

Endoparasitic diversity from the Southern Ocean: is it really low in Antarctic fish?

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Research Paper

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Author for correspondence:G. Muñoz, E-mail: gabriela.munoz@uv.cl**Abstract**

The biodiversity and composition of endoparasites in fish obtained from the Antarctic and subantarctic zones are compared in this study. Several fish were collected in the summer from Antarctica (King George Island) and the Southern Pacific coast (Strait of Magellan and Almirante Montt Gulf). This database was complemented with published information on fish endoparasite communities from both zones, with specimens of fish sample size $n \geq 15$. Thus, 31 fish species were analysed in this study, which altogether had 79 parasite species. Diversity indices were calculated for the parasite community of each fish species. Then they were compared between the Antarctic and subantarctic zones. Parasite species composition and host specificity (as the number of fish species used by a parasite species) were also analysed and compared between zones. The diversity indices and the abundance of parasites were significantly higher in the Antarctic than the subantarctic fish. Few parasite species (7.6%) were shared between fish from both zones, showing significant differences in parasite composition. Antarctic parasites were less host-specific than subantarctic parasites, which allowed the coexistence of several parasite species in the fish. The high parasite abundance in Antarctic fish could trigger sympatric speciation in certain parasitic lineages or the exploitation of new resources, resulting in more parasite species than those in subantarctic environments. The high abundance of Antarctic parasites implies different methods and rates of transmission than those of subantarctic parasites. In addition, more alternative fish hosts were used by the Antarctic than subantarctic parasites. This altogether indicates that host–parasite interaction dynamics significantly differ between the Antarctic and subantarctic systems.

Introduction

Parasites are small organisms that depend on free-living organisms (called hosts) to develop and reproduce. Also, many parasites may use several host species throughout their lives, and many others experience cosmopolitan living in different host species and habitats. However, parasite diversity has not been adequately integrated into ecological studies (Poulin & Morand, 2000; Gómez & Nichols, 2013) because it has been treated as part of free-living communities. Therefore, parasite diversity has been underestimated for many places and taxonomic groups of hosts. In addition, most free-living species in the world may not be free of parasites, and thus, parasite diversity is likely much higher than that of free-living species (Poulin & Morand, 2000; Poulin, 2014). In this context, parasites contribute to the biodiversity of every ecosystem (Windsor, 1995). Thus, including them in ecological studies is necessary, especially in conservation plans and places with high endemism of flora and fauna (Poulin, 2014).

In a census of species from the Southern Ocean (De Broyer *et al.*, 2014), the diversity of approximately 9000 different species of organisms – including algae, invertebrates and vertebrates, and excluding parasites – was considered. Nevertheless, approximately 270 parasite species have been recorded in 145 fish species, as shown in a checklist of parasites provided by Oğuz *et al.* (2015), complemented with other sources (Kabata, 1965; Rokicki & Skorá, 1986; Sosiński & Janusz, 1986; Rokicki & Zdzitowiecki, 1991; Rokicki *et al.*, 1992; Rohde *et al.*, 1998; Walter *et al.*, 2002; Kuhn *et al.*, 2018). However, the number of species is insufficient to analyse biodiversity, which refers to the variability of life on Earth, and different methods have been widely discussed (e.g. Magurran, 1988; Toumisto, 2010). Two components must be considered to measure biodiversity: species richness and the abundance proportion of each species (Toumisto, 2010). For that, many algorithms can be used to calculate diversity (e.g. Magurran, 1988) based on the number and species of the parasites. In contrast, other indices measure taxonomical distances among the species comprising a community (Clarke & Warwick, 2001), which gives valuable information about biodiversity from a different perspective. So far, no such kind of study exists in the Southern Ocean, including the Antarctic.

Antarctic parasite diversity must be contrasted with another area to understand how and why biodiversity is structured. One such zone is the subantarctic, which is the closest zone

to Antarctica. The subantarctic zone is distributed from 40°S to 60°S, with some variation between the Atlantic and Pacific coasts because of the geography, weather and kinds of currents of each place. The subantarctic zone is influenced by different water masses that affect the temperature of the upper water mass, varying between 4°C and 10°C in the winter and up to 14°C in the summer (Pickard & Emery, 1990). Conversely, Antarctic waters are characterized by low temperatures (−2°C to 2.5°C), with little variations in temperature and salinity during the year (Pickard & Emery, 1990). For a long time, extreme environmental conditions such as those found in the polar zones have been considered as having reduced biodiversity (Rohde, 1984; Adams, 2009). However, in recent studies, the Antarctic zone has been presented with high productivity that held large biomass and species diversity (Pickard & Emery, 1990; De Broyer *et al.*, 2014).

While several studies have indicated that parasite species richness is high in Antarctic fish, no data have validated this claim, making it necessary to contrast such richness with those in other places. Therefore, this assertion may represent subjective appreciations based on parasite communities composed of more than ten species (e.g. Walter *et al.*, 2002; Münster *et al.*, 2017; Muñoz & Rebolledo, 2018). However, we found several antecedents suggesting a contrary hypothesis, which is that the parasite diversity of Antarctic fish is lower than that of subantarctic fish – a statement supported by five facts: (1) parasite richness declines from tropical to Antarctic environments (Rohde, 1984); (2) the species diversity of marine fish decreases from the Northern Ocean to the Southern Ocean along the coast of Chile because of water temperature (Ojeda *et al.*, 2000; Navarrete *et al.*, 2014); (3) the taxonomic diversity of fish is narrow in the Antarctic because ten families are present in this zone – the family Nototheniidae comprises more than 50% of the benthic fish species, which is more than the zones outside of Antarctica (Eastman, 1993, 2005); meanwhile, for the subantarctic coastal zone, there are approximately 30 fish families, and 24% of the benthic fish belong to Nototheniidae (Reyes & Hüene, 2012); (4) the species of parasites and hosts are directly related to one another, as seen in terrestrial (Krasnov *et al.*, 2004) and aquatic organisms (Sassal *et al.*, 1998) – thus, low host diversity corresponds to low parasite diversity; and (5) low taxonomic parasite diversity can also be found in Antarctic fish because two parasitic groups, digeneans and acanthocephalans, have been the most representative parasites with high richness and abundance (Zdzitowiecki & White, 1992; Rocka, 2006; Oğuz *et al.*, 2015). Therefore, in this study, we propose analysing the composition and diversity of fish parasites using different methods and comparing them in the Antarctic and subantarctic zones.

Material and methods

Fish and parasite samples

Three fish species (ten specimens of *Harpagifer antarcticus*, 45 of *Notothenia rossii* and 22 of *Notothenia coriiceps*) were collected from Fildes Bay (King George Island, Antarctica) from the rocky intertidal zone during a field campaign supported by the Chilean Antarctic Institute (INACH) in January 2017. Other fish species were collected at the subantarctic zone in January 2017 and 2018. Three fish species were obtained from the Strait of Magellan (53°19′44.0832″S, 70°45′30.6576″W) using fishing lines onboard an artisanal boat: 20 specimens of *Salilota australis*, 28 of *Sprattus fueguensis* and seven of *Genypterus blacodes*,

whereas three fish species were collected with hand nets from the rocky intertidal zone of southern Chile: four specimens of *Austrolycus depressiceps*, 100 of *Patagonotothen cornucola*, 49 of *Harpagifer bispinis* and 15 of *Notothenia* sp. from Rinconada Bulnes, Punta Arenas (53°35′55.446″S, 70°56′0.4704″W), along with 117 specimens of *Patagonotothen tessellata* from Almirante Montt Gulf (51°44′17.34″S, 72°30′25.5564″W), fished by lines from a platform at the coast.

One-third of the fresh fish sample was dissected. Small fish (length <15 cm) were euthanized with an anaesthetic overdose of clove oil, whereas larger fish were euthanized by pithing the spinal cord with a large needle. Both methods were used following the bioethical protocols of the Universidad de Valparaíso (Chile). Other fish were frozen at −20°C and dissected posteriorly. All metazoan parasites were collected from each fish and then fixed in 10% formalin or 70% ethanol, according to the processes applied for identification. Posteriorly, the parasites (e.g. digeneans, cestodes, nematodes, acanthocephalans) were identified, counted and determined according to the morphological descriptions of species given in different specialized literature (Zdzitowiecki, 1990, 1997; Paggi *et al.*, 2000; Rocka, 2004; Laskowski & Jeżewski, 2008; Jeżewski *et al.*, 2014; Laskowski & Rocka, 2014; Paschoal *et al.*, 2014; Laskowski & Zdzitowiecki, 2017). The abundance of parasitic species in each host specimen was recorded and then averaged for each fish species sample. Databases were made using the new data collected in this study and complemented with 19 published articles about fish parasites in both zones of interest: the Antarctic and subantarctic systems (George-Nascimento & Arancibia, 1994; Walter *et al.*, 2002; Brickle *et al.*, 2005; González *et al.*, 2006; Laskowski *et al.*, 2007; Palm *et al.*, 2007; George-Nascimento *et al.*, 2009, 2011; Timi *et al.*, 2009; Vales *et al.*, 2011; Carballo *et al.*, 2012; Mackenzie *et al.*, 2013; Zdzitowiecki & Ozouf-Costaz, 2013; Santoro *et al.*, 2014; Flores *et al.*, 2016; Gordeev & Sokolov, 2016; Oliva *et al.*, 2016; Münster *et al.*, 2017; Kuhn *et al.*, 2018). A data matrix was made of 28 Antarctic and 18 subantarctic fish species, with different sample sizes ranging from two to 199 (table 1).

It is well known that fish sample sizes affect the numerical descriptors of parasites (Guegan & Kennedy, 1996; Jovani & Tella, 2006). Therefore, to avoid the effect of host sampling size, a minimum of 15 specimens per fish species was considered in this study (Bosch *et al.*, 2007). After excluding the small sample sizes, species richness and the abundance of parasites were correlated with fish sample size (via Spearman correlation tests) to confirm whether they were independent of one another. Most data used in this study did not fit normal distributions and did not show homoscedasticity of variances; therefore, nonparametric analyses were applied to obtain the statistical results (Zar, 1996). The significance level was $P < 0.05$ for all the analyses used and performed with the software PAST 3.13 (<https://folk.uio.no/ohammer/past/index.html>).

Parasite diversity

Because species richness and abundance are involved in biodiversity (Magurran, 1988; Toumisto, 2010), parasite richness and abundance were also calculated separately for each fish species. Using data from the literature, total parasite richness was obtained for each fish species sample according to the number of taxa declared in each article. All parasite taxa (independent of their hierarchical taxonomic level of identification) were used for diversity indices. Metacercariae were not considered because several

studies did not examine this parasitic stage, and thus, records on it are few. Mean parasite abundance was calculated as the total number of parasitic individuals divided by the host sample size.

The abundance of each parasite taxon was used to calculate the biodiversity for the entire parasite community of each fish species through the indices of Simpson and Shannon entropy. The Simpson index ($D = \sum(pi)^2$) measures dominance, with values from 0.1 to 1, indicating the lowest (several species with similar abundance) and highest species dominance (one species present or highly abundant in comparison to others), respectively. The Shannon entropy index (H) was calculated as $H' = -\sum[(pi) \times \ln(pi)]$, where pi is the relative abundance of the i -parasite species present in the community (Magurran, 1988). Its values range from 0 to $H_{max} = \ln S$ (indicating minimum and maximum diversity, respectively), where S = total number of parasite taxa in a host sample. The Shannon evenness index was calculated through H/H_{max} , with values from 0 to 1, meaning the lowest and the highest evenness abundance of parasite species, respectively. The other diversity index was the reciprocal of the Simpson diversity index (as true diversity = $1/D$), with values from 1 to 10 (for this study), meaning the lowest and the highest diversity, respectively. All parasite taxa of a fish species were considered for all the diversity descriptors mentioned here, which were calculated for each fish sample.

The taxonomic distinctness index (Clarke & Warwick, 2001) for parasites was also calculated, which required the phylogenetic hierarchy of parasites. The information on parasite taxonomy was obtained from the electronic publication of the World Register of Marine Species (WoRMS; www.marinespecies.org). Because of different taxonomical classifications among parasitic phyla, the information used was for six levels: phylum, class, order, family, genus and species. We calculated the average taxonomic distinctness (Av TD), which indicates the hierarchy levels of differences among parasites of a community. A value = 6 indicates that parasite species belong to different phyla, whereas a value = 1 indicates that parasites belong to the same genus. The variance of taxonomic distinctness (Var TD) was also calculated, and its values range from 0 (all parasite taxa belong to the same hierarchical level) to ≥ 1 (parasites belong to different hierarchical levels).

The average length was taken from several fish species when available in the article where parasitological information was obtained. The class mark was used when the body length range was indicated. When the fish body length was not provided in the papers used, the datum was obtained from Iwami and Kock (1990). Fish body length was compared between the Antarctic and subantarctic zones. All parasitological descriptors were also correlated to determine the influence of this variable on parasite diversity. If differences were observed in the correlation of variables between zones, comparisons between correlation coefficients were applied using Fisher r -to- z transformation (Wilcox, 2009).

Fish diversity was calculated using the taxonomic distinctness index. Fish taxonomy was obtained from Nelson (1994) and WoRMS (www.marinespecies.org). Six hierarchical levels were considered for fish (i.e. superorder, order, suborder, family, genus and species); thus, the index values of Av TD and Var TD varied from 0 to 6.

Parasite species composition

To compare parasite compositions between the Antarctic and subantarctic fish, all parasites identified at the species level were considered. When a parasite was undetermined for a particular

genus, if that genus was not recorded in any other fish, then that parasite was also considered. Unidentified parasites for a specific phylum, class or order were not used in this part of the study. The taxa richness, mean abundance and relative abundance (%) of parasites were calculated for four groups: digeneans, cestodes, nematodes and acanthocephalans. They were then compared separately between the Antarctic and subantarctic fish through Kruskal–Wallis tests to detect which of these parasite groups were more representative in each zone.

Host specificity was also calculated, considered as the number of hosts used by each parasite species. In this study, the host specificity values varied from 1 to 16 (meaning that a parasite species was found in 1 to 16 fish species). The host specificity value for a parasite species was the same for all host species with that parasite. For example, if a fish species sample had the parasites A, B and C with host specificity values 2, 4 and 10, this means these parasites were in two, four and ten host species, respectively. Then, the basic statistics of host specificity were obtained using the host specificity values of all the parasites found in a host species. For the aforementioned example, the average host specificity would be 5.3 in the parasite community of the fish sample. A Mann–Whitney test was then applied for the host specificity between parasites of the Antarctic and subantarctic fish. Spearman correlations were also applied between parasite diversity indices and the host specificity of different sampling zones.

The parasite composition between the two groups of fish was compared through a non-metric multidimensional scaling analysis (NMDS) using the Jaccard similarity coefficient (Chao *et al.*, 2006) based on the presence/absence of parasite taxa in the two fish groups. Another analysis was performed with the Bray–Curtis similarity index using the average abundance of each parasite taxon for ordination analysis (Clarke & Warwick, 1994). The scores of the two main ordinations' NMDS axes were compared separately between the Antarctic and subantarctic fish through a Mann–Whitney test.

Results

Fish and parasite samples

From the original database constructed for this study and after deleting small fish sample sizes ($n < 15$), the database was composed of 15 and 16 fish species for the Antarctic and subantarctic zones, respectively (table 1). In this database, no significant difference was found between zones in terms of sample size ($U_{15,16} = 71$; $P = 0.20$), and neither was a significant correlation found between parasite taxa richness and fish sample size (Antarctic: $n = 15$; $r_s = 0.360$; $P > 0.2$; subantarctic: $n = 16$; $r_s = 0.367$; $P > 0.2$).

Parasite diversity

Most of the parasitological descriptors were significantly different between sampling zones, such as species richness, mean abundance and diversity indices, which were higher in the Antarctic than the subantarctic fish (fig. 1). Parasite dominance was higher in the subantarctic than the Antarctic fish ($P = 0.029$). The Shannon evenness of parasite communities ($P = 0.231$) and taxonomy distinctness (average and variance) did not differ between both fish groups (fig. 1).

The host body length did not differ between zones ($U_{15,16} = 93.5$; $P = 0.299$) and did not correlate with the fish sample size for any sampling zone ($-0.091 < r_s < 0.306$; $P > 0.05$). The taxa

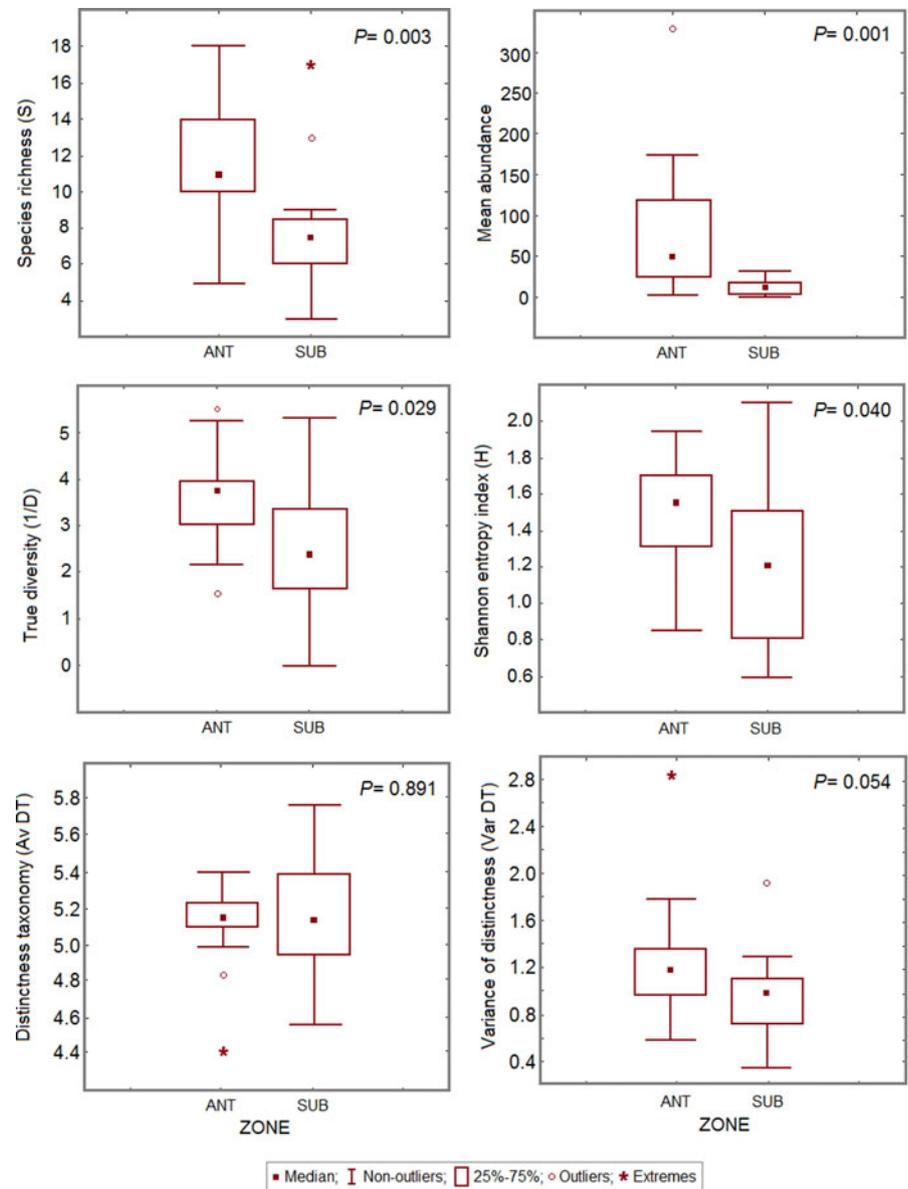


Fig. 1. Diversity descriptors of endoparasite communities for Antarctic (ANT) and Subantarctic (SUB) fish. The probability of the Mann-Whitney comparison tests is given for each descriptor.

richness and diversity indices of the fish did not correlate with the fish body length of both sampling zones. However, the average abundance of parasites was significantly correlated with the host body length of the subantarctic fish (table 2). Nonetheless, the correlation coefficients of average parasite abundance versus host body length did not differ between zones ($Z = -1.4$; $P = 0.161$).

Fish from the Antarctic zone were less diverse than those from the subantarctic zone in terms of the number of families, genera and species (table 3). Consequently, the taxonomic distinctness (Av TD) of the hosts was significantly smaller in the Antarctic than the subantarctic fish (table 3).

Parasite species composition

Seventy-nine parasite species were found in the 31 fish species: 38 in the Antarctic fish, and 47 in the subantarctic fish, with six species in both zones (7.6% of the parasites in common). The

maximum similarity of the composition of parasite communities between the pairs of fish species was relatively high between fish of the same zone (e.g. 90% of similarity between *N. coriiceps* and *N. rossii* from the Antarctic and 54% of similarity between *P. cornucola* and *H. bispinis* from the subantarctic zone). However, between fish species from different zones, the maximum similarity of parasite composition was 17% between *Dissostichus eleginoides* and *Merluccius australis*. Concordant with these results, differences in the parasite composition of fish were also observed between zones analysed by an NMDS. The two main axes show low-stress values ($= 0.334$) for the presence/absence of the parasite species (fig. 2), which usually implies a poor representation of the data by the two-dimensional axis. Only the first axis of this ordination analysis was significantly different between the Antarctic and subantarctic fish (Mann-Whitney: $U = 8$, $P < 0.001$ for axis 1; $U = 97$, $P = 0.363$ for axis 2). For the NMDS based on mean parasite abundance, a poor representation was also observed between the two main axes (stress values $= 0.338$) (fig. 2), because the first axis of this ordination analysis was the only significantly

Table 1. Fish species and bibliographic source from where data of endoparasites were obtained.

Fish species	Fam	Fish sample size (n)	Average/class mark of fish body length	Parasite taxa richness	Source
ANTARCTIC					
<i>Parachaenichthys charcoti</i>	Bat	47	16.9	13	Münster <i>et al.</i> (2017)
<i>Gerlachea australis</i>	Bat	5	22.0	2	Münster <i>et al.</i> (2017)
<i>Gymnodraco acuticeps</i>	Bat	8	26.5	7	Zdzitowiecki and Ozouf-Costaz (2013)
<i>Racovitzia glacialis</i>	Bat	7	27.6	6	Münster <i>et al.</i> (2017)
<i>Chinodraco hamatus</i>	Cha	100	35	16	Santoro <i>et al.</i> (2014)
<i>Chaenodraco wilsoni</i>	Cha	33	26.4	5	Kuhn <i>et al.</i> (2018)
<i>Chaenocephalus aceratus</i>	Cha	21	36	18	Palm <i>et al.</i> (2007)
<i>Champscephalus gunnari</i>	Cha	25	32.1	5	Kuhn <i>et al.</i> (2018)
<i>Cryodraco antarcticus</i>	Cha	2	36.6	3	Zdzitowiecki and Ozouf-Costaz (2013)
<i>Neopagetopsis ionah</i>	Cha	3	41.2	4	Kuhn <i>et al.</i> (2018)
<i>Pagetopsis macropterus</i>	Cha	4	23.8	3	Kuhn <i>et al.</i> (2018)
<i>Pseudochannichthys georgianus</i>	Cha	15	49.1	11	Kuhn <i>et al.</i> (2018)
<i>Paradiplospinus gracilis</i>	Gem	11	41	2	Palm <i>et al.</i> (2007)
<i>Harpagifer antarcticus</i>	Har	10	11.8	7	This study
<i>Macrouronus whitsoni</i>	Mac	25	32	12	Walter <i>et al.</i> (2002)
<i>Muraenolepis microps</i>	Mur	12	31	15	Palm <i>et al.</i> (2007)
<i>Pagothenia borchgrevinki</i>	Not	2	14.4	5	Zdzitowiecki and Ozouf-Costaz (2013)
<i>Gobionotothen gibberifrons</i>	Not	12	37	8	Palm <i>et al.</i> (2007)
<i>Lepidonotothen larseni</i>	Not	51	14	16	Palm <i>et al.</i> (2007)
<i>Lepidonotothen nudifrons</i>	Not	40	12	14	Palm <i>et al.</i> (2007)
<i>Lepidonotothen squamifrons</i>	Not	31	18	12	Palm <i>et al.</i> (2007)
<i>Trematomus eulepidopus</i>	Not	9	22	11	Palm <i>et al.</i> (2007)
<i>Trematomus newnesi</i>	Not	16	16.5	11	Laskowski <i>et al.</i> (2007)
<i>Trematomus bernachi</i>	Not	3	16.6	8	Zdzitowiecki and Ozouf-Costaz (2013)
<i>Notothenia coriiceps</i>	Not	22	32.5	9	This study
<i>Notothenia rossi</i>	Not	45	29.7	10	This study
<i>Dissostichus mawsoni</i>	Not	20	128	10	Gordeev and Sokolov (2016)
<i>Dissostichus eleginoides</i>	Not	18	82	10	Brickle <i>et al.</i> (2005)
SUBANTARCTIC					
<i>Odontesthes nigricans</i>	Ath	22	22.1	7	Flores <i>et al.</i> (2016)
<i>Odontesthes smitti</i>	Ath	31	14	7	Carballo <i>et al.</i> (2012)
<i>Brama australis</i>	Bra	90	34.5	6	Oliva <i>et al.</i> (2016)
<i>Sprattus fueguensis</i>	Clu	28	9.8	4	This study
<i>Eleginops maclovinus</i>	Ele	33	43.9	3	George-Nascimento <i>et al.</i> (2009)
<i>Micromesistius australis</i>	Gad	41	48	13	George-Nascimento <i>et al.</i> (2011)
<i>Harpagifer bispinis</i>	Har	49	5.4	8	This study
<i>Macruronus magellanicus</i>	Mer	278	64.6	8	Oliva (2001)

(Continued)

Table 1. (Continued.)

Fish species	Fam	Fish sample size (n)	Average/class mark of fish body length	Parasite taxa richness	Source
<i>Merluccius australis</i>	Mer	199	70	9	George-Nascimento and Arancibia (1994)
<i>Salilota australis</i>	Mor	20	40.6	17	This study
<i>Patagonotothen cornucola</i>	Not	100	7.1	9	This study
<i>Patagonotothen tessellata</i>	Not	117	13.0	7	This study
<i>Notothenia</i> sp.	Not	15	7.6	6	This study
<i>Raneya brasiliensis</i>	Oph	107	24.47	8	Vales <i>et al.</i> (2011)
<i>Genypterus blacodes</i>	Oph	7	68.5	8	This study
<i>Pinguipes brasilianus</i>	Pin	50	33.88	7	Timi <i>et al.</i> (2009)
<i>Sebastes capensis</i>	Seb	37	28	7	González <i>et al.</i> (2006)
<i>Austrolycus depreciceps</i>	Zoa	4	23.7	4	This study

Fam, Fish family; Ath, Atherinopsidae; Bat, Bathydraconidae; Bra, Bramidae; Cha, Channichthyidae; Clu, Clupeidae; Ele, Eleginopsidae; Gad, Gadidae; Gem, Gempylidae; Har, Harpagiferidae; Mac, Macrouridae; Mer, Merlucciidae; Mor, Moridae; Mur, Muraenolepididae; Not, Nototheniidae; Ophi, Ophidiidae; Pin, Pinguipedidae; Seb, Sebastidae; Zoa, Zoarcidae.

Table 2. Spearman correlations between several variables of parasite diversity and fish body length for Antarctic and subantarctic.

Variables of parasite diversity vs. fish body length	Antarctic (= 15)	Subantarctic (= 16)
Taxa richness (S)	-0.261	0.274
Average abundance	0.415	0.762*
Simpson dominance (D)	0.345	0.014
Shannon Entropy index (H)	-0.571*	-0.071
Shannon evenness (H'/H _{max})	-0.425	-0.117
True diversity (1/D)	-0.345	0.014
Average distinctness (Av TD)	0.017	0.008
Variation of distinctness (Var TD)	-0.260	-0.288

*significant correlation ($P < 0.05$).

different one between the Antarctic and subantarctic fish (Mann-Whitney: $U = 9$, $P < 0.001$ for axis 1; $U = 96$, $P = 0.342$ for axis 2).

Cestodes and acanthocephalans had greater richness in the Antarctic than the subantarctic fish (Mann-Whitney: $P < 0.045$), whereas the highest mean abundance and relative abundance were only given for the cestodes of the Antarctic fish (Mann-Whitney: $P < 0.035$). No significant differences were found for the species richness, mean abundance and relative abundance of nematodes and digeneans between the zones and databases (Mann-Whitney: $P > 0.12$).

Significant differences were observed in terms of host specificity between zones based only on parasite species ($U_{15,16} = 54$; $P < 0.008$). Host specificity was lower (i.e. euryxenous parasites) in the Antarctic than the subantarctic fish (table 4 and fig. 3). Host specificity was significantly correlated with parasite richness ($r_s = 0.523$, $P < 0.05$), the diversity indices of Shannon entropy ($r_s = 0.593$, $P < 0.03$) and true diversity ($r_s = 0.508$, $P < 0.05$), but was inversely correlated with parasite dominance ($r_s = -0.508$, $P < 0.05$) and Av DT ($r_s = -0.547$, $P < 0.05$) for subantarctic fish only. The host specificity of parasites from Antarctic fish was

Table 3. Differences of taxonomic hierarchies of fish between Antarctic and subantarctic zones.

Fish taxonomical data	Antarctic	Subantarctic
Number of families	4	12
Number of genera	10	14
Number of species	15	16
Av TD	3.04	5.09*
Var TD	1.00	0.75
* $U = 2823.5$; $P < 0.001$		

*Significant difference (Mann-Whitney test for comparison of average distinctness, Av DT).

not significantly correlated with any descriptor of the parasite community (r_s ranged from -0.012 to 0.237 ; $P > 0.05$). However, the correlation coefficients between host specificity and the community descriptors of parasites did not differ between zones ($Z > 1.91$; $P \geq 0.056$).

Discussion

The Antarctic fish had higher parasite diversity than the subantarctic fish, which was contrary to the assumptions given at the beginning of this study based on several antecedents communicated in previous studies (e.g. Rohde, 1984). Several patterns of the parasites and their fish hosts previously found along the latitudinal coast associated with water temperature gradients apply up to the subantarctic zone but not the Antarctic zone. The relative isolations of the Antarctic environment, given by surrounding currents that keep the mass of water around the continent, retain organisms highly adapted to the particular conditions of this pole; therefore, the patterns of distribution and diversity in this area may be different from those of other places. Approximately 80% of the Antarctic flora and fauna are endemic (Eastman, 2005; De Broyer *et al.*, 2014), including the parasite species (Rocka, 2006). In this study, we found that 7.6% of the parasite fauna was shared between the two zones, supporting the endemism of Antarctic parasites.

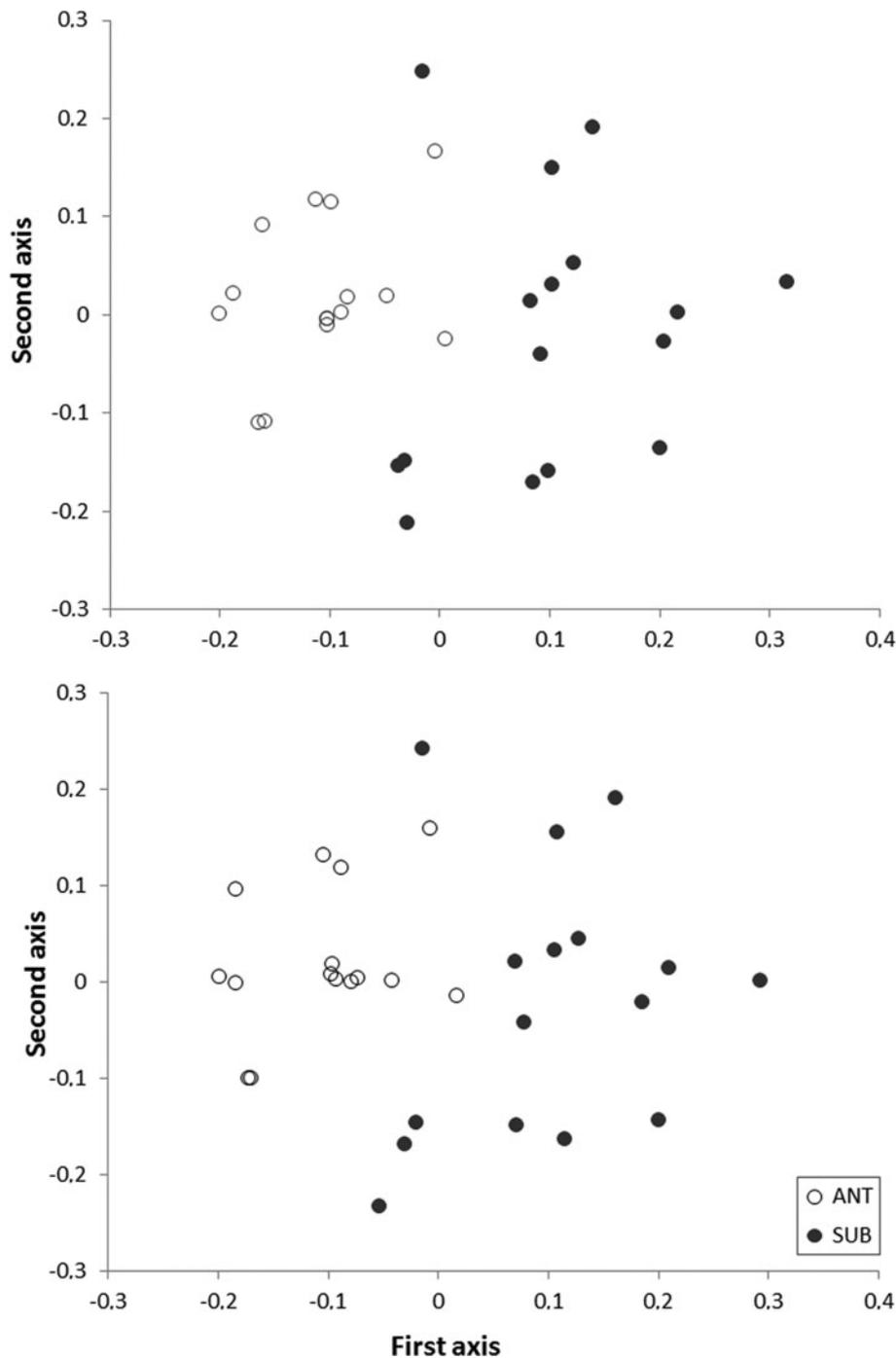


Fig. 2. Two dimensional ordination of NMDS for endoparasite composition of Antarctic (ANT) and Subantarctic (SUB) fish; presence-absence of parasites (Stress value = 0.334) was used in the analysis for the upper graph, and mean abundance of parasites (Stress value= 0.338) was used for the lower graph.

The high parasite abundance in the Antarctic fish was unexpected. Some Antarctic fish had hundreds of parasite individuals (e.g. Zdzitowiecki & Ozouf-Costaz, 2013; Santoro *et al.*, 2014). Multiple causes are related to the physiology and ecology of the hosts, which may affect the specific dynamic infections between the parasites and the hosts. The particular characteristics of the Antarctic climate have strongly affected the physiology of organisms that live there. Different organisms depress their physiological activities in certain periods. Notothenioid fish from the Southern Ocean have low metabolism (measured as oxygen consumption), which is correlated with low environmental temperature (Sandersfeld *et al.*, 2017). For example, the Antarctic fish *N. coriiceps* pass through a sort of hibernation period during winter

(May to November), when physiological responses are depressed (Campbell *et al.*, 2008). Thus, the low metabolism of Antarctic organisms should also influence the endoparasite metabolism because they depend energetically on the hosts. Some studies have shown that parasites have circadian rhythms that oscillate in periods of 24 h and may adjust their timing in response to environmental variables (Rijo-Ferreira *et al.*, 2017). Thus, parasites may also depress their metabolic activities according to their environment, related to the host body and external habitat. This way, parasites could increase their longevity. If so, fish may accumulate endoparasites, resulting in high parasitic abundances.

In our results, cestodes at larval stages from the intestine were the most abundant parasites in the Antarctic fish. Some parasite

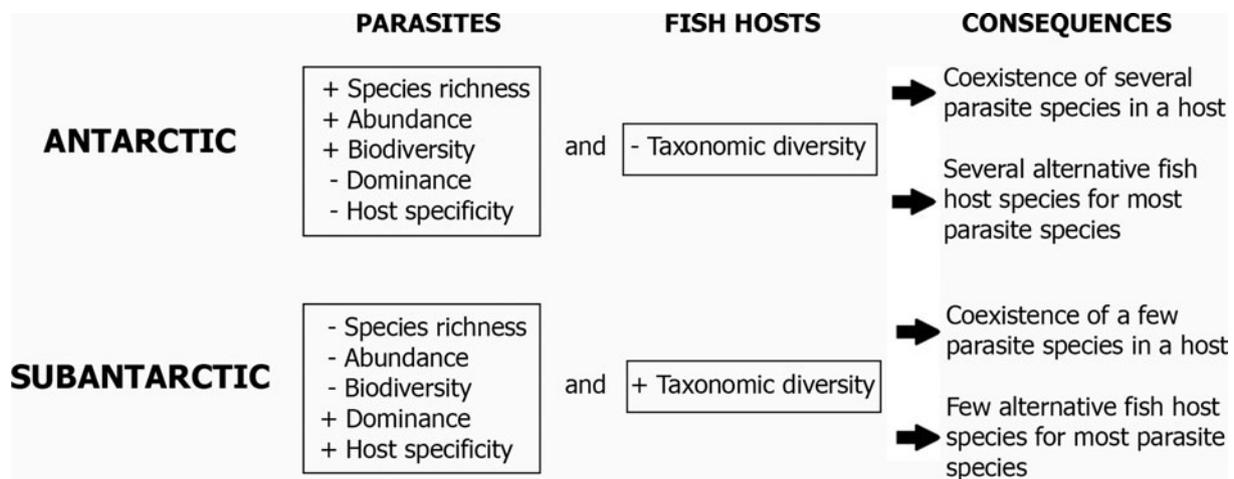


Fig. 3. Synthesis of the main results found in the Antarctic and subantarctic zones in the present study.

Table 4. Number of parasitic taxa per zone and median of host specificity (average of the number of fish species used by parasitic taxa \pm standard deviation (SD)) for each zone and data set.

	Per fish species		Per matrix (no. parasites \times no. fish)	
	Parasite species	Average range	Mode/median	Average \pm SD
Antarctic zone	38	4.4–9.6	11/5	6.5 \pm 4.2
Subantarctic zone	47	1–7.6	1/3	4.7 \pm 4.5

groups live in the host gut, such as digeneans and cestodes, which might be regularly lost, so their high abundance can also be caused by the high number of parasites that use the hosts via predation. Therefore, the constant acquisition of parasites can be possible through a relatively high predation rate on intermediate hosts, although this may be not usual for Antarctic fish, which have low metabolism rates. Another possibility is if the intermediate hosts are highly parasitized, then the parasites enter the hosts 'in packages', generating high parasite abundance (Poulin, 2007). The Antarctic fish used in this study feed mainly on planktonic crustaceans (DeWitt *et al.*, 1990), but little information exists about parasites in crustaceans of this habitat. Laskowski *et al.* (2010) indicated that the total prevalence of acanthocephalans in amphipods was 1.19%, unusually with one parasite individual per amphipod. Therefore, the reason for high parasite abundance in Antarctic fish is unclear.

Parasite abundance can exert significant influence not only on parasite community structure but also on parasite diversity, because high parasite abundance increases parasite interaction, inducing intra- and interspecific competitions, and splits the use of resources among species with different ecological consequences. Indeed, sympatric speciations have been found in specific parasitic lineages because of the exploitation of new resources (Summers *et al.*, 2003). Parasites in high abundance may explore new conditions to acquire more resources (e.g. new host species, microhabitats, macro-habitats) and to relax the interaction among them (Poulin, 2007). Also, the generational

durations of parasites are often short, from weeks to a couple of years; therefore, the ecological differentiation of parasites among species may quickly be isolated from one another in reproductive terms, leading to new species (Summers *et al.*, 2003). Thus, the characteristics of the new environments exert pressure on parasites, making genetic, physiological and ecological changes to them and allowing them to prevail under new conditions (Frank, 1993), such as new hosts and habitats.

Antarctic parasites are mostly euryxenous and endemic (Münster *et al.*, 2017), related to the low taxonomic diversity and endemism of the fish. Most Antarctic fish are taxonomically related because at least 50% of them belong to the family Nototheniidae, and 70% of them belong to the suborder Notothenioidei (Eastman, 2005). Therefore, these fish may be very similar in terms of their physiological characteristics, and thus, different species may have the same parasite species. In contrast, subantarctic parasites are stenoxenous, several monoxenous. Also, the taxonomic diversity of fish is broad in the subantarctic zone. In other words, host–parasite interactions are different between both zones. Antarctic parasites have more alternative hosts because they are less specific to them (table 4). Thus, several parasite species coexist in Antarctic fish (i.e. high species richness) associated with low dominance and euryxenous parasites (fig. 3). Instead, the dominant presence of stenoxenous parasites in a more taxonomically diverse fish community indicates that the life cycles of parasites have a narrow spectrum of hosts. Thus, changes in fish abundance may strongly affect the parasite populations of the subantarctic more than the Antarctic zone.

The main conclusion of this study is that parasite diversity is high in Antarctic fish, even when the latitudinal data suggest low parasite diversity. Moreover, parasite species composition differs between zones. Antarctic climate characteristics, low temperatures and currents surrounding the white continent are different from those of other oceanographic zones, forming a natural barrier for most organisms. As a result, all organisms, including parasites, are remarkably adapted to this environment. Consequently, host–parasite interaction dynamics likely differ between the Antarctic and subantarctic systems. The primary antecedents of parasites, such as specific life cycles and longevity, as well as processes underlying host–parasite relationships in the Antarctic, are hardly known and need to be further understood.

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Conflicts of interest. None.

Ethical standards. The capture and dissection procedure were approved by the Bioethic committee of the Universidad de Valparaíso (certificate N° 058/2016), and the capture of fish in Antarctica was allowed by the Chilean Antarctic Institute (certificate N° 69/2017), according to the Protocol on Environmental Protection to the Antarctic Treaty, and the Principles of the Scientific Committee on Antarctic Research.

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