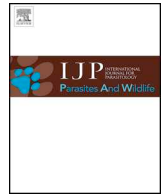




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Arthropod parasites of Antarctic and Subantarctic birds and pinnipeds: A review of host-parasite associations

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ABSTRACT

Due to its cold and dry climate and scarcity of ice-free land, Antarctica has one of the most extreme environments on our planet. To survive in the Antarctic region, parasitic arthropods must either remain closely associated with their hosts throughout the entire life cycle or develop physiological adaptations to survive in the terrestrial habitat while their hosts are away foraging at sea or overwintering at lower latitudes. Forty-eight species of birds and seven species of pinnipeds breed in the Antarctic region, with 158 species/subspecies of parasitic arthropods recorded thus far, comprising: sucking lice (Echinophthiriidae), chewing lice (Menoponidae, Philopteridae), fleas (Ceratophyllidae, Pygiopsyllidae, Rhopalopsyllidae), pentastomes (Reighardiidae), hard ticks (Ixodidae), nest-associated haematophagous mites (Laelapidae), nasal mites (Halarachnidae, Rhinonyssidae) and feather mites (Alloptidae, Avenzoariidae, Xolalgidae, Freyanidae). In this review, we provide an updated compilation of the available information on the host-parasite associations of arthropods infesting birds and pinnipeds in the Antarctic region, and discuss some over-arching ecological patterns and gaps of knowledge.

1. Introduction

Antarctica has one of the most extreme environments on our planet. Ice-free areas comprise c. 2.4% of the continent (Drewry et al., 1982), and the biomass generated in these scarce ice-free terrestrial ecosystems is dwarfed by the astonishing productivity of the Southern Ocean (Siegfried et al., 1985). As a result, vertebrates breeding in Antarctica and Subantarctic islands rely primarily on marine resources, playing a vital ecological role in transferring biomass from the marine to the terrestrial environment (Siegfried et al., 1985). Parasites are also important constituents of the biodiversity of the Antarctic region, and can also have relevance for the conservation of their hosts as they act as stabilizers or destabilizers depending on ecosystem interactions (Combes, 1996; Kerry and Riddle, 2009; Diaz et al., 2017). Owing to the relative scarcity of biomass production on the terrestrial environment of Antarctica, parasites of vertebrates represent a substantial component of the invertebrate fauna of Antarctica as they are able indirectly to exploit the marine productivity, even those which remain on land during their entire life cycle.

Freezing and desiccation are key challenges for the survival of invertebrates in the Antarctic region (Wharton, 2003; Teets and Denlinger, 2014). Most free-living Antarctic arthropods are endemic

and are believed to have established prior to the last glacial maximum, displaying a variety of physiological adaptations to these extreme environmental conditions (Convey, 2010; Mortimer et al., 2011; Teets and Denlinger, 2014). For parasitic arthropods, survival in the Antarctic environment may be achieved by remaining closely associated with the host throughout the entire life cycle, including when the host forages at sea, or to develop physiological adaptations to survive in the terrestrial habitat while the host is away (e.g. cold-hardiness in ticks; Lee and Baust, 1987).

Studies on arthropod parasites of Antarctic birds and pinnipeds date back to the 19th century (e.g. White, 1852; Giebel, 1876; Taschenberg, 1880), and extensive taxonomic studies were developed well into the 20th century (e.g. Kéler, 1952; Meillon, 1952; Timmermann, 1965; Clay and Moreby, 1967; Gressitt, 1967; Smit, 1987). However, with a few notable exceptions (e.g. Stefan et al., 2014; Palma, 2017), the 21st century has arguably seen a decline in the research effort dedicated to describe and catalogue the parasitic arthropod fauna of Antarctica. This is undoubtedly a reflection of the broader problem of the 'taxonomic impediment', i.e. the global shortage of professional taxonomists and systematists (Brooks and Hoberg, 2001; Giangrande, 2003). Furthermore, the focus of Antarctic research has gradually shifted towards technology-based methods (e.g. autonomous and remote sensors) and

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climate change research (Kennicutt et al., 2014, 2015). Considering the high costs associated with maintaining research bases and organizing field expeditions to Antarctica and Subantarctic islands, research projects in the region often have to compete for logistical support. Unfortunately, in recent decades the research on the diversity and ecology of parasites has lost prominence when competing with more ‘global’ or ‘cutting-edge’ topics.

On the other hand, we have recently seen a great improvement in our knowledge about the distribution of the terrestrial Antarctic fauna through satellite imagery (e.g. Lynch and LaRue, 2014; Borowicz et al., 2018) and at sea through satellite tracking and geolocation tagging (e.g. Delord et al., 2019; Granroth-Wilding and Phillips, 2019), and about phylogenetic relationships and taxonomy (e.g. Penhallurick and Wink, 2004; Cole et al., 2019). Furthermore, the development of computational tools to process geographic information (Durr and Gatrell, 2004) and analyse networks (Poulin, 2010) has also provided new insight into the complex relationships among parasites and their hosts. Here, we provide an updated compilation of the available information on the host-parasite associations of arthropods infesting birds and pinnipeds in the Antarctic region (including Subantarctic islands), and use modern analytical tools to evaluate our current state and gaps of knowledge and to identify over-arching ecological patterns.

2. Definitions and methods

Because there are conflicting definitions of the Antarctic region, for the purpose of this review we will refer to the area of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR),

which comprises the Antarctic continent and most Subantarctic islands. Fig. 1 represents the Antarctic sub-regions as defined in this study (adapted from the CCAMLR statistical areas).

All birds and mammals breeding on land in the Antarctic region were considered as ‘Antarctic hosts’, comprising 55 species (48 birds and 7 mammals), of which 14 breed exclusively in the Antarctic region (10 birds and 4 mammals) (Table 1). The taxonomy and the geographic distribution were derived from public datasets (BirdLife International and Handbook of the Birds of the World, 2019; International Union for Conservation of Nature and Natural Resources, 2019). Information about arthropod parasites was obtained from the peer-reviewed literature and the collection of the Museum of New Zealand (Te Papa) (<https://collections.tepapa.govt.nz/>).

We compiled a dataset of host-parasite-location associations within the Antarctic region and host-parasite associations outside the Antarctic region (Multimedia Component 1). Subspecies was used as the taxonomic unit for parasites that show consistent geographical or host distribution differences at this rank (e.g. species of *Ixodes*, *Notiopsylla*, *Saemundsonia*, *Quadriceps*). We use “stragglers” to refer to parasites found occasionally on a bird but which appear not to be regular parasites of that host (e.g. ground-nesting birds being temporarily infested by parasites from other species breeding nearby), and “contaminants” to refer to parasites transferred to a bird by human agency (e.g. parasites transferred due to careless handling of carcasses or museum specimens) (Pilgrim and Palma, 1982).

Gephi 0.9.2 (Bastian et al., 2009) was used to analyse the network of host-parasite associations (excluding stragglers and contaminants). The ForceAtlas2 algorithm (Jacomy et al., 2014) was used to graphically

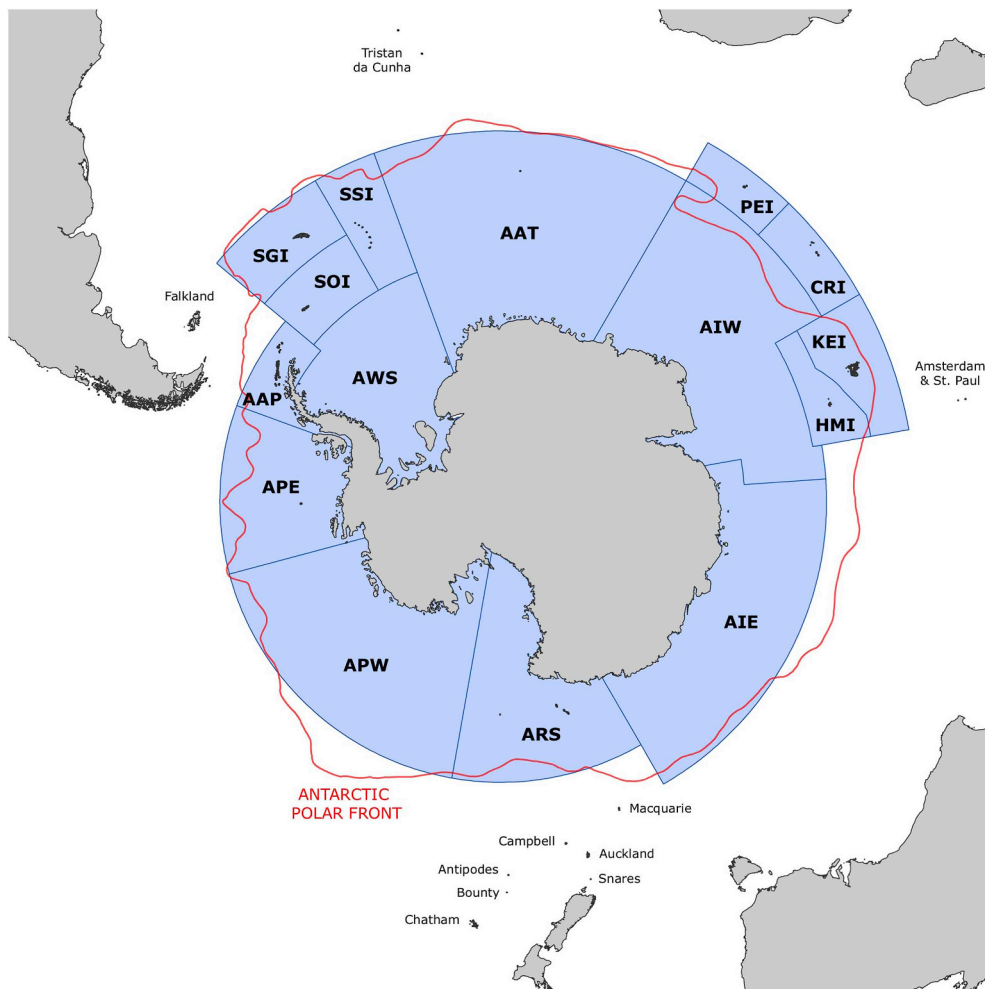


Fig. 1. Sub-areas of the Antarctic region. Legend: AAP = Antarctic Peninsula (including South Shetland Islands and Palmer Archipelago), AWS = Antarctica Weddell Sea sector, AAT = Antarctica Atlantic Ocean sector (including Bouvet Island), AIW = Antarctica Indian Ocean West sector, AIE = Antarctica Indian Ocean East sector, ARS = Antarctica Ross Sea sector (including Scott and Balleny Islands), APW = Antarctica Pacific Ocean West sector, APE = Antarctica Pacific Ocean East sector (including Peter I Island), SOI = South Orkney Island, SGI = South Georgia Island, SSI = South Sandwich Islands, PEI = Prince Edward Islands, CRI = Crozet Islands, KEI = Kerguelen Islands, HMI = Heard and McDonald Islands. The Antarctic Polar Front was drawn from Moore et al. (1999).

Table 1

Summary of the bird and pinniped species breeding in the Antarctic region, with the number of parasite species/subspecies recorded within the Antarctic region (“Antarctica”) or exclusively outside with the Antarctic region or at unreported location (“Elsewhere”), excluding stragglers and contaminants. The betweenness centrality may be interpreted as a measure of the potential influence a species has over the spread of vector-borne pathogens through the network.

Family	Species	Common name	Parasites recorded		Betweenness centrality
			Antarctica	Elsewhere	
Otariidae	<i>Arctocephalus gazella</i>	Antarctic fur seal	0	0	0%
	<i>Arctocephalus tropicalis</i>	Subantarctic fur seal	0	1	0%
Phocidae	<i>Hydrurga leptonyx</i>	Leopard seal	1	0	0%
	<i>Leptonychotes weddellii</i>	Weddell seal	1	0	0%
	<i>Lobodon carcinophagus</i>	Crabeater seal	1	0	0%
	<i>Mirounga leonina</i>	Southern elephant seal	2	0	0%
	<i>Ommatophoca rossii</i>	Ross seal	1	0	0%
Chionidae	<i>Chionis albus</i>	Snowy sheathbill	4	0	2.5%
	<i>Chionis minor</i>	Black-faced sheathbill	5	0	6.5%
Laridae	<i>Larus dominicanus</i>	Kelp gull	6	10	9.0%
	<i>Sterna virgata</i>	Kerguelen tern	2	0	0.8%
	<i>Sterna vittata</i>	Antarctic tern	3	5	5.9%
Stercorariidae	<i>Catharacta antarctica</i>	Brown skua	8	5	5.8%
	<i>Catharacta maccormicki</i>	South polar skua	9	0	1.2%
Diomedeidae	<i>Diomedea exulans</i>	Wandering albatross	7	6	6.6%
	<i>Phoebastria fusca</i>	Dark-mantled sooty albatross	0	7	1.3%
	<i>Phoebastria palpebrata</i>	Light-mantled sooty albatross	6	4	1.6%
	<i>Thalassarche carteri</i>	Indian yellow-nosed albatross	1	2	0.3%
	<i>Thalassarche chrysostoma</i>	Grey-headed albatross	7	8	4.7%
	<i>Thalassarche melanophris</i>	Black-browed albatross	11	3	4.6%
Procellariidae	<i>Aphrodroma brevirostris</i>	Kerguelen petrel	3	5	2.7%
	<i>Daption capense</i>	Pintado petrel	7	4	6.7%
	<i>Fulmarus glacialisoides</i>	Southern fulmar	5	0	1.7%
	<i>Halobaena caerulea</i>	Blue petrel	7	1	1.9%
	<i>Macronectes giganteus</i>	Southern giant petrel	8	4	4.4%
	<i>Macronectes halli</i>	Northern giant petrel	3	5	1.9%
	<i>Pachyptila belcheri</i>	Slender-billed prion	3	4	0.8%
	<i>Pachyptila crassirostris</i>	Fulmar prion	0	7	2.0%
	<i>Pachyptila desolata</i>	Antarctic prion	13	2	6.5%
	<i>Pachyptila salvini</i>	Salvin's prion	1	3	0.1%
	<i>Pachyptila turtur</i>	Fairy prion	3	12	6.2%
	<i>Pagodroma nivea</i>	Snow petrel	5	1	1.5%
	<i>Pelecanoides georgicus</i>	South Georgia diving petrel	8	0	3.9%
	<i>Pelecanoides urinatrix</i>	Common diving petrel	7	7	3.6%
	<i>Procellaria aequinoctialis</i>	White-chinned petrel	5	7	2.1%
	<i>Procellaria cinerea</i>	Grey petrel	2	11	4.0%
	<i>Pterodroma lessonii</i>	White-headed petrel	2	13	5.8%
	<i>Pterodroma macroptera</i>	Great-winged petrel	2	1	0.9%
	<i>Pterodroma mollis</i>	Soft-plumaged petrel	5	3	1.6%
	<i>Thalassoica antarctica</i>	Antarctic petrel	5	1	2.1%
Oceanitidae	<i>Fregetta tropica</i>	Black-bellied storm-petrel	3	4	3.2%
	<i>Garrodia nereis</i>	Grey-backed storm-petrel	2	2	1.7%
	<i>Oceanites oceanicus</i>	Wilson's storm-petrel	6	2	2.7%
Spheniscidae	<i>Aptenodytes forsteri</i>	Emperor penguin	1	0	0%
	<i>Aptenodytes patagonicus</i>	King penguin	3	1	1.8%
	<i>Eudyptes chrysocome</i>	Southern rockhopper penguin	5	7	2.2%
	<i>Eudyptes chrysolophus</i>	Macaroni penguin	6	6	2.6%
	<i>Pygoscelis adeliae</i>	Adelie penguin	4	0	2.0%
	<i>Pygoscelis antarcticus</i>	Chinstrap penguin	3	0	0.5%
	<i>Pygoscelis papua</i>	Gentoo penguin	3	3	1.3%
Phalacrocoracidae	<i>Leucocarbo atriceps</i>	Imperial shag	4	1	3.3%
	<i>Leucocarbo verrucosus</i>	Kerguelen shag	2	0	0.1%
Motacillidae	<i>Anthus antarcticus</i>	South Georgia pipit	0	0	0%
Anatidae	<i>Anas eatoni</i>	Southern pintail	0	0	0%
	<i>Anas georgica</i>	Yellow-billed pintail	1	4	0%

represent the network. Degrees (number of connections of a given node) are evaluated as a measure of the host breadth of a given parasite species or the parasite diversity of a given host species. Betweenness centrality (proportion of shortest paths between nodes that pass through a given node, i.e. shortest path betweenness) is evaluated as a measure of the potential influence a species has over the spread of vector-borne pathogens through the network (Newman, 2005, 2018).

3. Overview of the parasite groups

A total of 158 species/subspecies of parasitic arthropods

representing 15 families was recorded infesting Antarctic hosts (Fig. 2, Table 2); of these, 116 species/subspecies were recorded within the Antarctic region and 42 were only recorded outside the region. Additionally, another 11 species/subspecies of parasitic arthropods were recorded only as stragglers/contaminants of Antarctic hosts; of these, three were recorded within the Antarctic region and eight were only recorded outside the region.

Figs. 3 and 4 provide a summary of the different parasite genera to infest each host species, including stragglers and contaminants. These figures highlight the associations that have yet to be recorded in the Antarctic region, providing clues as to which hosts and parasites have

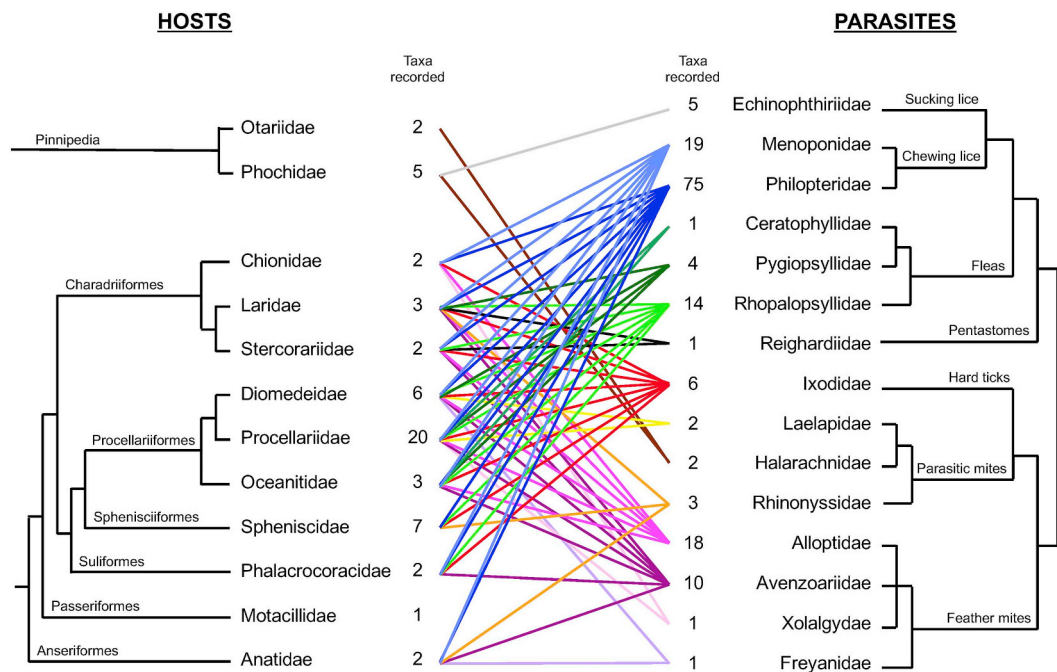


Fig. 2. Host-parasite associations at the family level between Antarctic birds and mammals and arthropods, excluding stragglers and contaminants. Phylogenetic trees are not drawn to scale (adapted from Dabert and Mironov, 1999; Whiting, 2002; Dowling and O'Connor, 2010; Zhang, 2011; Prum et al., 2015).

Table 2

Summary of the arthropod parasite groups recorded on Antarctic hosts. Asterisks are used to indicate the number of species or subspecies that were recorded on Antarctic hosts only as stragglers or contaminants. The genus *Freyana* (indicated with a cross) was recorded but the species could not be determined.

Family	Genera (number of species or subspecies)
Echinophthiriidae	<i>Antarctophthirus</i> (4), <i>Lepidophthirus</i> (1)
Menoponidae	<i>Actornithophilus</i> (2), <i>Ancistrona</i> (1), <i>Austromenopon</i> (13 + 2*), <i>Eidmanniella</i> (1), <i>Longimenopon</i> (1), <i>Trinoton</i> (1)
Phloptoridae	<i>Anaticola</i> (1), <i>Anatocetus</i> (1), <i>Austrogoniodes</i> (11 + 2*), <i>Bedfordiella</i> (1), <i>Docophoroides</i> (4), <i>Episbates</i> (1), <i>Haffneria</i> (1), <i>Halipeurus</i> (3 + 3*), <i>Harrisoniella</i> (2), <i>Naubates</i> (6), <i>Nesiotinus</i> (1), <i>Paraclisis</i> (4), <i>Pectinopygus</i> (1), <i>Pelmatocerandra</i> (2), <i>Perineus</i> (4 + 1*), <i>Philoceanus</i> (3), <i>Piagetella</i> (1), <i>Pseudonirmus</i> (3), <i>Quadriceps</i> (8), <i>Saemundssonina</i> (15), <i>Trabeculus</i> (2)
Ceratophyllidae	<i>Ceratophyllus</i> (1*), <i>Glaciopsyllus</i> (1)
Pygiopsyllidae	<i>Notiopsylla</i> (4 + 1*), <i>Pagipsylla</i> (1*)
Rhopalopsyllidae	<i>Listronis</i> (1), <i>Parapsyllus</i> (11)
Reighardiidae	<i>Reighardia</i> (1)
Ixodidae	<i>Ixodes</i> (4)
Laelapidae	<i>Androlaelaps</i> (2)
Halarachnidae	<i>Halarachne</i> (1), <i>Orthohalarachne</i> (1)
Rhinonyssidae	<i>Larinyssus</i> (1), <i>Rhinonyssus</i> (2)
Alloptidae	<i>Alloptes</i> (7), <i>Brephosceles</i> (5), <i>Echinacarus</i> (2), <i>Microspalax</i> (2), <i>Oxyalges</i> (2)
Avenzoariidae	<i>Bdellorhynchus</i> (1), <i>Promegnina</i> (1), <i>Rhinozachvatkinia</i> (2), <i>Scutomegninia</i> (1), <i>Zachvatkinia</i> (5)
Xolalgidae	<i>Ingrassia</i> (1)
Freyanidae	<i>Diomedacarus</i> (1), <i>Freyana</i> †

been understudied in the region and which parasites have a greater propensity to be recorded as stragglers/contaminants. For example, northern giant petrels (*Macronectes halli*), fulmar prions (*Pachyptila crassirostris*) and fairy prions (*Pachyptila turtur*) stand out as hosts of several species of chewing lice, and yet no such parasites were recorded infesting these hosts in the Antarctic region; further studies are warranted to evaluate whether this is due to an insufficient sampling effort or if it is related to an inability of these parasites to survive in the harsh Antarctic environment. Similarly, it is noteworthy that species of chewing lice of the genus *Naubates* have often been recorded as stragglers/contaminants, which may indicate a greater mobility and active host-seeking behaviour than other chewing lice.

3.1. Lice (Echinophthiriidae, Menoponidae and Phloptoridae)

Sucking lice (suborder Anoplura) feed on the blood of mammals (Durden, 2001), whereas chewing lice (suborders Amblycera and

Ischnocera) feed on the feathers and skin (a few species on blood and mucus) of their avian and mammalian hosts (Clayton et al., 2007). These parasites complete their entire life cycle on the body of their host, and will usually die within a short period if removed (Durden, 2001; Clayton et al., 2007). As a result, louse transmission usually requires direct animal-to-animal contact, or at least a high level of proximity (e.g. predation or scavenging, roosting or nesting in adjacent areas) (Clayton et al., 2007). Some Ischnocera can also be transmitted by phoresis through hippoboscid flies (Keirans, 1975), and although these vectors are not present in the Antarctic region, they do occur at Auckland and Campbell Islands (Gressitt, 1965) where some of the same species of Antarctic birds are also present.

Five species of sucking lice from two genera were recorded on Antarctic hosts (Table 2). These were representatives of Echinophthiriidae, a family with species living on aquatic mammals such as otters, seals, fur seals, sea lions and walrus (Leonardi and Palma, 2013). Interestingly, sucking lice have been recorded only on Antarctic ‘true

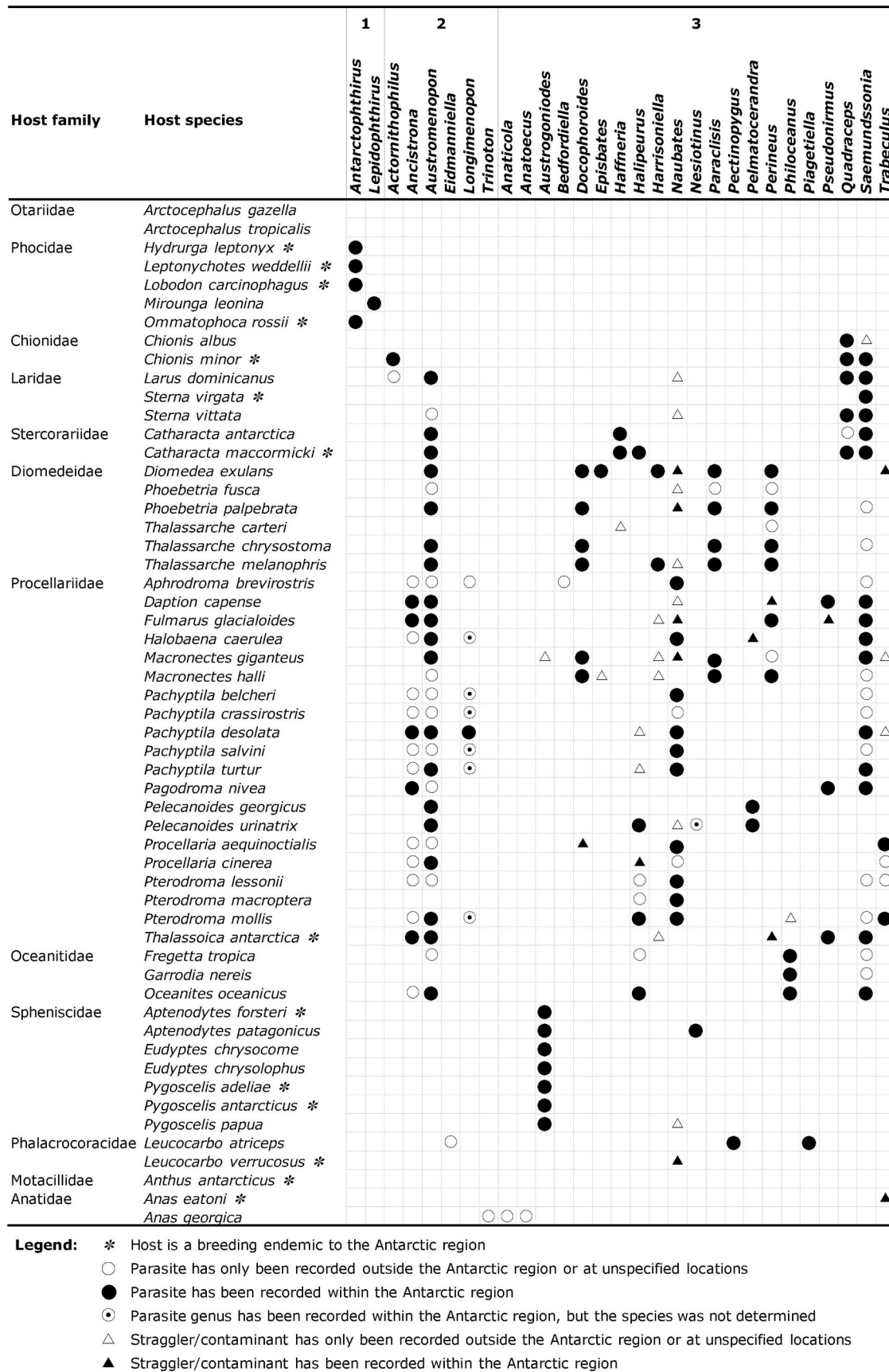


Fig. 3. Genera of sucking lice (Echinophthiriidae – 1) and chewing lice (Menoponidae – 2, Philopteridae – 3) recorded infesting Antarctic birds and mammals.

Host family	Host species	1	2	3	4	5	6	7	8	9	10	11	12
		<i>Ceratophyllus</i> <i>Glaciopsyllus</i> <i>Notiopsylla</i> <i>Pagiopsylla</i>	<i>Listronius</i> <i>Parapsyllus</i>	<i>Reighardia</i>	<i>Ixodes</i>	<i>Androlaelaps</i>	<i>Halarachne</i>	<i>Orthohalarachne</i>	<i>Larinyssus</i> <i>Rhinionyssus</i>	<i>Alloptes</i> <i>Brephosceles</i> <i>Echinacarus</i> <i>Microspalax</i> <i>Oxyalges</i>	<i>Bdellorhynchus</i> <i>Promegninia</i> <i>Rhinozachvatkinia</i> <i>Scutomegninia</i>	<i>Zachvatkinia</i>	<i>Diomedacarus</i>
Otariidae	<i>Arctocephalus gazella</i> <i>Arctocephalus tropicalis</i>							○					
Phocidae	<i>Hydrurga leptonyx</i> * <i>Leptonychotes weddellii</i> * <i>Lobodon carcinophagus</i> * <i>Mirounga leonina</i> <i>Ommatophoca rossii</i> *							●					
Chionidae	<i>Chionis albus</i> <i>Chionis minor</i> *					●				●			●
Laridae	<i>Larus dominicanus</i> <i>Sterna virgata</i> * <i>Sterna vittata</i>		●		○	●	○		○	●			○
Stercorariidae	<i>Catharacta antarctica</i> <i>Catharacta maccormicki</i> *			●	●	●				●		●	
Diomedeidae	<i>Diomedea exulans</i> <i>Phoebetria fusca</i> <i>Phoebetria palpebrata</i> <i>Thalassarche carteri</i> <i>Thalassarche chrystostoma</i> <i>Thalassarche melanophris</i>		○		○	●	○			●		○	○
Procellariidae	<i>Aphrodroma brevirostris</i> <i>Daption capense</i> <i>Fulmarus glacialis</i> <i>Halobaena caerulea</i> <i>Macronectes giganteus</i> <i>Macronectes halli</i> <i>Pachyptila belcheri</i> <i>Pachyptila crassirostris</i> <i>Pachyptila desolata</i> <i>Pachyptila salvini</i> <i>Pachyptila turtur</i> <i>Pagodroma nivea</i> <i>Pelecanoides georgicus</i> <i>Pelecanoides urinatrix</i> <i>Procellaria aequinoctialis</i> <i>Procellaria cinerea</i> <i>Pterodroma lessonii</i> <i>Pterodroma macroptera</i> <i>Pterodroma mollis</i> <i>Thalassoica antarctica</i> *	●	●	●	○	●	○						
Oceanitidae	<i>Fregetta tropica</i> <i>Garrodia nereis</i> <i>Oceanites oceanicus</i>	●	○	●		●				○		○	
Spheniscidae	<i>Aptenodytes forsteri</i> * <i>Aptenodytes patagonicus</i> <i>Eudyptes chrysolome</i> <i>Eudyptes chrysolophus</i> <i>Pygoscelis adeliae</i> * <i>Pygoscelis antarcticus</i> * <i>Pygoscelis papua</i>	●		●		●						●	
Phalacrocoracidae	<i>Leucocarbo atriceps</i> <i>Leucocarbo verrucosus</i> *			●		●						●	
Motacillidae	<i>Anthus antarcticus</i> *												
Anatidae	<i>Anas eatoni</i> * <i>Anas georgica</i>								●		○		○

Legend: * Host is a breeding endemic to the Antarctic region
 ○ Parasite has only been recorded outside the Antarctic region or at unspecified locations
 ● Parasite has been recorded within the Antarctic region
 ⊙ Parasite genus has been recorded within the Antarctic region, but the species was not determined
 △ Straggler/contaminant has only been recorded outside the Antarctic region or at unspecified locations
 ▲ Straggler/contaminant has been recorded within the Antarctic region

Fig. 4. Genera of fleas (Ceratophyllidae – 1, Pygiopsyllidae – 2, Rhopalopsyllidae – 3), pentastomes (Reighardiidae – 4), hard ticks (Ixodidae – 5), parasitic mites (Laelapidae – 6, Halarachnidae – 7), Rhinionyssidae – 8) and feather mites (Alloptidae – 9, Avenzoariidae – 10, Freyanidae – 11, Xolalgidae – 12) recorded infesting Antarctic birds and mammals.

seals' (*Hydrurga leptonyx*, *Leptonychotes weddellii*, *Lobodon carcinophagus*, *Mirounga leonina* and *Ommatophoca rossii*), but were not recorded from the two Antarctic species of fur seals (*Arctocephalus gazella* and *Arctocephalus tropicalis*). However, considering that three species of Echinophthiriidae have been recorded infesting three species of *Arctocephalus* spp. in South America, Africa and New Zealand (Leonardi and Palma, 2013; Palma, 2017), it is plausible that lice may be found on Antarctic species of fur seals in the future.

Chewing lice were by far the most diverse group of parasitic arthropods recorded in the Antarctic region, with 94 species/subspecies. Menoponidae (Amblycera) is represented by 19 species from 6 genera and Philopteridae (Ischnocera) is represented by 75 species/subspecies from 21 genera (Table 2). An additional two species of Menoponidae and six species of Philopteridae were also recorded on Antarctic hosts; however, those records were considered stragglers or contaminants. Of these, two were recorded within the Antarctic region: *Austromenopon edwardsi* Price and Clay, 1972 and *Halipeurus heraldicus* Timmermann, 1960. *Austromenopon edwardsi* is regularly parasitic on shearwaters (*Puffinus* spp.) but was atypically recorded on a soft-plumaged petrel (*Pterodroma mollis*) at Kerguelen Island (Price and Clay, 1972). Since shearwaters do not breed in the Antarctic region, however, it seems unlikely that this parasite would occur naturally in the region. *Halipeurus heraldicus* is regularly parasitic on gadfly petrels (*Pterodroma* spp.) in the Indian and Pacific Oceans (Palma, 2011), and was atypically recorded on a soft-plumaged petrel at Kerguelen Island (Clay and Moreby, 1970). It is unclear whether this record is a straggler, a contaminant or perhaps a misidentification of *Halipeurus procellariae* (J.C. Fabricius, 1775) (Palma, 2011). The remaining six species recorded on Antarctic hosts as stragglers or contaminants were exclusively found outside the Antarctic region, and therefore are unlikely to occur in the region.

Although chewing lice are generally considered to have a high host specificity, *Ancistrona vagelli* J.C. Fabricius, 1787 is a clear exception. This monotypic species has been recorded on a broad variety of Procellariiformes hosts (Palma, 2017). It does not appear to be particularly abundant in any host (Palma, 2017), but in the Antarctic region infests 16 recorded hosts. *Ancistrona vagelli* lacks significant morphological features that would justify subdividing it (Palma, 2017), however it remains to be determined whether there are significant genetic differences among its populations from different hosts or geographical areas.

The taxonomy of the *Longimenopon* spp. infesting seabirds in the Antarctic region is unclear (Palma, 2017). This genus currently comprises six species, all parasitic on Procellariiformes (Timmermann, 1957; Nakagawa, 1959). *Longimenopon galeatum* Timmermann, 1957 was described from specimens collected from a white-faced storm-petrel (*Pelagodroma marina*) at Tristan da Cunha Islands (Timmermann, 1957). Although this species has since been recorded on a number of Antarctic hosts, only the records of *L. galeatum* on Antarctic prion (*Pachyptila desolata*) and Kerguelen petrel (*Aphrodroma brevirostris*) at South Orkney, Macquarie and Gough Islands (Timmermann, 1957; Watson, 1967) are considered valid. A complete revision of the genus is necessary before the species infesting other Antarctic hosts (*Halobaena caerulea*, *Pachyptila* spp. and *Pterodroma mollis*) can be identified (Palma, 2017).

Two species of chewing lice have been recorded infesting the Georgia pintail (*Anas georgica*) in mainland South America (Hinojosa-Sáez et al., 2009), *Anaticola crassicornis* (Scopoli, 1763) and *Anatoecus dentatus* (Scopoli, 1763), both of which are cosmopolitan as frequent parasites of dabbling ducks (*Anas* spp.) (e.g. Dik and Uslu, 2012; Grossi et al., 2014; Naz et al., 2016). It remains to be determined whether the records of *Anaticola* sp. and *Anatoecus* sp. from Bird Island, South Georgia (Clay and Moreby, 1970; Bonner and Croxall, 1988) correspond to *Anaticola crassicornis* and *Anatoecus dentatus*. It also seems plausible that these species could infest the southern pintail (*Anas eatonii*), an understudied dabbling duck endemic to the Crozet and

Kerguelen Islands.

3.2. Fleas (*Ceratophyllidae*, *Pygiopsyllidae* and *Rhopalopsyllidae*)

Fleas are haematophagous parasites of mammals and birds (Durden and Hinkle, 2019). Fleas of seabirds are predominantly nest-dwelling (Meillon, 1952; Bell et al., 1988), and as a result even though they can be generalists with regards to their hosts within an island group, their populations are often isolated between different island groups (Meillon, 1952).

Seventeen species/subspecies were recorded from Antarctic birds (Table 2): Ceratophyllidae was represented by one species, Pygiopsyllidae by four species/subspecies from two genera and Rhopalopsyllidae by 12 species/subspecies from two genera. The genera *Notiopsylla* (Pygiopsyllidae) and *Parapsyllus* (Rhopalopsyllidae) comprise most of the flea diversity in the Antarctic region, infesting predominantly Procellariiformes birds at Subantarctic islands. It is worth noting that the subspecies of *Parapsyllus magellanicus* Jordan, 1938 show clear differences in their geographic distribution. Based on current records, *P. m. heardi* is restricted to the Indian Ocean (Prince Edward, Crozet, Kerguelen and Heard Islands), *P. m. largificus* is endemic to the Bounty Islands and *P. m. magellanicus* occurs in the Southwest Atlantic (South Georgia and Falkland Islands) and Pacific Oceans (Antipodes, Snares and Macquarie Islands) (Smit, 1979, 1984; Chastel and Beaucournu, 1992). The subspecies of *Notiopsylla kerguelensis* (Taschenberg, 1880) also show considerable differences in geographic distribution: *N. k. kerguelensis* is a common parasite of Procellariiformes in Subantarctic islands throughout the Southern Ocean, including the Antipodes Islands (Jordan and Rothschild, 1908; Meillon, 1952; Beaucournu and Rodhain, 1990; Chastel and Beaucournu, 1992), whereas *N. k. tenuata* is an abundant parasite of the Antipodes parakeet (*Cyanoramphus unicolor*) and frequently shifts onto Procellariiformes nesting in the Antipodes Islands, but has not been recorded elsewhere (Smit, 1979).

Glaciopsyllus antarcticus Smit and Dunnet, 1962 (Ceratophyllidae) stands out among fleas as the only species able to thrive in the extreme conditions of the Antarctic continent, being commonly found in the nests of Procellariidae (and occasionally Oceanitidae) (Murray et al., 1967; Whitehead et al., 1991; Steele et al., 1997). It has been speculated that this species survives through the Antarctic winter by overwintering on the hosts (Bell et al., 1988; Whitehead et al., 1991), however the observation that some of adult fleas survive after having been stored at -20°C for 4 months suggests that it may have unexpected physiological characteristics that could allow it to overwinter in Antarctica (Steele et al., 1997).

It is worth noting that although *Listronius robertsonianus* (Jordan, 1938) (Rhopalopsyllidae) is considered a valid species, its host is not entirely clear. This species was described from specimens collected in 1936 from a burrow with a shared entrance for white-chinned petrel (*Procellaria aequinoctialis*) and Magellanic penguin (*Spheniscus magellanicus*) at the Falkland Islands (Jordan, 1938), and has not been recorded since. The other four species of the genus *Listronius* are parasitic on rodents (Lewis, 1973; Beaucournu and Gallardo, 1991; Beaucournu et al., 2014). There are no native rodents in the Falkland Islands, and the only native terrestrial mammal of the archipelago, the Falklands wolf (*Dusicyon australis*), became extinct in 1876 (Sillero-Zubiri et al., 2004). However, Norway rats (*Rattus norvegicus*) and black rats (*Rattus rattus*) were introduced to the Falkland Islands by whaling and sealing vessels in the late 1700s and are known to enter the burrows of white-chinned petrels to predate on their eggs and chicks (Poncet et al., 2011). Therefore, whether *L. robertsonianus* is parasitic of seabirds or rodents remains to be determined.

It should be noted that although *Ceratophyllus gallinae* (Schrank, 1803) and *Pagipsylla galliralli* (Smit, 1965) were reported respectively on a fairy prion (*Pachyptila turtur*) in mainland New Zealand and on a royal penguin (*Eudyptes chrysolophus schlegelii*) at the Snares Islands,

both of these fleas are primarily parasites of domestic poultry and terrestrial birds (Smit, 1979). Therefore, these records probably correspond to stragglers and it is unlikely that these flea species could be established in the Antarctic region.

3.3. *Pentastomes (Reighardiidae)*

Pentastomes, also known as tongue worms, are parasites of almost all vertebrate classes (Dabert, 2005; Poore, 2012). This group presents a mixture of annelid and crustacean characteristics, and genetic studies suggest they are most closely related to fish ectoparasites (Branchiura), representing a basal clade of Crustacea that diverged in the Cambrian period (Sanders and Lee, 2010). *Reighardia sterna*e (Diesing, 1864) is one of two pentastome species that infest birds as their definitive host, parasitizing the respiratory tract of Charadriiformes birds such as gulls and terns (Laridae), auks (Alcidae) and skuas (Stercorariidae) (Threlfall, 1971; Riley, 1973; Hoberg, 1987). Although the life cycle of other pentastomes often involves larval development in an intermediate host (usually fishes), this is not the case for *R. sterna*e, for which larval development appears to occur in the definitive host (Riley, 1973; Banaja et al., 1976). As a result, transmission probably occurs directly through vomiting (during chick feeding or due to oesophageal irritation), coughing and sneezing (Banaja et al., 1976; Dabert, 2005). In skuas, predation of infested gulls and terns could also serve as a potential route of transmission.

*Reighardia sterna*e was recorded infesting kelp gulls (*Larus dominicanus*) and south polar skuas (*Catharacta maccormicki*) at Anvers Island, near the Antarctic Peninsula (Hoberg, 1987). These are the only records of this parasite in the Antarctic region; however, it is likely that it also occurs in kelp gulls and south polar skuas throughout their distribution in the Antarctic region. Furthermore, brown skuas (*Catharacta antarctica*), Kerguelen terns (*Sterna virgata*) and Antarctic terns (*Sterna vittata*) are other potential hosts that have yet to be thoroughly evaluated.

3.4. Ticks (*Ixodidae*)

Although both soft ticks (Argasidae) and hard ticks (Ixodidae) are frequent parasites of seabirds (Dietrich et al., 2011), only hard ticks have been recorded as parasites of Antarctic seabirds. These parasites can exploit up to three different host individuals during their life cycle (larva, nymph and adult stages), with intervals between hosts ranging from weeks to years (Randolph, 1998). Although they may remain attached to their seabird hosts when they forage at sea and potentially ‘hitchhike’ over great distances, seabird ticks are believed to be predominantly nest-dwelling during the wintering period (Olsen et al., 1995; Dietrich et al., 2011). These characteristics, combined with relatively low host specificity, make hard ticks highly effective vectors for pathogens of seabirds between hosts within the same site and between distant sites (Olsen et al., 1995; Dietrich et al., 2011; Muñoz-Leal and González-Acuña, 2015).

Four species/subspecies of ticks were recorded in the Antarctic region, all hard ticks of the *Ixodes* genus. *Ixodes uriae* White, 1852 has the most extensive geographical distribution and one of the greatest host ranges of all ticks, having been recorded on almost 100 avian and mammalian hosts in all continents (including the northern hemisphere) (Muñoz-Leal and González-Acuña, 2015). This species has a remarkable resistance to dehydration and cold-hardiness, being able to tolerate temperatures as low as $-30\text{ }^{\circ}\text{C}$ (Lee and Baust, 1987), and is able to become established in rocky areas without any vegetation (Barbosa et al., 2011). These characteristics help explain why it is the only tick species able to survive in the Antarctic Peninsula, and why it also scores the highest host range of the external parasites recorded from Antarctic hosts, with 27 avian hosts.

Ixodes kerguelensis André & Colas-Belcour, 1942 might not be as widely distributed as *I. uriae*, but it is a common parasite of seabirds in the Southern Ocean (Arthur, 1960; Wilson, 1970a), having been

recorded from 12 Antarctic species. It is worth noting that Wilson (1970a) found that several records of seabird ticks (*I. auritulus*, *I. percavatus* and *I. zumpti*) were based on misidentified specimens of *I. kerguelensis*, and also concluded that *Ixodes pterodromae* was a synonym of *I. kerguelensis*. *Ixodes kerguelensis* has not yet been recorded in Subantarctic island groups with scarce vegetation (e.g. Bouvet, South Orkney, South Sandwich); however, it is difficult to ascertain whether this is due to a dependency of plant substrate to provide protection from desiccation, to differences in avian community composition (e.g. absence of albatrosses and several species of burrowing petrels), or if it is reflective of the relatively lower sampling effort conducted at those locations.

The distribution of *Ixodes auritulus zealandicus* Dumbleton, 1953 extends close to the margins of the Southern Ocean, with records at Macquarie, Antipodes and Auckland Islands, as well as on mainland New Zealand and the Chatham Islands (Nuttall, 1916; Dumbleton, 1953; Heath et al., 2011). Considering that it has been recorded from 12 Antarctic bird species that were sampled outside of the Antarctic region, it seems likely that this tick species could also be established within the region. *Ixodes auritulus* sensu lato was recorded infesting ‘penguins’ at the Antarctic Peninsula; however, the subspecies was not determined (Gressitt and Weber, 1959). Considering the locality, this record probably corresponds to *Ixodes auritulus auritulus* Neumann, 1904, which is common in South America (Kohls and Clifford, 1966), rather than *I. a. zealandicus*. It is worth noting that although *I. a. auritulus* is generally considered a parasite of terrestrial birds, it is also capable of infesting seabirds such as the Magellanic diving-petrel (*Pelecanoides magellani*) (González-Acuña et al., 2005). Both *I. auritulus* and *I. kerguelensis* are members of the *Ixodes auritulus-percavatus* group, for which the phylogeny and nomenclature are unclear (Arthur, 1960; Wilson, 1970a); it seems likely that future reviews might change the taxonomy of these parasites, which in turn will reflect on our knowledge of their ecology in the Antarctic region.

Lastly, *Ixodes laridis* Heath and Palma, 2017 has only been recorded on Antarctic hosts outside of the Antarctic region. This species infests a broad variety of seabirds, including four species of Antarctic seabirds, but its records are restricted to Australia, mainland New Zealand and the Chatham Islands (Heath and Palma, 2017), and therefore to date it does not appear to have established in the Antarctic region. It is worth noting that it has been speculated that *I. a. zealandicus* and *I. laridis* might be capable of producing neurotoxins, leading to muscle paralysis (Heath, 2006).

3.5. Parasitic mites (*Halarachnidae*, *Rhinonyssidae* and *Laelapidae*)

Parasitic mites comprise nasal mites (Halarachnidae and Rhinonyssidae), which are found in the respiratory tract, and nest-associated haematophagous mites (Laelapidae). The complete life cycle of nasal mites develops within their hosts, relying on direct transmission via oral route (during chick feeding or courtship) or indirectly across water, perches, or other contaminated surfaces (Bell, 1996). Five species of nasal mites have been recorded from Antarctic birds and mammals (Table 2): two species in two genera of the Halarachnidae and three species in two genera of the Rhinonyssidae.

Halarachnidae comprises mites living in the respiratory tract of mammals, with *Halarachne* spp. infesting true seals (Phocidae) and sea otters (*Enhydra lutris*) (Domrow, 1962; Furman and Dailey, 1980) and *Orthohalarachne* spp. infesting fur seals and sea lions (Otariidae) and walruses (Odobenidae) (Popp, 1961). *Halarachne miroungae* (Ferris, 1925) has been recorded infesting southern elephant seals (*Mirounga leonina*) in the Antarctic region (Domrow, 1962; Wilson, 1967, 1970b), and specimens of an undetermined species of *Halarachne* have also been recovered from the Weddell seal (*Leptonychotes weddellii*) (Newell, 1947). Considering the difficulty in studying other species of true seals that breed sparsely on pack ice around Antarctica, it seems plausible that *H. miroungae* (or other yet undescribed *Halarachne* spp.) might

parasitize other hosts in the Antarctic region. Although *Orthohalarachne* spp. have not been recorded in the Antarctic region yet, *Orthohalarachne diminuata* (Doetschmann, 1944) was reported from Subantarctic fur seals (*Arctocephalus tropicalis*) in South Africa and at Gough and Amsterdam Islands (Bester, 1989), and would therefore be likely to occur in breeding sites of Subantarctic fur seals within the Antarctic region (i.e. Prince Edward and Crozet Islands), perhaps with opportunities of transmission to Antarctic fur seals (*Arctocephalus gazella*).

Rhinonyssidae comprises mites living in the respiratory tract of birds. It is unclear whether *Rhinonyssus schelli* (Fain and Hyland, 1963) – which was recorded in Adelie penguins (*Pygoscelis adeliae*) and gentoo penguins (*Pygoscelis papua*) in the Antarctic region (Wilson, 1967, 1970b) – should be reclassified as a subspecies of *Rhinonyssus sphenisci* Fain and Mortelmans, 1959, which infests other penguin species in South America and Africa (Vanstreels et al., 2019). On the other hand, species of *Larinyssus* are parasites of Charadriiformes, with *Larinyssus orbicularis* Strandmann, 1948 infesting a number of gull (*Larus* spp.) and tern species (*Sterna* spp., *Thalasseus* spp.) (Strandmann, 1948; Mitchell, 1961). *Larinyssus orbicularis* has not yet been recorded in the Antarctic region, but it is known to infest kelp gulls in South Africa and South America (Zumpt and Till, 1955; González-Acuña et al., 2011). Considering that rhinonyssid mites can go unnoticed for decades even when they are abundant in extensively studied hosts (González-Acuña et al., 2011; Dimov, 2013; Vanstreels et al., 2019), it seems probable that the occurrence of these parasites has been underestimated in the Antarctic region.

Laelapidae comprises both free-living and parasitic mites, with the haematophagous mites of the genus *Androlaelaps* frequently found on mammals, especially rodents, but some species are also known to parasitize birds (Strandmann, 1949). These parasites are predominantly nest-bound, feeding on their seabird hosts during incubation and chick-rearing. *Androlaelaps pachyptilae* (Zumpt and Till, 1956) has been recorded on a variety of Antarctic procellariiform birds, and within the Antarctic region it was recorded in the nest of Antarctic prions (*Pachyptila desolata*) at Heard Island (Zumpt and Till, 1956). Additionally, *Androlaelaps farenholzi* Berlese, 1911 was also recorded in the nest of fairy prions (*Pachyptila turtur*) in Australia (Domrow, 1977). Because most studies of parasites from seabirds at Subantarctic islands have focused on collecting parasites from the hosts, rather than their nests, it seems probable that nest-associated haematophagous mites might be more widely distributed than currently known.

3.6. Feather mites (Alloptidae, Avenzoariidae, Freyanidae and Xolalgidae)

There is debate on whether feather mites should be considered parasites or mutualistic ectosymbionts, because representatives of most families live in different microhabitats of the plumage of their host and normally do not cause any visible damage to birds. While there is evidence that in rare cases feather-inhabiting mites may cause itching, discomfort and premature breakage of feathers (Proctor, 2003), some authors have argued that they might benefit their hosts by contributing to the cleaning of their feathers (Blanco et al., 2001; Jovani, 2003). In this context, the relationship between feather mites and their hosts may depend on the species involved, infestation intensity and environmental conditions (Proctor, 2003). Feather mites complete their entire life cycle on the skin and feathers of their host, and as in the Psoroptidia they lack a phoretic deutonymphal stage, that is present in other Astigmata (Proctor, 2003). This condition, in combination with their relatively limited mobility, implies that direct animal-to-animal contact (e.g. chick-rearing and mating) is the primary means of transmission between feather mites and their hosts (Proctor, 2003), which is reflected on their close co-evolutionary relationships (Dabert and Mironov, 1999). Nevertheless, it should be noted that some taxa of feather mites are transmitted by phoresis through hippoboscid flies and chewing lice (Harbison et al., 2009).

Feather mites have been recorded from all orders of Antarctic birds

except penguins (Spheniscidae) and the South Georgia pipit (*Anthus antarcticus*). It is worth noting that although it was previously believed that penguins could not host feather mites due to their strongly modified plumage and highly aquatic lifestyle (Atyeo and Peterson, 1970; Proctor, 2003), a more recent study demonstrated the occurrence of feather mites on penguins in Australia (Mironov and Proctor, 2008). Forty species of feather mites have been recorded from Antarctic birds (Table 1): Alloptidae (Analgoidea) was represented by 18 species from five genera, Avenzoariidae (Analgoidea) was represented by 10 species from five genera and Xolalgidae (Analgoidea) and Freyanidae (Pterolichoidea) were represented by one species each. Additionally, immatures of *Freyana* sp. have also been recorded in the Antarctic region (Atyeo and Peterson, 1970), adding one more genus of the family Freyanidae.

Among the four families of feather mites recorded on birds of Antarctica, species of three families (Alloptidae, Avenzoariidae and Freyanidae) are restricted to orders of aquatic birds, while species of Xolalgidae infest a wider range of hosts and occur both on aquatic and terrestrial birds (Gaud and Ateyo, 1996; Proctor, 2003). Members of the families Alloptidae and Avenzoariidae stand out as particularly frequent parasites of Antarctic seabirds, with species of Alloptidae infesting Charadriiformes and Procellariiformes, whereas those of Avenzoariidae have been recorded on these orders but also on Suliformes and Anseriformes. Despite such a broad range of hosts at the family level, at the species level these mites are generally limited to infesting hosts of the same genus, corroborating the interpretation that they have coevolved and cospeciated along with their hosts (Dabert and Mironov, 1999).

Members of the families Xolalgidae and Freyanidae were not as frequent among Antarctic hosts. Species of *Ingrassia* (Xolalgidae) have been recorded from several species of Procellariiformes and Sphenisciformes (Mironov and Proctor, 2008) and, in the Antarctic region, *Ingrassia antarctica* (Gaud, 1952) was described from South Georgia diving-petrels (*Pelecanoides georgicus*) at Kerguelen Island (Gaud, 1952). Unidentified specimens of *Ingrassia* have also been recorded on snowy sheathbills (*Chionis albus*) and Salvin's prions (*Pachyptila salvini*) (Atyeo and Peterson, 1970; Bishop and Heath, 1998), suggesting that the diversity and prevalence of these mites in the Antarctic region has been underreported. *Diomedacarus gigas* (Trouessart, 1895) (Freyanidae) was recorded on black-browed albatrosses (*Thalassarche melanophris*) at South Georgia Islands (Atyeo and Peterson, 1970). Considering the wide host and geographic distribution of this parasite on albatrosses (Diomedidae) in the northern hemisphere, it seems probable that the occurrence of *D. gigas* in albatrosses in the Antarctic region has also been underreported.

It should be noted that although quill mites (Cheyletoidea: Syringophilidae) have not been recorded on Antarctic birds, they are relatively frequent parasites of other species of the families Anatidae, Diomedidae, Laridae, Motacillidae, Phalacrocoracidae and Procellariidae (Schmidt and Skoracki, 2007; Glowska et al., 2015; Zmudzinski et al., 2016). It is therefore plausible that these parasites occur in the Antarctic region but were not yet recorded due to insufficient research effort.

4. Host-parasite relationships from a network and epidemiological perspective

Fig. 5 provides a graph of the associations between Antarctic hosts and parasites; a larger version of this graph with labels for species names is provided in Multimedia Component 2. The Antarctic host-parasite network is predominantly organized in a manner that reflects the host families, with parasites radiating to host-specific relationships. Most Procellariidae (petrels, shearwaters, prions and diving-petrels) were grouped into a compact network, with a complex web of partly-shared parasites. Interestingly, three species of Procellariidae that breed on the Antarctic continent (Antarctic petrel *Thalassoica antarctica*, snow

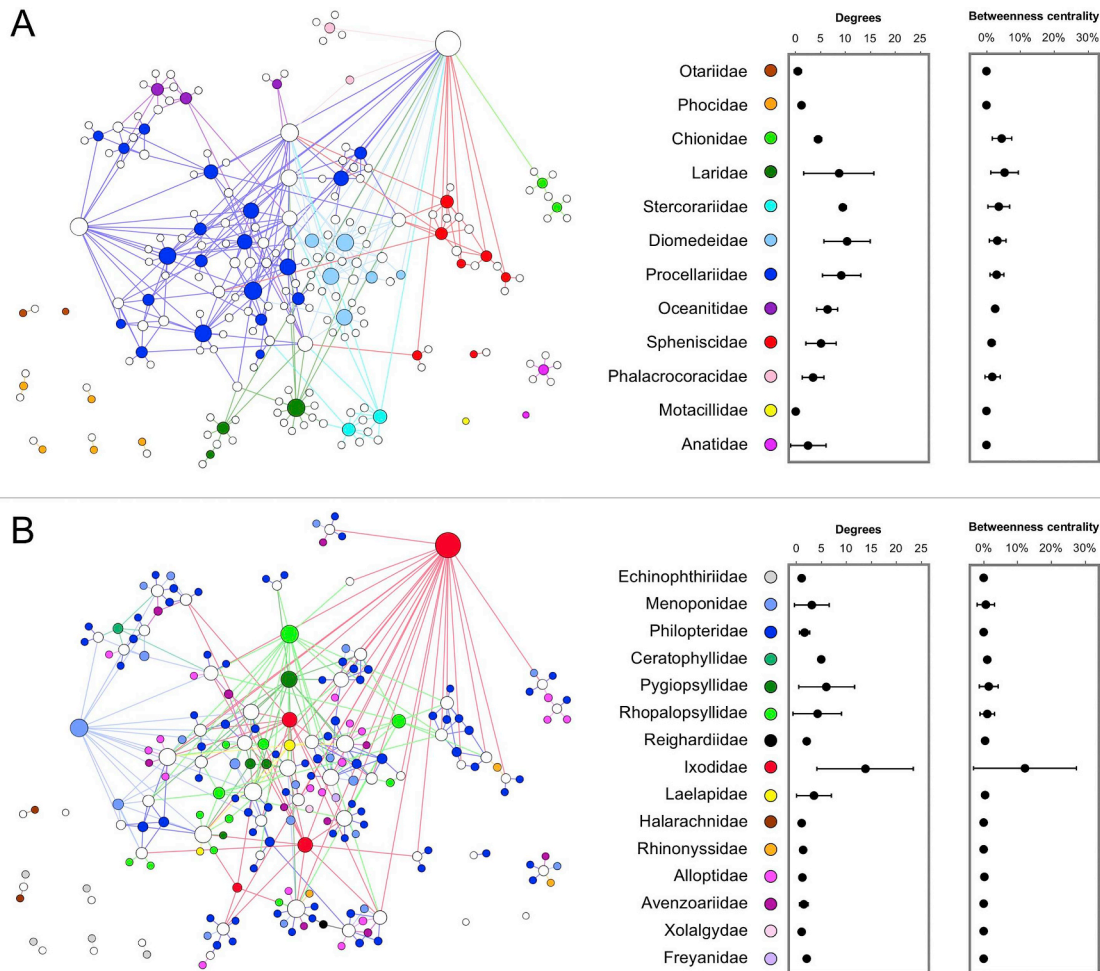


Fig. 5. Network representation and mean and standard deviation of degrees and betweenness centrality of the host-parasite associations by host families (A) and parasite families (B), excluding stragglers and contaminants. Degrees (number of connections of a given node) may be interpreted as a measure of the host breadth of a given parasite species or the parasite diversity of a given host species; node size is drawn proportional to the number of degrees. Betweenness centrality (proportion of shortest paths between nodes that pass through a given node) may be interpreted as a measure of the potential influence a species has over the spread of vector-borne pathogens through the network.

petrel *Pagodroma nivea* and southern fulmar *Fulmarus glacialis* were more closely associated with members of Oceanitidae than with other Procellariidae, except for the grey-backed storm-petrel (*Garrodia nereis*) which was relatively isolated from other Oceanitidae. Diomedeidae (albatrosses) showed substantial connectivity to Procellariidae but also had its own internal network connectivity of partly-shared parasites. In contrast, most other bird families were relatively isolated, being connected only through a few generalist parasites. A notable exception is the kelp gull (Laridae), which displayed significant connectivity to Procellariidae through a variety of parasite families. Pinnipeds and dabbling ducks were entirely isolated, not showing connectivity to one another nor to other hosts.

Among the parasites, Ixodidae, Pygiopsyllidae and Rhopalopsyllidae stood out for their role in connecting the host-parasite network. This was largely attributable to a few generalist parasites: *Ixodes uriae* (27 recorded hosts, 34.5% centrality), *Parapsyllus magellanicus heardi* (16 hosts, 7.3% centrality), *Notiopsylla kerguelensis kerguelensis* (14 hosts, 5.5% centrality), *Ixodes auritulus zealandicus* (12 hosts, 8.2% centrality) and *Ixodes kerguelensis* (12 hosts, 5.1% centrality). Additionally, although Menoponidae had a generally high host specificity (average = 3.0 hosts, 0.7% centrality), *Ancistrona vagelli* stood out for its high connectivity (16 hosts, 11.2% centrality), even though its host niche was restricted to Procellariidae and Oceanitidae.

The low host specificity and high connectivity displayed by *Ixodes*

spp. places these parasites in an exceptional position to act as vectors of pathogens of seabirds in the Antarctic region. Ticks transmit a greater variety of infectious agents than any other group of arthropods worldwide (Jongejan and Uilenberg, 2004), and it seems that they are equally well-equipped to play a similar role in the Antarctic region, especially considering the ability of *I. uriae* to withstand the extreme winter conditions of the Antarctic continent (Lee and Baust, 1987). This is supported by the fact that *I. uriae* has been documented as the vector of viruses (St George et al., 1985; Major et al., 2009), bacteria (Chastel et al., 1993; Olsen et al., 1995; Schramm et al., 2014) and protozoa (Peirce and Prince, 1980; Montero et al., 2016). However, most studies on the epidemiological role of *I. uriae* have focused on the parasite itself or on a single species of host, and further studies are necessary to clarify the extent to which this parasite serves as a reservoir and vector of infection among different hosts at the same island or island group, or among different Antarctic sub-regions. Furthermore, the potential role of other *Ixodes* spp. in the transmission of pathogens, especially *I. kerguelensis* and *I. a. zealandicus*, remains to be studied. It is worth noting, nonetheless, that *I. a. auritulus* was documented as the vector of *Borrelia* spp. in North America (Morshed et al., 2005; Scott and Foley, 2016).

Although fleas were not as widely connected and central to the host-parasite network as ticks, they might also provide opportunities for pathogen transmission in the Antarctic region. Fleas are vectors of a

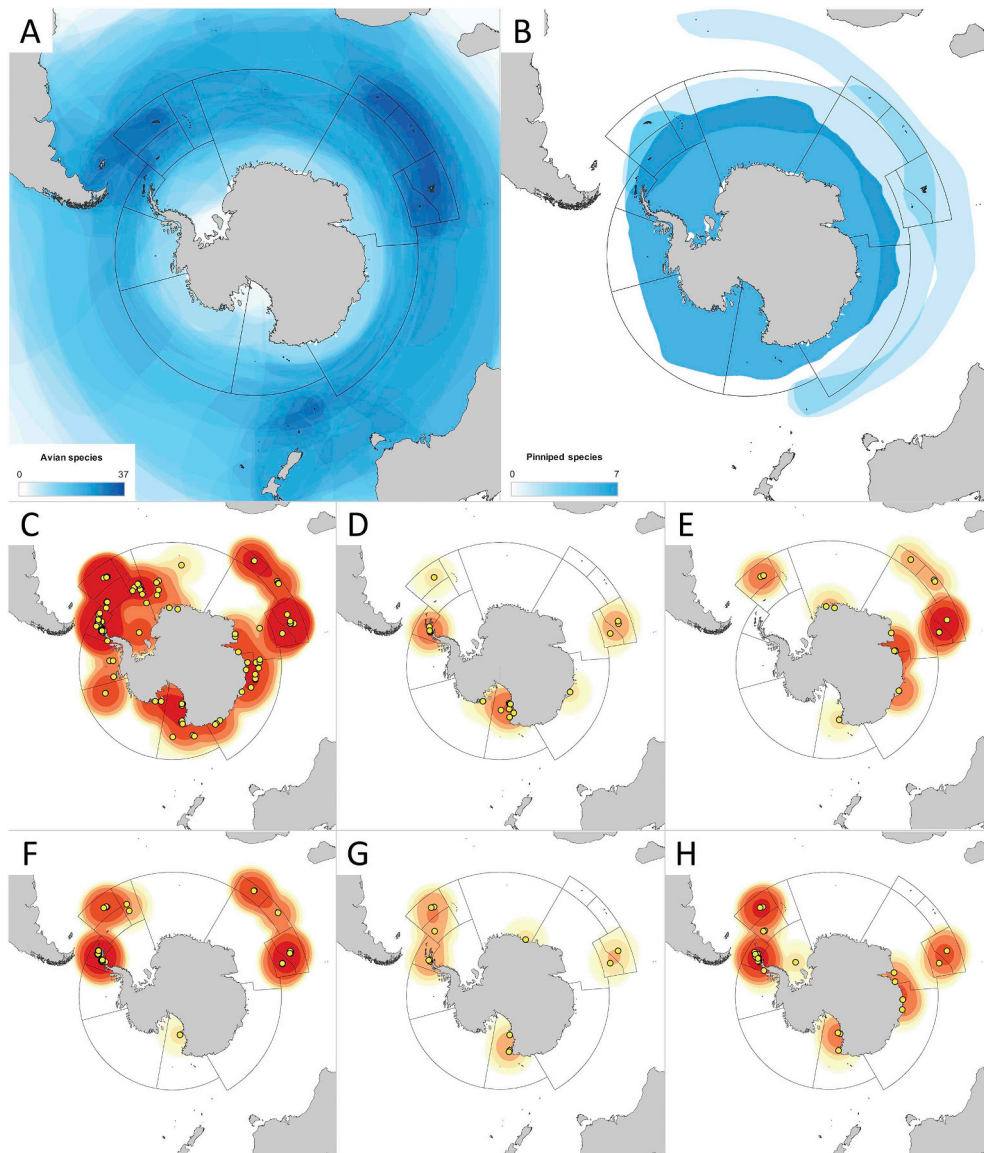


Fig. 6. Distribution of host species and host-parasite-location records in the Antarctic region, excluding stragglers and contaminants. Legend: (A) avian hosts, (B) pinniped hosts, (C) chewing lice, (D) sucking lice, (E) fleas, (F) ticks, (G) nasal mites, (H) feather mites.

number of viral and bacterial pathogens to birds and mammals (Bitam et al., 2010; Sekeyová et al., 2012; Durden and Hinkle, 2019), and can also serve as intermediate hosts for cestodes of mammals (Marshall, 1967). Although no evidence has yet been produced to show that they can play a similar role in Antarctic seabirds, *Parapsyllus* spp. may play a role in the transmission of *Poxviridae* and *Flaviviridae* to other penguin species in subtropical regions (Morgan et al., 1985; Kane et al., 2012).

Due to their higher host specificity and lower centrality, it seems improbable that other groups of parasites play a major role in the interspecies transmission of pathogens in the Antarctic region, perhaps with the exception of the chewing louse, *Ancistrona vagelli*, and the nest-associated mite, *Androlaelaps pachyptilae*. Chewing lice are known to vector viruses, bacteria and filarioid nematodes to other birds (Saxena et al., 1985; Clayton et al., 2007), and *Androlaelaps* spp. are known to transmit Rickettsiales bacteria under experimental conditions (Kocianová, 1989).

From a host-centred perspective, a few species stand out for their higher connectivity to hosts from other classes and could serve as target species for epidemiological surveillance of arthropod-borne pathogens. Considering their relatively high connectivity to other families, high betweenness centrality, and broad distribution among the Subantarctic

sub-regions, the following species can be highlighted: kelp gulls (16 recorded parasites, 9.0% centrality, occurrence in 13 sub-regions), Cape petrels (*Daption capense*; 11 parasites, 6.7% centrality, 11 sub-regions), southern giant petrels (*Macronectes giganteus*; 12 parasites, 4.4% centrality, 12 sub-regions) and brown skuas (*Catharacta antarctica*; 10 parasites, 5.8% centrality, 9 sub-regions). It is worth noting that kelp gulls, southern giant petrels and brown skuas are also predators/scavengers of other seabirds, and may therefore be well-suited for the epidemiological surveillance of pathogens that are transmitted through direct contact (e.g. avian influenza, Newcastle disease).

5. Geographic distribution of parasite records: biogeography or study effort bias?

Figs. 6 and 7 summarize the distribution of bird and pinniped hosts and their parasites in the Antarctic region. With the exception of emperor penguins, which use their feet to incubate their egg while standing on sea ice (Le Maho, 1977), other Antarctic birds rely on ice-free land for their reproduction. As a result, it is not surprising that their diversity in the Southern Ocean tends to be greatest near the main island groups. On the other hand, most Antarctic pinnipeds raise their

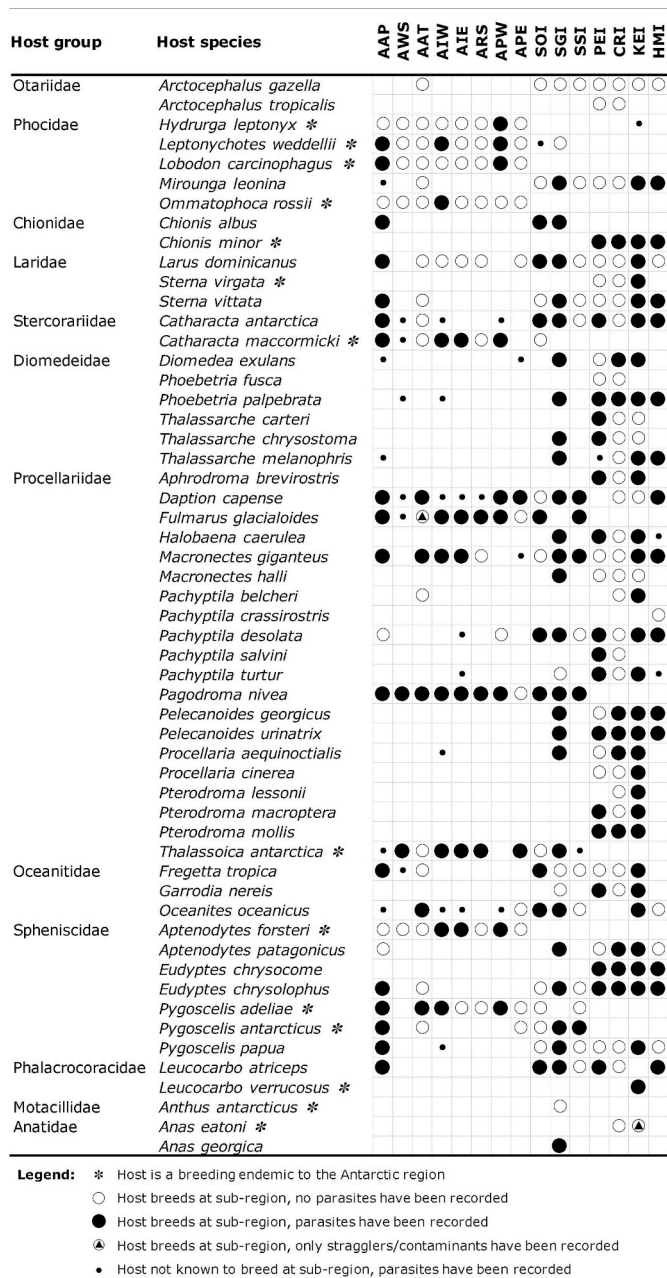


Fig. 7. Distribution of the records of parasitic arthropods in relation to host species and their distribution in the sub-regions of the Antarctic region. Legend: AAP = Antarctic Peninsula (including South Shetland Islands and Palmer Archipelago), AWS = Antarctica Weddell Sea sector, AAT = Antarctica Atlantic Ocean sector (including Bouvet Island), AIW = Antarctica Indian Ocean West sector, AIE = Antarctica Indian Ocean East sector, ARS = Antarctica Ross Sea sector (including Scott and Balleny Islands), APW = Antarctica Pacific Ocean West sector, APE = Antarctica Pacific Ocean East sector (including Peter I Island), SOI = South Orkney Island, SGI = South Georgia Island, SSI = South Sandwich Islands, PEI = Prince Edward Islands, CRI = Crozet Islands, KEI = Kerguelen Islands, HMI = Heard and McDonald Islands.

pups on pack ice (Kelly, 2001), and therefore the diversity for these species is greatest south of the Antarctic Circumpolar Current.

Although the geographic distribution of parasite records in the Antarctic region did follow the general patterns in the distribution of their hosts, some significant differences may be noted. Parasites that remain closely associated with their hosts during their life cycle (chewing lice, sucking lice, nasal and feather mites) have been

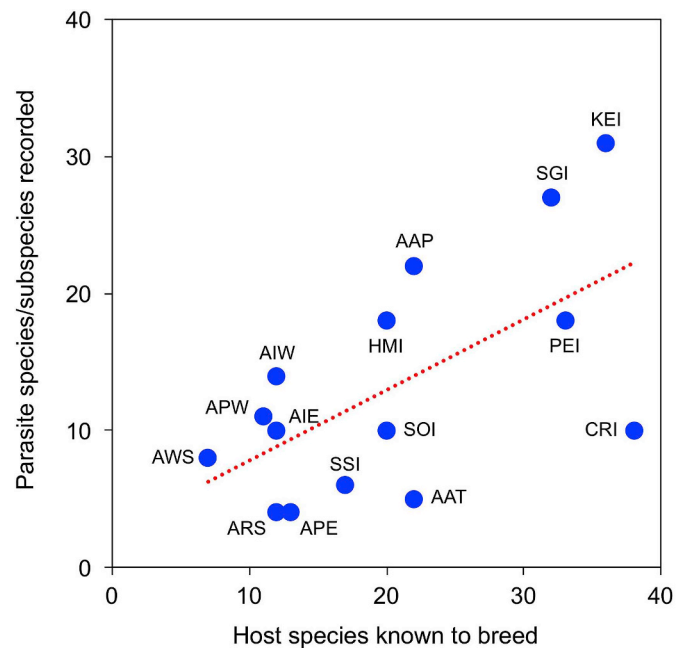


Fig. 8. Distribution of the number of parasite species/subspecies recorded in relation to the number of host species known to breed at the different Antarctic sub-regions, excluding stragglers and contaminants. Legend: AAP = Antarctic Peninsula (including South Shetland Islands and Palmer Archipelago), AWS = Antarctica Weddell Sea sector, AAT = Antarctica Atlantic Ocean sector (including Bouvet Island), AIW = Antarctica Indian Ocean West sector, AIE = Antarctica Indian Ocean East sector, ARS = Antarctica Ross Sea sector (including Scott and Balleny Islands), APW = Antarctica Pacific Ocean West sector, APE = Antarctica Pacific Ocean East sector (including Peter I Island), SOI = South Orkney Island, SGI = South Georgia Island, SSI = South Sandwich Islands, PEI = Prince Edward Islands, CRI = Crozet Islands, KEI = Kerguelen Islands, HMI = Heard and McDonald Islands.

abundantly recorded on the Antarctic continent, whereas parasites that are nest-bound during some stages of their life cycle (fleas, ticks and nest-associated haematophagous mites) are scarcely recorded on the Antarctic continent, with the exception of the Antarctic Peninsula. The only true exception to this rule is the flea *G. antarcticus*, which has been abundantly recorded on the Antarctic continent; as previously discussed, it is unclear whether this species survives winter by attaching to their hosts or by being able to survive freezing, or a combination of both (Whitehead et al., 1991; Steele et al., 1997). In contrast, although the tick *I. uriae* is remarkably resistant to low temperatures and desiccation (Lee and Baust, 1987), the only record of this species on the Antarctic continent outside of the Peninsula was that of a brown skua infested at Ross Island (Wilson, 1967). However, because brown skuas are not known to breed in the Ross Sea sub-region (BirdLife International and Handbook of the Birds of the World, 2019), it seems probable that the tick was carried by a bird from a Subantarctic island or from the Antarctic Peninsula. The lack of more tick records on the Antarctic continent outside of the Peninsula therefore suggests that freezing and dehydration during polar winter might be an unsurpassable barrier even for these extraordinarily resilient parasites.

It is also interesting that records of parasites along the coast of the Antarctic continent are often concentrated near permanent research stations, especially at the Antarctic Peninsula (multiple stations), MacRobertson Land (Mawson station), Princess Elizabeth Land (Davis station), Wilkes Land (Casey station) and Ross Sea (McMurdo station and Scott base). In contrast, the low frequency of parasite records on the Weddell Sea, Dronning Maud Land, King Edward VII Land, Marie Byrd Land and Ellsworth Land is likely a reflection of the scarcity of research stations in these regions. It therefore seems reasonable to presume that the parasites that were recorded elsewhere along the coast

of the Antarctic continent are also present in those regions.

Among the Subantarctic island groups, the South Sandwich, Bouvet, Balleny, Scott and Peter I Islands stand out for the scarcity of parasite records. These islands are breeding sites to a substantial number of species, hence the lack of parasite records is probably related to the logistical difficulties related to conduct of biological research at those islands. It is worth noting that these islands also have a substantially poorer flora than other Subantarctic islands, probably resulting in an environment with limited availability of sheltered microhabitats for nest-bound parasites. Nonetheless, there is no reason to believe that host-bound parasites such as chewing lice and feather mites, which are able to thrive in even harsher environments on the Antarctic continent, would be absent from the seabirds nesting at those islands.

As would be expected, the number of parasite species/subspecies recorded in an Antarctic sub-region is correlated to the number of host species that are known to breed in that sub-region (Fig. 8; $R^2 = 0.380$). However, it is interesting to note that some Subantarctic island groups and Antarctic sub-regions have a lower number of recorded parasites than expected based on their host diversity, suggesting an effect attributable to a decreased research effort: CRI (linear regression residual = -12.3), AAT (-9.0), SSI (-5.4), APE (-5.3), ARS (-4.8), SOI (-3.0) and PEI (-1.7). Further parasitological studies focusing on those sub-regions are likely to improve our knowledge on the ecology and distribution of parasites in the Antarctic region.

6. Other arthropods associated with Antarctic birds and mammals

A number of other arthropods have been recorded in association with Antarctic birds and pinnipeds, but which are not believed to be parasitic. The goose barnacles *Conchoderma auritum* Linnaeus, 1767, *Lepas australis* Darwin, 1851 and *Lepas hilli* (Leach, 1818) are sessile crustaceans known to attach to the skin, plumage or fur of Antarctic penguins and pinnipeds (Barnes et al., 2004; Setsaas and Bester, 2006; Reisinger and Bester, 2010). Even though goose barnacles are filter-feeders, in large numbers they may have negative aerodynamic or hydrodynamic effects (Aznar et al., 1994; Nascimento et al., 2010).

The prostigmatid mite, *Paralorryia leptonychotes* (Womersley, 1937), was described from specimens collected from the intestines of a Weddell seal (*Leptonychotes weddellii*) (Womersley, 1937; Baker, 1968). There is no information on the life cycle of this mite, though members of the family Tydeidae are not generally considered parasites of vertebrates (Silva et al., 2016). Another prostigmatid mite, *Copidognathus johnstoni* (Womersley, 1937), was also described from specimens collected from the intestines of a Weddell seal (Womersley, 1937; Dalenius, 1965). Considering that members of the family Halacaridae are frequently parasites of marine invertebrates (Dabert, 2005), this record is believed to have been related to a displaced specimen (Pugh, 1993).

A variety of insects and mesostigmatic mites can be found in the nest material of seabirds (Dalenius, 1965; Watson, 1967; Hunter, 1970; Crafford et al., 1986; Fain and Galloway, 1993a). These are not considered parasitic, except perhaps for the fly, *Fannia canicularis* (Linnaeus, 1761), which has been found on nests of seabirds at the Prince Edward Islands and whose larvae are known to occasionally cause secondary myiasis in vertebrates (Crafford et al., 1986). Lastly, it is worth mentioning that deutonymphs of mites of the genera *Notiopsyllopus* and *Psylloglyphus* may attach to fleas of the genus *Parapsyllus*, but the mites are not parasitic on the birds (Fain, 1977; Fain and Beaucournu, 1984; Fain and Galloway, 1993b).

7. Conclusion

Arthropod parasites are important components of the biodiversity of the Antarctic region, comprising nearly three times as many species as the hosts they rely on. There are still many important gaps in our knowledge about the basic ecology of these parasites, their host and

geographic distribution, and the impacts that they may have on the health and population dynamics of their hosts. Investigating these host-parasite interactions will be important in order to better understand the Antarctic ecosystem. Furthermore, the study of Antarctic parasite communities and how they evolved under extremely adverse environmental conditions can provide clues as to how this ecosystem will respond to future climate change and other anthropogenic impacts.

Declaration of competing interest

The authors declare they do not have conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jppaw.2020.03.007>.

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