study is somewhat expected and is reasonable as bigger fish provide a more resource-rich ecological niche for helminths (Rocka 2006, 2017; Klimpel et al. 2017). Also, it was documented for different Antarctic fish species in previous research (Hoogester and White 1981; Palm et al. 1998; Zdzitowiecki and Laskowski 2004; Münster et al. 2017; Muñoz and Rebolledo 2018; Muñoz and Cartes 2020; Kuzmina et al. 2020; Alt et al. 2022) that bigger individuals, which are usually older than smaller ones, accumulate a larger number of larval stages of helminths compared to smaller specimens.

Thus, the results of our study show that despite the presence of small but significant changes in the climatic factors (mean air and water temperature and water salinity) between 2014–2015 and 2020–2021, there were no significant differences in helminth of *N. coriiceps* component community patterns between these years. On the other hand, we believe that some differences in infection patterns revealed in the present study may be associated with the influence of biotic factors that affect the helminths' transmission such as changes in the populations of intermediate, paratenic, and definitive hosts of helminths (marine invertebrates, mammals, and birds) in Antarctic ecosystems.

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Author contribution All authors contributed to the study conception and design. Conceptualisation: Yaroslav Y. Syrota, Yuriy I. Kuzmin, and Tetiana A. Kuzmina. Material collection and processing were performed by Oleksander O. Salganskiy and Ihor V. Dykyy; helminth identifications and data processing were performed by Tetiana A. Kuzmina, Olga I. Lisitsyna, Eleonora M. Korol, Louis H. du Preez, and Ivanna G. Dmytrieva. Data analysis: Yaroslav Y. Syrota, Yuriy I. Kuzmin, and Tetiana A. Kuzmina. The first draft of the manuscript was written by Yaroslav Y. Syrota, Yuriy I. Kuzmin, and Tetiana A. Kuzmina, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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