

Chapter 9

Macroparasites in Antarctic Penguins

Julia I. Diaz, Bruno Fusaro, Virginia Vidal, Daniel González-Acuña, Erli Schneider Costa, Meagan Dewar, Rachael Gray, Michelle Power, Gary Miller, Michaela Blyton, Ralph Vanstreels, and Andrés Barbosa

9.1 Introduction

Parasites are the majority of species on Earth (Windsor 1998). The total number of parasite species is likely to be huge, because practically all free-living metazoan species harbor at least one parasite species and almost every individual of every species is parasitized by at least one parasite during its life cycle (Poulin and Morand 2004). The number of parasite species has been estimated as a range from 30 to 71 %

Julia I. Diaz, Daniel González-Acuña, Erli Schneider Costa, Meagan Dewar, Rachael Gray, Michelle Power, Gary Miller, Ralph Vanstreels, and Andrés Barbosa are Working Group of Health Monitoring of Birds and Marine Mammals of the SCAR.

J.I. Diaz (✉)

Centro de Estudios Parasitológicos y de Vectores (CEPAVE), FCNyM, UNLP, CONICET, La Plata, Argentina
e-mail: jidiaz@cepave.edu.ar

B. Fusaro

Instituto Antártico Argentino (IIA), Plan Anual, Argentina

V. Vidal • A. Barbosa (✉)

Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales – CSIC, Madrid, Spain
e-mail: barbosa@mncn.csic.es

D. González-Acuña

Facultad de Ciencias Veterinarias, Universidad de Concepción, Concepción, Chile

E.S. Costa

Universidade Estadual do Rio Grande do Sul and APECS-Brazil, Porto Alegre, Brazil

M. Dewar

Deakin University, Waurn Ponds, Australia

R. Gray

Faculty of Veterinary Science, School of Life and Environmental Sciences,
The University of Sydney, Sydney, Australia

M. Power

Department of Biological Sciences, Macquarie University, Sydney, Australia

G. Miller

Institute for Marine and Antarctic Studies, University of Tasmania, Sandy Bay, TAS,
Hobart, Australia

M. Blyton

Western Sydney University, Richmond, Australia

R. Vanstreels

Department of Pathology, Faculty of Veterinary Medicine and Animal Science,
University of São Paulo, São Paulo, Brazil

of the living species (Price 1980; de Meeus and Renaud 2002). Therefore, parasites can be considered a selective pressure affecting different aspects of the host life which can modulate host populations (Morand and Deter 2009). Moreover, parasite diversity provides insights into the history and biogeography of other organisms, into the structure of ecosystems, and into the processes behind the diversification of life (Poulin and Morand 2004).

Helminths and ectoparasites are the main macroparasites of birds. Helminth is a Greek word that means “worm” and is a conventional name, but not a taxon of animal classification (Miyazaki 1991). Among helminth parasites are included those metazoan “worms” that in any stage of their life cycle live in or on other metazoan species (host). Helminths living inside bird hosts are represented by the major groups, Digenea, Cestoda, Nematoda, and Acanthocephala.

Helminths occupy diverse sites within the host including the gastrointestinal, respiratory, and urinary systems and in organs and tissue spaces of their host. Depending on the parasitic species, their intensity of infection, the host immune status, and the environmental conditions, their presence might not lead to obvious clinical manifestations, or it may manifest itself in terms of individual morbidity and mortality or produce more subtle negative effects on host fitness (Hoberg 2005).

Ectoparasites include arthropod parasites such as ticks, mites (Acari), lice, bugs, fleas, and flies (Insecta). The effects of ectoparasites may include anemia (Gauthier-Clerc et al. 1998; Mangin et al. 2003), feather damage (Barbosa et al. 2002), transmission of pathogens (Allison et al. 1978; Morgan et al. 1981; Siers et al. 2010; Yabsley et al. 2012), and, in the case of some ticks, injection of neurotoxins (Gothe et al. 1979). The consequences of these infestations can vary greatly depending on their intensity and on host health and immune status, and can include negative impacts in terms of mortality, breeding success, and behavior (Gauthier-Clerc et al. 1998; Mangin et al. 2003).

Animals living in Antarctica including penguins are also affected by parasites; however, there is limited knowledge available on their presence, their distribution, epidemiology, life cycles, and health effects on the host in Antarctic fauna (Barbosa and Palacios 2009; Kerry and Riddle 2009). Among Antarctic vertebrates, penguins represent more than 90% of the terrestrial biomass and are the most studied group on this matter. However, available information is sparse and fragmented. In this chapter, we examine the published information on macroparasites of Antarctic penguins, using these species as a model to understand the broader picture on the parasitology of Antarctic birds.

9.2 Diversity and Richness of Helminth Parasites

Former Antarctic expeditions, such as the ones led by James Clark Ross (1839–1843), Jean-Baptiste Charcot (1903–1905), and Robert Falcon Scott (1910–1913), among others, already collected parasites and left us a valuable source of information. One of the most thorough publications on helminths from that time was the one written by Johnston in 1937–1938, dealing with parasites collected during the 1911–1914 Australian Antarctic expedition. He not only supplied descriptions and drawings of helminths, but also included the review and history of each one of them. In general, former published surveys on helminths parasitizing Antarctic penguins often provided only a list of hosts and the parasites collected from them and with few cases reporting on the proportion of infected hosts (Johnston and Mawson 1945; Mawson 1953). Nevertheless, data about their prevalence, intensity, or abundance are scarce, and have only started to be provided in the last decades (Fonteneau et al. 2011; Vidal et al. 2012; Diaz et al. 2013, 2016). Despite this apparent gap, there is a sufficient number of publications that, when compiled and compared, allow as a fairly comprehensive assessment of the richness of helminths present in Antarctic penguins.

Antarctic and Sub-Antarctic penguins act as definitive host of only 13 recognized helminth species (Table 9.1). The core component of the helminth fauna of Antarctic penguins are cestodes, mainly *Parorchites zederi* (Dilepididae). This species is the only cyclophyllidean present in pelagic birds and is widely distributed among Antarctic penguins, including the three pygoscelid species and the Emperor penguin (Cielecka et al. 1992; Vidal et al. 2012; Diaz et al. 2013, 2016; Kleinertz et al. 2014). The presence of Cyclophyllidea eggs has also been demonstrated in the feces of Adélie penguins (Fredes et al. 2008), and it is reasonable to presume these were *P. zederi*.

Members of the Tetrabothriidea are also important components of the helminth communities of Antarctic penguins (Baer 1954). *Tetrabothrius pauliani* Joyeux and Baer 1954 was registered parasitizing all pygoscelid species and also the King penguin, *Tetrabothrius joubini* Railliet and Henry, 1912 was only reported in the Chinstrap penguin (Prudhoe 1969; Cielecka et al. 1992; Georgiev et al. 1996), and *Tetrabothrius wrighti* Leiper and Atkinson 1914 was registered in Adélie, King, and Emperor penguins (Leiper and Atkinson 1914; Johnston 1937; Prudhoe 1969; Fonteneau et al. 2011).

Table 9.1 Summary of macroparasites recorded in Antarctic penguins

	Emperor <i>Aptenodytes forsteri</i>	King <i>Aptenodytes patagonicus</i>	Adélie <i>Pygoscelis adeliae</i>	Chinstrap <i>Pygoscelis antarctica</i>	Gentoo <i>Pygoscelis papua</i>	Macaroni <i>Eudyptes chrysolophus</i>	Southern Rockhopper <i>Eudyptes chrysocome</i>	Royal <i>Eudyptes schlegeli</i>
Breeding distribution	Antarctic	**Sub- Antarctic	Antarctic	Antarctic/ Sub-Antarctic	Antarctic/ Sub-Antarctic	Sub-Antarctic	Sub- Antarctic	Sub- Antarctic
Diet (% by weight)								
Fishes	96.8	68.7–99.8	67.3–100	0.1–38.8	0.2–70.0	2.0–25.0	1.9–28.3	45.8
Crustaceans	0.4	0.1	54.6–99.6	55.1–99.9	30.0–99.8	75.0–98.3	45.1–99.7	51.4
Cephalopods	2.7	0.2–31.3	0–0.4	0	0.5–2.1	0.1–2.2	0.3–53.0	2.8
Cestoda								
<i>Parorchites zedleri</i>	X (1, 2)		X (1, 18, 19)	X (18, 24, 25)	X (18, 26, 29, 34)			
<i>Tetrabothrius joubini</i>				X (18, 23, 24)				
<i>Tetrabothrius pauliani</i>		X (1)	X (18)	X (18, 25, 26, 27)	X (1)			
<i>Tetrabothrius wrightii</i>	X (1)	X (8)						
<i>Tetrabothrius</i> sp.	X (2)		X (19, 21)	X (31, 32)		X (27)		
<i>Diphyllobothrium</i> sp.	X (2)				X (34)			
Nematodes								
<i>Stegophorus macronectes</i>			X (19, 20)	X (25)	X (7, 29)	X (7)	X (7)	
<i>Stegophorus adeliae</i>					X (34)			
<i>Tetrameres wetzeli</i>		X (8)			X (29)			
<i>Tetrameres</i> sp.			X (19)					
<i>Contracaecum heardi</i>		X (8)			X (7)	X (7)		
<i>Contracaecum</i> sp.		X (7)			X (31, 32)		X (7)	
<i>Terranova piscium</i>								X (7) ^a
<i>Streptocara</i> sp.			X (21)		X (31)			

<i>Stomachus = Anisakis</i> sp.												X (7) ^a
Acanthocephalans												
<i>Corynosoma shackletoni</i>										X (29, 33, 34)		
<i>Corynosoma hamanni</i>										X (29) ^a		
<i>Corynosoma bullosum</i>										X (29) ^a		
<i>Corynosoma pseudohamanni</i>										X (28) ^a		
<i>Corynosoma</i> sp.										X (25)		
Chewing lice												
<i>Austragonioides antarcticus</i>										X (3, 4, 5, 10)		
<i>A. brevipes</i>										X (4, 5, 9, 10)		
<i>A. bicornutus</i>												X (4, 5, 10)
<i>A. bifasciatus</i>										X (4, 5)		
<i>A. concii</i>												X (4, 5)
<i>A. cristati</i>												X (3, 4, 5, 10, 11)
<i>A. demersus</i>												X (5, 10)
<i>A. gressitti</i>												X (3, 4, 5, 10, 11)
<i>A. keleri</i>												X (4)
<i>A. macquariensis</i>												X (4)
<i>A. struthesus</i>												X (3, 4, 5, 10, 34)
<i>A. mawsoni</i>												X (3, 4, 5, 10, 11)
												X (3, 4, 5)
												X (3, 4, 5, 9, 10, 11)
												X (4, 5)

(continued)

Table 9.1 (continued)

	Emperor <i>Aptenodytes forsteri</i>	King <i>Aptenodytes patagonicus</i>	Adélie <i>Pygoscelis adeliae</i>	Chinstrap <i>Pygoscelis antarctica</i>	Gentoo <i>Pygoscelis papua</i>	Macaroni <i>Eudyptes chrysolophus</i>	Southern Rockhopper <i>Eudyptes chrysocome</i>	Royal <i>Eudyptes schlegeli</i>
<i>A. hamiltoni</i>						X (11)	X (4, 5, 10, 11)	X (4, 5, 9, 10)
<i>Nesiotinus demersus</i>		X (11)						
<i>Naubates prioni</i>					X (11)			
Ticks								
<i>Ixodes uriae</i>		X (10, 12, 13, 14, 15, 16, 17)	X (10, 23)	X (23)	X (10, 23, 34)	X (10, 12, 15, 38, 40)	X (10, 12, 38, 39)	X (10)
Mites			X (22)					
<i>Rhinonyssus scheeli</i>								
<i>Ayersacarus tilbrooki</i>					X (36)			
<i>Gamasellus antarcticus</i>					X (37)			
<i>Gamasolaelaps arenosus</i>					X (36)			
Fleas						X (10)	X (10)	
<i>Parapsyllus heardi</i>								
<i>Parapsyllus longicornis</i>					X (35)		X (10)	
<i>Parapsyllus magellanicus</i>							X (10, 12)	

Diet from Williams (Williams 1995)

Numbers in brackets refers to references in the table notes

^aDenotes immature individuals

References: (1) Prudhoe (1969), (2) Kleinertz et al. (2014), (3) Clay and Moreby (1967), (4) Clay and Moreby (1970), (5) Clay (1967), (7) Mawson (1953), (8) Fonteneau et al. (2011), (9) Banks et al. (2006), (10) Murray et al. (1991), (11) Palma and Horing (2002), (12) Murray and Vestjens (1967), (13) Gauthier-Clerc et al. (1998), (14) Gauthier-Clerc et al. (1999), (15) Frenot et al. (2001), (16) Gauthier-Clerc et al. (2003), (17) Mangin et al. (2003), (18) Cielecka et al. (1992), (19) Diaz et al. (2016), (20) Zdzitowiecki and Drózd (1980), (21) Fredes et al. (2008), (22) Wilson (1967), (23) Barbosa et al. (2011), (24) Ippen et al. (1981), (25) Vidal et al. (2012), (26) Georgiev et al. (1996), (27) Andersen and Lysfjord (1982), (28) Dimitrova et al. (1996), (29) Diaz et al. (2013), (31) Fredes et al. (2006), (32) Fredes et al. (2007), (33) Hoberg (1986), (34) Gonzalez-Acuña et al. (2013), (35) De Meillon (1952), (36) Hunter (1970), (37) Tragardh (1908), (38) Brooke (1985), (39) Schultz and Petersen (2003), (40) Bergstrom et al. (1999)

Undetermined species of *Tetrabothrius* were also mentioned in Antarctic and Sub-Antarctic regions (Barbosa and Palacios 2009; Kleinertz et al. 2014).

Eggs of *Diphyllobothrium* sp. have been documented in fecal samples of Emperor (Kleinertz et al. 2014) and only in one Gentoo penguin specimen (Gonzalez-Acuña et al. 2013). Recently, some mature and gravid specimens identified as *Diphyllobothrium* sp. were recovered from different colonies of the three pygoscelid species (Fusaro and Diaz unpublished data), and in some instances these parasites can be found on the penguin nests (Barbosa unpublished data). Diphyllbothriidae is a very common group in Antarctic marine mammals but does not seem as common in seabirds. It is worth noting that even though *Diphyllobothrium scoticum* (see Meggitt 1924; Markowski 1952) has been registered as parasites of pygoscelid penguins (Adélie and Chinstrap), this finding was later denied by Johnston (1937).

Spirurid nematodes occur in the esophagus and stomach of seabirds and are one of the more abundant components in the helminth communities of penguins. *Stegophorus macronectes* (Johnston and Mawson 1942) (Acuariidae) is the best represented species. This acuarid nematode has a wide host and geographical distribution, having been reported in all pygoscelid species (Vidal et al. 2012; Diaz et al. 2013, 2016) and in the Rockhopper and Macaroni penguins in Sub-Antarctic regions (Johnston and Mawson 1945; Mawson 1953; Zdzitowiecki and Drózd 1980). The taxonomical and nomenclatural history of this species is complex, and different synonyms were employed in the past including *Stegophorus adeliae* Johnston and Mawson 1945 and *Stegophorus paradelia* Johnston, 1938 sensu Petter, 1959 (see Vidal et al. 2016).

In addition to acuarids, nematodes of the genus *Tetrameres* (Spirurida, Tetrameriidae) parasitized the proventricular glands in Antarctic penguins (Schmidt 1965). *Tetrameres wetzeli* (Schmidt 1965) is the only species on the genus described parasitizing penguin hosts, Rockhopper, King, and Gentoo penguins (Schmidt 1965; Fontaneau et al. 2011; Diaz et al. 2013). Undetermined species of *Tetrameres* were also found in Adélie penguins (Diaz et al. 2016).

Contracaecum ascaridoid nematodes are commonly found in the stomach of piscivorous birds (Garbin et al. 2007, 2008; Diaz et al. 2010). *Contracaecum heardi* Johnston and Mawson 1942 is the species best documented among Sub-Antarctic penguins infecting King, Macaroni, and Gentoo penguins (Mawson 1953; Fontaneau et al. 2011).

Other nematode species have been found in Antarctic and Sub-Antarctic penguins. However, most of these reports were based on eggs, few, immature, or fragmented specimens, or corresponded to fish or mammal parasites, so their identification was not possible or is doubtful (e.g., *Contracaecum* spp., *Stomachus* = *Anisakis* sp., *Streptocara* sp., *Terranova* sp., *Capillaria* sp., among others (Mawson 1953; Fredes et al. 2006, 2007, 2008).

Acanthocephalans are not common in pelagic birds. Only *Corynosoma shackletoni* Zdzitowiecki 1978 has been found at the adult stage in Gentoo penguins (Hoberg 1986; Diaz et al. 2013). Other *Corynosoma* species were registered in pygoscelid penguins (e.g., *Corynosoma bullosum*, *Corynosoma hamanni*, and *Corynosoma pseudohamanni*). However, all those reports correspond to immature

specimens (see Zdzitowiecki 1991; Dimitrova et al. 1996; Vidal et al. 2012; Diaz et al. 2013), and it is thought that these parasites only reach maturity in cetaceans or pinnipeds with penguin infections being accidental (Holloway and Bier 1967; Hoberg 2005).

Digenea parasites have not been recorded in Antarctic or Sub-Antarctic penguins. This likely occurs due to the limitation of their life cycle, the focal nature of transmission near island systems, and the dilution effect of the marine coastal environment, which diminishes their ability to thrive in this kind of hosts (Hoberg 2005).

It is well established that pelagic birds generally support a depauperate parasite fauna, with a much lower diversity than that of birds inhabiting in neritic and littoral waters (Hoberg 2005). A noticeable pattern that emerges by comparing the community of helminths present in Antarctic penguins to that of seabirds from other continents is that the helminth community of penguins is remarkably less diverse. For instance, seabirds of the Alcidae family there are reported in more than 40 helminth species (Muzaffar and Jones 2004), while Antarctic penguin species are parasitized by a total of 10 species (Barbosa and Palacios 2009). Nevertheless, such comparison should be taken with caution as the different number host species might allow more parasite species; in addition, differences in research effort could also affect the comparison. Within penguins, differences in helminths richness between Antarctic and non-Antarctic penguins are similar. Non-Antarctic penguins harbor 12 helminth species, while Antarctic penguins present eight recognized species and seven species parasitize penguin species distributed in the Sub-Antarctic region (Clarke and Kerry 2000; Barbosa and Palacios 2009). Moreover, penguins included in the genus *Spheniscus* (non-Antarctic) have helminth communities richer than those of *Pygoscelis* genus (Clarke and Kerry 2000; Barbosa and Palacios 2009; Brandão et al. 2014). Infracommunities of three pygoscelid species present in the Antarctic Peninsula harbor between one or three helminth species, while those of the Magellanic penguins in Patagonia harbor up to five species (Diaz et al. 2010, 2013, 2016; Vidal et al. 2012). In general, the low number of helminths found in pygoscelid penguins can be explained by the narrow range of variety of prey present in their diet which is form mainly by krill and some few species of squid and fishes (Williams 1995). A wider diet and/or foraging plasticity facilitate the exposure to a high number of parasite species through the ingestion of a high number of intermediate hosts (Hoberg 1996).

9.3 Life Cycles and Source of Infection of Helminths

Most helminths that infect seabirds have indirect life cycles, involving a definitive host, the bird in which adults develop and sexual reproduction occurs, and one or more intermediate/paratenic hosts (invertebrates, fishes) carrying the larval stages. As a result, infestations by helminths are strongly influenced by the trophic relationships of the hosts (Hoberg 1996). Specialized foragers, such as some Antarctic

penguins, can therefore be expected to be infested by fewer parasites than more generalist species.

The trophic webs of the Southern Ocean have macrozooplankton such as euphausiids (krill) playing a key role as an intermediate between primary producers and top predators. Krill (especially *Euphausia* spp.) are the main prey item for most Antarctic penguins (Cherel and Kooyman 1998) and are therefore plausible intermediate hosts for their helminths (Hoberg 2005; Bush et al. 2012).

Larval stages of penguin cestodes use a variety of prey crustaceans/fishes as intermediate hosts (Hoberg 2005). *Parorchites zederi* is probably widely distributed among Antarctic penguins due to a broad oceanic distribution of euphausiids (Hoberg 2005; Vidal et al. 2012; Diaz et al. 2013).

The complete life cycle of *Tetrabothrius* species remains unclear and further investigations are needed. It has been suggested that the first intermediate host of tetrabothriidean cestodes are marine crustaceans and second intermediate or paratenic host could be cephalopods or fishes (Baer 1954; Hoberg 1987). Larval stages identified as Tetrabothriidae were found in nototheniid fishes in Sub-Antarctic waters (Rocka 2003). Presence of tetrabothrids could therefore be higher in penguin species that include cephalopods or fishes in their diets (Diaz et al. 2016).

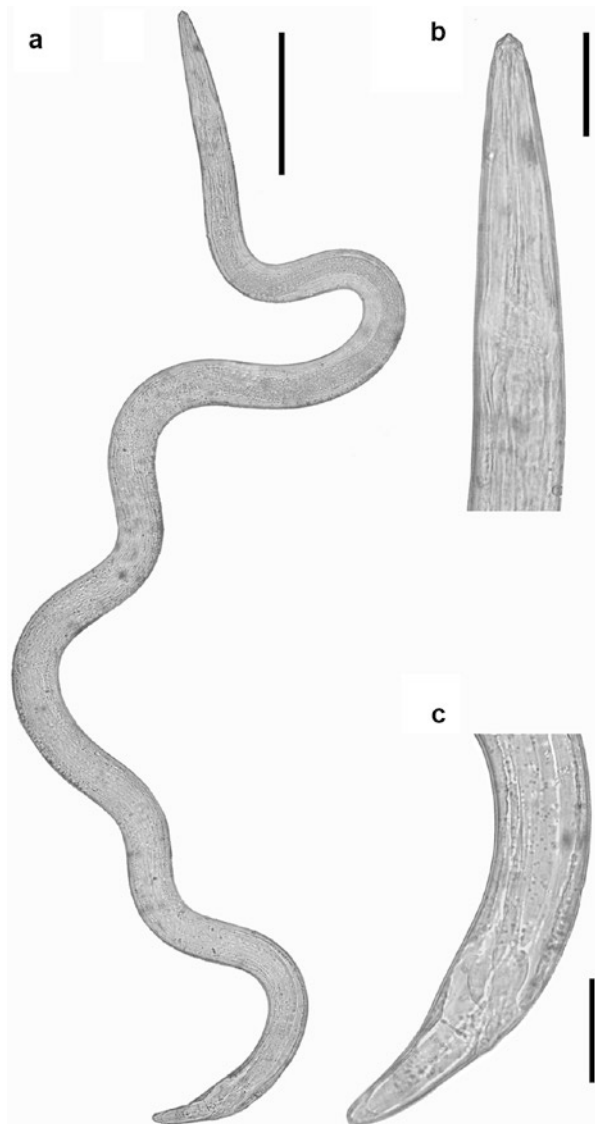
Acuariid and tetramerid nematodes that parasitize aquatic vertebrates are known to develop to the third infective stage in the hemocoel of crustaceans (Anderson 2000). The high prevalence of *S. macronectes* in Antarctic penguins could thus be a consequence of the broad oceanic distribution of euphausiids and their key role in the Southern Ocean trophic web, since they likely serve as suitable intermediate/paratenic hosts. This is corroborated by the observation of a third stage nematode larva in a krill specimen during a survey from Punta Stranger (Diaz pers. obs.). Morphological features observed in that case (Fig. 9.1) are consistent with those of an Acuariidae third stage larva (see Anderson 2000).

However, considering that this larva was the only parasite specimen found after having dissected hundreds of krill individuals (Vidal and Barbosa unpublished data) prevalence of helminth larvae in krill is likely very low. In fact, it is striking that Kagei et al. (1978) found no helminth stages in two large samples of more than 35000 and 55000 Antarctic krill (*E. superba*) each one.

Fishes serve as paratenic hosts for the infective third stage larvae of Anisakidae nematods, which mature after being ingested by the definitive hosts. Species of Nototheniidae have been registered as intermediate hosts of *Contracaecum* larvae in the Antarctic region (Kloser et al. 1992; Rocka 2004). The diet of Antarctic penguins includes varying proportion of nototheniid fish, particularly like *Pleuragramma antarcticum* in different proportions (Adams and Klages 1989; Pütz 1995; Ainley et al. 1998; Leschröel et al. 2004), and it is reasonable to speculate that these species may be involved in the transmission of *Contracaecum* to penguins. However, considering that Antarctic penguins generally do not have a strictly piscivorous diet, reports of Anisakidae are very scarce.

Acanthocephalans appear to be almost absent from pelagic birds (Anderson 2000). *Corynosoma* matures in the gut of mammals and birds, whereas fishes and

Fig. 9.1 Acuariidae third stage larvae found in the hemocoel of *E. superba*.
(a) Complete specimen.
(b) Detail of anterior end.
(c) Detail of posterior end.
Scale bars: (a) 500 μ ;
(b, c) 100 μ



aquatic invertebrates serve as intermediate hosts. However, since euphausiids are not part of the life cycle of *Corynosoma*, infestation rates are low in krill-dependent species like penguins (Muzaffar and Jones 2004). Notothenid fishes such as *Notothenia coriiceps* have been reported harboring cystacanths of *C. shackletoni* in the studied area (Laskowski and Zdzitowiecki 2005; Laskowski et al. 2012), and therefore are likely to play a role in the transmission of *Corynosoma* spp. to penguins in the Antarctic.

Finally, it should be noted that many helminth species that were reported parasitizing Antarctic penguins only develop to maturity on mammal definitive hosts.

However, taking account that some marine mammals (i.e., pinnipeds, cetaceans) and penguins feed on the same prey items, several larvae or immature stages could appear in the intestinal tract of the birds (e.g., *C. bullosum*, *C. hammani*, and *C. pseudohammani* (Mawson 1953; Zdzitowiecki 1991).

9.4 Ectoparasites

Due to the harsh conditions in Antarctica, the number of species of ectoparasites present in Antarctic penguins is relatively small and limited to ticks, fleas, and chewing lice (Barbosa and Palacios 2009) (Table 9.1). There is only one tick species (*Ixodes uriae*) which is distributed in both Sub-Antarctic (Gauthier-Clerc et al. 1998) and Antarctic regions (Barbosa et al. 2011). Flea species of Antarctic penguins (*Parapsyllus heardi*, *P. longicornis*, *P. magellanicus*) are only present in Sub-Antarctic islands (De Meillon 1952; Murray and Vestjens 1967; Murray et al. 1991). Finally, chewing lice species are the more diverse group of ectoparasites with 17 species (*Austrogoniodes antarcticus*, *A. bicornutus*, *A. bifasciatus*, *A. brevipes*, *A. chrysolophus*, *A. concii*, *A. cristati*, *A. gressitti*, *A. hamiltoni*, *A. keleri*, *A. mawsoni*, *A. macquariensis*, *A. strutheus*, *A. vanalphenae*, *A. watersoni*, *Naubates prioni*, *Nesiotinus demersus*) only five of which occur in the Antarctic continent and adjacent islands (*Austrogoniodes antarcticus*, *A. bifasciatus*, *A. chrysolophus*, *A. gressitti*, *A. mawsoni*) (Clay 1967; Clay and Moreby 1967, 1970; Murray et al. 1991; Palma and Horning 2002; Banks et al. 2006).

9.5 Prevalence and Parasitism Intensity

Information on the prevalence or infection intensity of helminths and ectoparasites of Antarctic penguins is scarce, with only 12 out of 33 published studies examined in this chapter providing information on prevalence (Table 9.2). Prevalence of metazoan parasites can differ considerably among parasites species, host species, regions, years and season. As a result, the interpretation of the prevalence data herein compiled should be cautious, especially because most of the information is based on relatively small sample sizes.

A remarkable trend is that penguin helminths tend to occur at higher prevalence than ectoparasites, with a maximum prevalence in several worm species (*P. zederi*, *T. pauliani*, *S. macronectes*). Current data indicate that *P. zederi* has the widest distribution of prevalence information, from East Antarctica showing the lowest prevalence in the Emperor penguin to Avian Island and Deception Island with the highest prevalence in both Adélie and Chinstrap penguins. Among penguin species, *P. zederi* parasitizing Gentoo penguin seems to be more prevalent in the South Shetlands than in more Southern locations although the opposite is shown in Adélie penguin with the higher prevalence in the more Southern location in Avian Island than in the Northern populations. *Stegophorus macronectes* does not show any clear geographical pattern

Table 9.2 Parasite prevalences in Antarctic penguins

Host species	Location	N	Parasite	P %	Reference	
<i>Eudyptes chrysolophus</i>	Sub-Antarctic ±		<i>Ixodes uriae</i>	6	Bergstrom et al. (1999)	
	Antarctic Peninsula	13	<i>Tetrabothrius</i> sp.	23	Andersen and Lysfjord (1982)	
<i>Aptenodytes patagonicus</i>	Crozet ± Archipelago	41	<i>Tetrabothrius wrighti</i>	100	Fonteneau et al. (2011)	
			<i>Tetrameres wetzeli</i>	41.5		
			<i>Contraecaecum heardi</i>	14.6		
			<i>Ixodes uriae</i>	15	Gauthier-Clerc et al. (1999)	
<i>Aptenodytes forsteri</i>	East Antarctica	50f	<i>Parorchites zederi</i>	2	Kleinertz et al. (2014)	
			<i>Tetrabothrius</i> sp.	24		
			<i>Diphyllobothrium</i> sp.	2		
<i>Pygoscelis adeliae</i>	Hope Bay	7C	<i>Stegophorus macronectes</i>	50	Diaz et al. (2016)	
			<i>Tetrameres</i> sp.	33		
	Avian Is.	2	<i>Parorchites zederi</i>	100		
			<i>Tetrabothrius</i> sp.	50		
	25 de Mayo/ King George Is.	7/19C	<i>Parochites zederi</i>	29/16C		
			<i>Stegophorus macronectes</i>	14/21C		
	3	<i>Parochites zederi</i>	33	Cielecka et al. (1992)		
		<i>Tetrabothrius pauliani</i>	33			
		<i>Ixodes uriae</i>	9*	Barbosa et al. (2011)		
<i>Pygoscelis antarctica</i>	Bouvet Is.	9	<i>Tetrabothrius pauliani</i>	88	Andersen and Lysfjord (1982)	
	Deception Is.	4/61C	<i>Parorchites zederi</i>	100/26C	Vidal et al. (2012)	
			<i>Tetrabothrius pauliani</i>	100/13C		
				<i>Stegophorus macronectes</i>	67/72C	
				<i>Ixodes uriae</i>	26*	Barbosa et al. (2011)
	Ronge Is.			<i>Ixodes uriae</i>	2*	
	Livingston Is.			<i>Ixodes uriae</i>	10*	
<i>Tetrabothrius joubini</i>				66	Georgiev et al. (1996)	
			<i>Tetrabothrius pauliani</i>	33		
25 de Mayo/ King George Is.	3		<i>Parorchites zederi</i>	100	Cielecka et al. (1992)	
			<i>Tetrabothrius pauliani</i>	100		
			<i>Tetrabothrius joubini</i>	100		

Table 9.2 (continued)

Host species	Location	<i>N</i>	Parasite	<i>P</i> %	Reference
<i>Pygoscelis papua</i>	Paradise Bay	5/100e	<i>Parorchites zederi</i>	20	Gonzalez-Acuña et al. (2013)
			<i>Stegophorus adeliae</i>	40	
			<i>Corynosoma shackletoni</i>	40	
			<i>Ixodes uriae</i>	5	
			<i>Austrogonioides gressitti</i>	4	
	Antarctic Peninsula	6/100e	<i>Parorchites zederi</i>	33	
			<i>Stegophorus adeliae</i>	16	
			<i>Corynosoma shackletoni</i>	33	
			<i>Austrogonioides gressitti</i>	1	
Ardley Is.	3/100e	<i>Diphyllobothrium</i> sp.	100		
		<i>Stegophorus adeliae</i>	33		
		<i>Austrogonioides gressitti</i>	1		
25 de Mayo/	3/8C	<i>Parorchites zederi</i>	100/0C	Cielecka et al. (1992)	
King George Is.	1	<i>Parorchites zederi</i>	100	Georgiev et al. (1996)	
	37	<i>Parorchites zederi</i>	54	Diaz et al. (2013)	
		<i>Stegophorus macronectes</i>	48.6		
		<i>Tetrameres wetzeli</i>	5.4		
		<i>Corynosoma shackletoni</i>	13.5		
		<i>Ixodes uriae</i>	9*		
Livingston Is.		<i>Ixodes uriae</i>	8–10*	Barbosa et al. (2011)	
Ronge Is.		<i>Ixodes uriae</i>	2*		

Only were considered those papers in which prevalences were provided or they were possible to be calculated, and those parasites that only reach maturity in birds

N number of birds examined, *P* prevalence, ± Sub-Antarctic Regions, *f* fecal samples, *C* chicks, * collected under stones, *e* external examination

in prevalence although seems to be more prevalent in chicks in Deception Island, while the remaining locations show prevalences around 50%. As was mentioned above, *P. zederi* and *S. macronectes* are the most prevalent and frequent helminth species among Antarctic and Sub- Antarctic penguins, which could be due to the potential role played by euphausiids, the mean prey item in this system, as intermediate hosts.

The prevalence of *Tetrabothrius* infections in Antarctic penguins varies greatly even at the species level, with higher prevalence being recorded in the Sub-Antarctic region and South Shetlands islands whereas more austral populations have less prevalence. Data from *Tetrameres* indicate that *T. wetzeli* is more prevalent in the Sub-Antarctic region (King penguins at Crozet Island) than in the South Shetlands

(Gentoo penguins at 25 de Mayo/King George Island). Finally, *Corynosoma* species show higher prevalence in the Southern locations than in the North.

Information on the prevalence of ectoparasites is even scarcer than for helminths. Ticks are present in both Sub-Antarctic and Antarctica regions, but they present different behavior that precludes any comparisons. In Sub-Antarctic islands, ticks are found on the penguins (Gauthier-Clerc et al. 1999), while in the Antarctic Peninsula they are much less common and are usually found under the stones close to the penguin colonies (Barbosa et al. 2011). Nevertheless, data from the Antarctic Peninsula indicates a North-South decrease in the abundance and prevalence of ticks present under the stones at the penguin rookeries (Barbosa et al. 2011). However, such pattern is not coherent with a hypothesis of tick colonization from North to South because genetic studies showed that there is no latitudinal genetic cline; on the contrary, results have shown two different genetic populations of ticks in these regions (McCoy et al. 2013).

In general, the data seem to indicate a broader trend of decreased macroparasite prevalence towards more southerly localities; however, this conclusion should be considered judiciously due to the small number of studies and in some cases their small sample size. With regard to age, prevalence appears to be generally higher in adults than in chicks that could be explained due to the longer time of exposure to the parasites in adult individuals and the shorter period of time for parasite development in chicks, but again caution should be taken with this conclusion due to the small sample size in the case of adults. In fact, the opposite patterns can also be found which is explained by the less development of the immune system in the case of chicks.

Information on parasite intensity is even scarcer than prevalence information. There are only four studies giving such information from Crozet archipelago in King Penguin (mean intensity (MI)=178.6) (Fonteneau et al. 2011), 25 de Mayo/King George Island in Gentoo penguin (MI=22.02) (Diaz et al. 2013), Deception Island in Chinstrap penguin (MI=23.21) (Vidal et al. 2012), and 25 de Mayo/King Gorge Island, Bahia Esperanza/Hope Bay, and Avian Island in Adélie penguin (MI=26) (Diaz et al. 2016). These studies are generally consistent with the interpretation that the mean intensity of infection is higher in penguins inhabiting the Sub-Antarctic region than those on the South Shetland Islands or at the Antarctic Peninsula. A similar result was found comparing the mean intensity between Antarctic and non-Antarctic penguin species with higher values for the latter (D'Amico et al. 2014).

9.6 Parasite Effects on Antarctic Penguins

The effect of macroparasites on the health and fitness of Antarctic penguins is a topic that barely has been addressed, with only a few studies dealing with ticks infecting penguins living in Sub-Antarctic islands and others investigating the potential effects of helminths in the South Shetlands Islands. Reported effects of ticks on penguins include mortality due to hyperinfestation (Gauthier-Clerc et al. 1998), reduced breeding success (Mangin et al. 2003), and transmission of

tick-borne diseases such as borreliosis (Olsen et al. 1995; Schramm et al. 2014; Barbosa et al. unpublished data) and babesiosis (Earle et al. 1993; Montero et al. 2016).

Helminth effects on Antarctic penguin have been reported at the level of the tissue damage, specifically, Martin et al. (2016) described lesions accompanied by hemorrhage, edema, degeneration, and necrosis of the intestine. More generally, using an experimental approach by means of the administration of anti-helminthic drugs, Palacios et al. (2012) estimated the effect of helminth parasites as a loss of 6% of the body mass in infected chicks of Chinstrap penguins. Body mass loss has been also reported in Gentoo penguin chicks in a similar experiment (Palacios et al. unpublished data). Effects on the immune system of Antarctic penguins have also been demonstrated in terms of an increased foot-web swelling response to phytohemagglutinin and a decreased concentration of eosinophils and monocytes in the blood of individuals treated with anti-helminthic drugs (Bertellotti et al. 2016).

9.7 Potential Effects of Climate Change

Climate change can affect the distribution, abundance, and/or virulence of parasites (Sutherst 2001). Antarctica, however, is a region where the effects of climate change are complex and sometimes even contradictory. While the Antarctic Peninsula is one of the parts of the Earth where the temperatures have increased more rapidly in recent decades (Meredith and King 2005) and as a consequence a substantial reduction in sea ice extent has been detected (Stammerjohn et al. 2008; Fan et al. 2014), the Eastern continental region has shown an opposite trend of gradual decrease in land air temperatures and increase in sea ice extent (Fan et al. 2014). As a result, the expected effects of climate on the Antarctic fauna, including penguins and their parasites, will certainly differ between these regions.

Climate change in the Antarctic Peninsula is producing profound environmental changes affecting the trophic web from the bottom to the top through a significant reduction in the primary production (Montes-Hugo et al. 2009). With the consequent reduction in krill abundance (Atkinson et al. 2004; Flores et al. 2012), top predators such as penguins are changing their population trends (Carlini et al. 2009; Trivelpiece et al. 2011; Barbosa et al. 2012). However, not all species inhabiting the same areas have responded similarly, as is notoriously the case of the ice-intolerant Gentoo penguins, which have often benefitted from climate change, whereas the ice-dependent Adélie penguins in the same areas have experienced sharp population decreases (Forcada et al. 2006; Forcada and Trathan 2009). Dietary changes as a response to climate change could be predicted based on changes occurred during past climate changes in which penguins change their diet from krill to squid during warm periods (Emslie et al. 1998). Such changes would certainly affect not only the overall nutritional and health status of these seabirds, but it would also affect the rate of ingestion of parasite cysts/larvae and of exposure to new parasites. Similarly, because the life cycles of ectoparasites are greatly influenced by ambient tempera-

ture, it is expected that the increase of temperatures affect these parasites. For instance, there are already data to suggest that warmer years produce an increase in the abundance of ticks in the Antarctic Peninsula (Benoit et al. 2009).

9.8 Conclusions and Future Prospective

Although Antarctic penguins have been far more studied than other Antarctic seabirds, the scarce and fragmented nature of the available information has limited our broader understanding on the pathogens and disease that affect them and how they may impact their ecology, conservation, and evolution (Barbosa and Palacios 2009).

Published information is based on a geographically uneven sampling area, with few areas (e.g., South Shetland Islands) having been the subject of extensive research whereas virtually no information is available for the most of the continent (e.g., Ross Sea). As a consequence, there is not enough information yet to allow us to establish biogeographical patterns of presence and abundance of parasites. An additional complicating factor is that the information has often been collected during relatively short and discontinuous periods of time and long-term studies or surveillance of the temporal variation of prevalence or parasitism intensity is nonexistent. Such information is crucial to evaluate how environmental changes affect the ecology of these parasites and their impacts to the health of penguins.

Another challenge faced in health studies of Antarctic penguins is the difficulty of obtaining high quality data that faithfully reflect the occurrence of pathogens and disease, often due to the logistical limitations that are inherent to the continent or to application of diagnostic methods that were not specifically designed or validated to be used for these species. For instance, an important limitation that may influence data quality is the difficulty to obtain information of helminth parasites from live penguins through coprological studies because of the high probability of false negative results (Vidal et al. 2012). This, along with the ethical and legal restrictions and the endangered status of many species, restricts the study of endoparasites to the postmortem examination of naturally deceased individuals. As a result, quantitative information on the epidemiology of these parasites (prevalence, intensity of infection, etc.) are likely to be heavily biased and might allow for an adequate interpretation of their ecology and health effects. To solve this problem, the application of molecular techniques could help in improving the applicability and reliability of helminthological studies to living animals (Vidal et al. 2016).

Another important gap in our knowledge on the parasites of Antarctic penguins is the generalized insufficiency of information about their life cycles. This implies that we do not know which could be the intermediate hosts and, as a result, it is not possible to evaluate the risk of infection or how environmental factors affect the epidemiological dynamics.

Finally, from an ecological standpoint, the mechanisms and extent to which parasites affect their hosts is a critical gap in our understanding of Antarctic penguin

parasites. Parasites can play a key role in the population dynamics of their hosts by affecting fitness traits such as survival, breeding success, or behavioral performance (Morand and Deter 2009). This can produce decline in host populations or affect host in different subtle ways through resources consumption and affecting metabolic rate, territorial behavior, phenology, intra- and interspecific interactions, mating and foraging success, etc. (Moller 1997). In addition, hosts can also adjust their behavior in order to avoid or reduce the effects of parasites (Perrot-Minnot and Cézilly 2009). The study of all these aspects has been virtually absent in Antarctica for decades, and only recently some studies have been published on this topic (see above).

It is therefore clear that an urgent effort is needed to obtain high quality data through long-term and geographically representative sampling effort, investigating not only the occurrence of parasites and pathogens but also deeper aspects of their ecology, life cycle, epidemiology, and health impacts. This will be a challenge not only for Antarctic researchers individually, but also reflects the need for broader instruments and policies by international and national Antarctic research programs to incorporate fauna health and pathogen studies as core components of scientific research in the Antarctic.

Acknowledgments This work is a contribution from the Genes to Geoscience funded workshop “Microbial and Parasitic impacts on Antarctic wildlife” held in August 2015 at Macquarie University, Sydney, Australia, and organized by the Working Group of Health Monitoring of Birds and Marine Mammals of the SCAR Expert Group of Birds and Marine Mammals. Macquarie University and the Standing Scientific group of Life Sciences of SCAR funded the workshop. JID is partially supported by PIP 0698 CONICET and N758 UNLP. AB is supported by the PINGUCLIM and CTM2011-24427 project funded by the Spanish Ministry of Economy and Competitiveness. RETV is supported by CAPES through the Department of Pathology (FMVZ-USP). DGA is supported by INACH T-12-13.

References

- Adams NJ, Klages NT (1989) Temporal variation of the diet of the gentoo penguin *Pygoscelis papua* at sub-antarctic Marion Island. *Col Waterbirds* 12:30–36
- Ainley DG, Wilson PR, Barton KJ, Ballard G, Nur N, Karl B (1998) Diet and foraging effort of Adélie penguin in relation to pack-ice conditions in the southern Ross Sea. *Polar Biol* 20:311–319
- Allison FR, Desser SS, Whitten LK (1978) Further observations on the life cycle and vectors of the haemosporidian *Leucocytozoon tawaki* and its transmission to the Fiordland crested penguin. *N Zeal J Zool* 5:371–374
- Andersen KI, Lysfjord S (1982) The functional morphology of the scolex of two Tetrabothrius Rudolphi 1819 species (Cestoda: Tetrabothriidae) from penguins. *Parasitol Res* 67:299–307
- Anderson RC (2000) Nematode Parasite of Vertebrates. Their development and Transmission, CAB International (ed) 2nd edn. Oxon, Wallingford, UK, 650 p
- Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103
- Baer JG (1954) Revision taxonomique et étude biologique des cestodes de la famille des Tetrabothriidae parasites d’oiseaux de haute mer et de mammifères marins, vol 1. Mémoires de l’Université de Neuchâtel, Neuchâtel, pp 4–122
- Banks JC, Palma RL, Paterson AM (2006) Cophylogenetic relationships between penguins and their chewing lice. *J Evol Biol* 19:156–166

- Barbosa A, Merino S, de Lope F, Moller AP (2002) Effects on feather lice on flight behavior of male barn swallow (*Hirundo rustica*). *Auk* 119:213–216
- Barbosa A, Palacios MJ (2009) Health of Antarctic birds: a revision of their parasites, pathogens and diseases. *Polar Biol* 32:1095–1115
- Barbosa A, Benzal J, Vidal V, D'Amico V, Coria NR, Diaz JI, Motas M, Palacios MJ, Cuervo JJ, Ortiz J, Chitimia L (2011) Seabird ticks (*Ixodes uriae*) distribution along the Antarctic Peninsula. *Polar Biol* 34:1621–1624
- Barbosa A, Benzal J, De León A, Moreno J (2012) Population decline of chinstrap penguins (*Pygoscelis antarctica*) on deception Island, South Shetlands, Antarctica. *Polar Biol* 35:1453–1457
- Benoit JB, Lopez-Martinez G, Elnitsky MA, Lee RE, Denlinger DL (2009) Increase in feeding by the tick *Ixodes uriae* on Adélie penguins during a prolonged summer. *Antarct Sci* 21:151–152
- Bergstrom S, Haemig PD, Olsen B (1999) Distribution and abundance of the tick *Ixodes uriae* in a diverse subantarctic community. *J Parasitol* 85:25–27
- Bertelotti M, D'Amico V, Palacios MG, Barbosa A, Coria NR (2016) Effects of antihelminthic treatment on cell-mediated immunity in Gentoo penguin chicks. *Polar Biol* 39:1207–1212
- Brandão ML et al (2014) Checklist of Platyhelminthes, Acanthocephala, Nematoda and Arthropoda parasitizing penguins of the world. *Check List* 10(3):562–573. doi:10.15560/10.3.562
- Brooke ML (1985) The effect of allopreening on tick burdens of molting Eudyptid penguins. *Auk* 102:893–895
- Bush MW, Kuhn T, Münster J, Klimple S (2012) Marine crustaceans as potential hosts and vectors for metazoan parasites. *Parasitol Res Monogr* 3:329–360
- Carlini R, Coria NR, Santos MM, Negrete J, Juarez MA, Daneri GA (2009) Responses of *Pygoscelis adeliae* and *P. papua* populations to environmental changes at Isla 25 de Mayo (King George Island). *Polar Biol* 32:1427–1433
- Cherel Y, Kooyman GL (1998) Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. *Mar Biol* 130:335–344
- Cielecka D, Wojciechowska A, Zdzitowiecki K (1992) Cestodes from penguins on King George Island (South Shetlands, Antarctic). *Acta Parasitol* 37:65–72
- Clarke J, Kerry K (2000) Diseases and parasites of penguin. *Penguin Conserv* 13:5–24
- Clay T (1967) Mallophaga (biting lice) and Anoplura (sucking lice). Part I: austrogoniodes (Mallophaga) parasitic on Penguins (Sphenisciformes). *Ant Res Ser* 10:149–155
- Clay T, Moreby C (1967) Mallophaga (biting lice) and Anoplura (sucking lice). Part II: keys and locality lists of Mallophaga and Anoplura. *Ant Res Ser* 10:157–196
- Clay T, Moreby C (1970) Mallophaga and Anoplura of Subantarctic islands. *Pac Insect Monogr* 23:216–220
- D'Amico VL, Bertelotti M, Diaz JI, Coria NR, Vidal V, Barbosa A (2014) Leucocyte levels in some Antarctic and non-Antarctic penguins. *Ardeola* 61:145–162
- De Meillon B (1952) The fleas of the seabirds in the Southern Ocean. ANARE Reports Series B Vol 1 Zoology
- Diaz JI, Cremonte F, Navone GT (2010) Helminths of the Magellanic penguin, *Spheniscus magellanicus* (Sphenisciformes), during the breeding season in Patagonian Coast, Chubut, Argentina. *Comp Parasitol* 77:172–177
- Diaz JI, Fusaro B, Longarzo L, Coria NR, Vidal V, Jerez S, Ortiz J, Barbosa A (2013) Gastrointestinal helminths of Gentoo Penguins (*Pygoscelis papua*) from Stranger Point, 25 de Mayo/King George Island, Antarctica. *Parasitol Res* 112:1877–1881. doi:10.1007/s00436-013-3341-3
- Diaz JI, Fusaro B, Longarzo L, Coria NR, Vidal V, D'Amico VL, Barbosa A (2016) Gastrointestinal helminths of Adélie Penguins (*Pygoscelis adeliae*) from Antarctica. *Polar Res* 35:28516
- Dimitrova ZM, Chipev NH, Georgiev BB (1996) Record of *Corynosoma pseudohamanni* Zdzitowiecki, 1984 (Acanthocephala, Polymorphidae) in birds at Livingston, and South Shetlands, with a Review of Antarctic Avian Acanthocephalans. *Bulg Antarct Res Life Sci* 1: 102–110
- Earle RA, Huchzermeyer FW, Brossy JJ (1993) *Babesia peircei* sp. nov. from the Jackass penguin. *S Afr J Zool* 28:88–90
- Emslie SD, Fraser W, Smith RC, Walker W (1998) Abandoned penguin colonies and environmental change in the Palmer Station area, Anvers island, Antarctic Peninsula. *Ant Sci* 10:257–268

- Fan T, Deser C, Schneider DP (2014) Recent Antarctic sea ice trends in the context of the Southern Ocean surface climate variation since 1950. *Geophys Res Lett* 41:2419–2426
- Flores H, Atkinson A, Kawagushi S, Krafft B, Milinevsky G, Nicol S, Reiss C, Tarling GA, Werner R, Bravo Rebolledo E, Cirelli V, Cuzin-Roudy J, Fielding S, Groeneveld J, Haraldsson M, Lombana A, Marschoff E, Meyer B, Pakhomov EA, Rombola E, Schmidt K, Siegel V, Teschke M, Tonkes H, Toullec J, Trathan P, Tremblay N, Van de Putte A, van Franeker JA, Werner T (2012) Impact of climate change on Antarctic krill. *Mar Ecol Prog Ser* 458:1–19
- Fonteneau F, Geiger S, Marion L, Le Maho Y, Robin JP, Kinsella JM (2011) Gastrointestinal helminths of King penguins (*Aptenodytes patagonicus*) at Crozet Archipelago. *Polar Biol* 34:1249–1252. doi:10.1007/s00300-011-0970-9
- Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Glob Chang Biol* 12:411–423. doi:10.1111/j.1365-2486.2006.01108.x
- Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. *Glob Chang Biol* 15:1618–1630
- Fredes F, Raffo E, Muñoz P, Herrera M (2006) Fauna parasitaria gastrointestinal en polluelos de Pinguino Papua (*Pygoscelis papua*) encontrados muertos en zona antártica especialmente protegida (ZAEP N°150). *Parasitol Latinoam* 61:179–182
- Fredes F, Madariaga M, Ravo E, Valencia J, Herrera M, Godoy C, Alcaíno H (2007) Gastrointestinal parasite fauna of Gentoo penguins (*Pygoscelis papua*) from the Península Munita, Bahía Paraíso, Antarctica. *Antarct Sci* 19:93–94
- Fredes F, Raffo E, Muñoz P, Herrera M, Godoy C (2008) Fauna parasitaria gastrointestinal en el pinguino Adelia (*Pygoscelis adeliae*) de zona antártica especialmente protegida (ZAEPN 150). *Parasitología latinoamericana* 63(1–2–3–4):64–68. doi:10.4067/S0717-77122008000100011
- Frenot Y, de Oliveira E, Gauthier-Clerc M, Deun V J, Bellido A, Vernon P (2001) Life cycle of the tick *Ixodes uriae* in penguin colonies: relationship with host breeding activity. *Int J Parasitol* 31:1040–1047
- Garbin L, Navone GT, Diaz JI, Cremonte F (2007) Further study of *Contraecaecum pelagicum* (Nematoda: Anisakidae) in *Spheniscus magellanicus* (Aves: Spheniscidae) from two Argentine coast sites. *J Parasitol* 93:143–150
- Garbin L, Diaz JI, Cremonte F, Navone GT (2008) *Contraecaecum chubutensis* n. sp. New anisakid species parasitizing the imperial cormorant *Phalacrocorax atriceps* from the North Patagonian coast, Argentina. *J Parasitol* 94:852–859
- Gauthier-Clerc M, Clerquin Y, Handrich Y (1998) Hyperinfestation by ticks *Ixodes uriae*: a possible cause of death in adult king penguins, a long-lived seabird. *Colonial Waterbird* 21:229–233
- Gauthier-Clerc M, Jaulhac B, Frenot Y, Bachelard C, Monteil H, Le Maho Y, Handrich Y (1999) Prevalence of *Borrelia burgdorferi* (the Lyme disease agent) antibodies in king penguin *Aptenodytes patagonicus* in Crozet Archipelago. *Polar Biol* 22:141–143
- Gauthier-Clerc M, Manguin S, Le Bohec C, Gendner JP, Le Maho Y (2003) Comparison of behaviour, body mass, haematocrit level, site fidelity and survival between infested and non-infested king penguin *Aptenodytes patagonicus* by ticks *Ixodes uriae*. *Polar Biol* 26:379–382
- Georgiev BB, Vasileva GP, Chipev NH, Dimitrova ZM (1996) Cestodes of seabirds at Livingston Island, South Shetlands. *Bulg Antarct Res Life Sci* 1:111–127
- Gonzalez-Acuña D, Hernandez J, Moreno L, Herrmann B, Palma R et al (2013) Health evaluation of wild gentoo penguins (*Pygoscelis papua*) in the Antarctic Peninsula. *Polar Biol* 36:1749–1760
- Gothe R, Kunze K, Hoogstraal H (1979) The mechanisms of pathogenicity in the tick paralysis. *J Med Entomol* 16:357–369
- Hoberg EP (1986) Aspects of ecology and biogeography of Acanthocephala in Antarctic seabirds. *Ann Parasit Hum Comp* 61:199–214
- Hoberg EP (1987) *Tetrabothrius shinii* sp. nov. (Eucestoda) from *Phalacrocorax atriceps bransfieldensis* (Pelecaniformes) in Antarctica with comments on morphological variation, host-parasite biogeography, and evolution. *Can J Zool* 65:2969–2975
- Hoberg EP (1996) Faunal diversity among avian parasite assemblages: the interaction of history, ecology and biogeography in marine systems. *Bull Scand Soc Parasitol* 6:65–89

- Hoberg EP (2005) Marine birds and their helminth parasites. In: Rohde K (ed) Marine parasitology, (Chapter 10, Economic, environmental and medical importance). CSIRO, Sydney, pp 414–421
- Hunter PE (1970) Acarina: Mesostigmata: free-living mites of South Georgia and Heard Island. Pacific Insects Monograph 23:43–70
- Holloway HL Jr, Bier W (1967) Notes on the host specificity of *Corynosoma hamanni* (Linstow, 1892). Bull Wildl Dis Assoc 3:76–78
- Ippen R, Odening K, Henne D (1981) Cestode *Parorchites zederi* and sarcosporidian *Sarcocystis* spp. Infections in penguins of the South Shetland Islands. Erkr Zootiere 22:203–210
- Johnston TH (1937) Australian Antarctic Expedition 1911–1914. Scientific Reports. Series C, Zoology and Botany, vol X, part 4. Cestoda, p 77
- Johnston TH, Mawson PM (1945) Parasitic nematodes. B.A.N.Z.A.R.E. Reports, Series B, vol. V, part 2, pp 73–160
- Kagei N, Asano K, Kihata M (1978) On the examination against the parasites of antarctic krill, *Euphausia superba*. Sci Rep Whales Res Inst 30:311–313
- Kerry KR, Riddle MJ (2009) Health of Antarctic wildlife: a challenge for science and policy. Springer, Berlin
- Kleinertz S, Christmann S, Silva LMR, Hirzmann J, Hermosilla C, Taubert A (2014) Gastrointestinal parasite fauna of Emperor Penguins (*Aptenodytes forsteri*) at the Atka Bay. Antarct Parasitol Res 113:4133–4139. doi:10.1007/s00436-014-4085-4
- Kloser H, Plotz J, Palm H, Bartsch A, Hubold G (1992) Adjustment of anisakid nematode life cycles to the high Antarctic food web as shown by *Contracaecum radiatum* and *C. osculatum* in the Weddell Sea. Antarct Sci 4:171–178
- Laskowski Z, Zdzitowiecki K (2005) The helminth fauna of some notothenioid fishes collected from the shelf of Argentine Islands, west Antarctica. Pol Polar Res 26:315–324
- Laskowski Z, Korczak-Abshire M, Zdzitowiecki K (2012) Changes in acanthocephalan infection of the Antarctic fish *Notothenia coriiceps* in Admiralty Bay, King George Island, over 29 years. Pol Polar Res 33:99–108
- Leiper RT, Atkinson EL (1914) Helminthes of the British Antarctic Expedition, 1910–13. P.Z.S., pp 222–226
- Lescröel A, Ridoux V, Bost C-A (2004) Spatial and temporal variation in the diet of the gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands. Polar Biol 27:206–216
- Mangin S, Gauthier-Clerc M, Frenot Y, Gendner JP, Le Maho Y (2003) Ticks *Ixodes uriae* and the breeding performance of a colonial seabird king penguin *Aptenodytes patagonicus*. J Avian Biol 34:30–34
- Markowski S (1952) The Cestodes of seals from the antarctica – vol 1 num 7. Published by Bulletin of the British Museum (Natural History) Zoology
- Martín MA, Ortiz JM, Seva J, Vidal V, Valera F, Benzal J, Cuervo J, de la Cruz C, Belliure J, Martínez AM, Diaz JI, Motas M, Jerez S, D'Amico VL, Barbosa A (2016) Mode of attachment and pathology caused by *Parorchites zederi* in three species of penguins: *Pygoscelis papua*, *Pygoscelis adeliae*, and *Pygoscelis antarctica* in Antarctica Journal of Wildlife Diseases, 52: 568–575. DOI: 10.7589/2015-07-200
- Mawson PM (1953) Parasitic nematoda collected by the Australian National Antarctic Research Expedition: Heard Island and Macquarie Island 1948–1951. Parasitology 43:291–297
- McCoy KD, Beis P, Barbosa A, Cuervo JJ, Fraser WR, Gonzalez-Solis J, Jourdain E, Poisbleau M, Quillfeldt P, Leger E, Dietrich M (2013) Population genetic structure and colonisation of the western Antarctic Peninsula by the seabird tick *Ixodes uriae*. Mar Ecol Prog Ser 459:109–120
- Meggitt FJ (1924) The cestodes of mammals. London, p 282
- de Mees T, Renaud F (2002) Parasites within the new phylogeny of eukariotes. Trends Parasitol 18:247–251
- Meredith MP, King JC (2005) Rapid ocean climate change at the WAP. Geophys Res Lett 32:L19604
- Miyazaki I (1991) An illustrated book of helminthic zoonoses. Southeast Asian Medical Information Center (International Medical Foundation of Japan) Nihon Kokusai Iryōdan

- Moller AP (1997) Parasitism and the evolution of host life history. In: Clayton DH, Moore J (eds) Host-parasite evolution. General principles and avian models. Oxford University press, New York. pp 105–127
- Montero E, Gonzalez LM, Chaparro A, Benzal J, Bertellotti M, Masero JA, Colominas-Ciuró R, Vidal V, Barbosa A (2016) First record of Babesia in Antarctic penguins. Ticks Tick Borne Dis 7(3):498–501
- Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic peninsula. Science 323:1470–1473
- Morand S, Deter J (2009) Parasitism and regulation of the host population. In: Thomas F, Guégan JF, Renaud F (eds) Ecology and evolution of parasitism. Oxford University Press, Oxford, pp 83–104
- Morgan IR, Westbury HA, Caple IW, Campbell J (1981) A survey of virus infection in sub-antarctic penguins on Macquarie Island, Southern Ocean. Aust Vet J 57:333–335
- Murray MD, Vestjens WJM (1967) Studies on the ectoparasites of seals and penguins. Aust J Zool 15:715–725
- Murray MD, Palma RL, Pilgrim RLD (1991) Ectoparasites of Australian, New Zealand and Antarctic birds. Appendix I. In: Marchant S, Higgins PJ (eds) Handbook of Australian, New Zealand and Antarctic birds, vol I, part A. Oxford University Press, Melbourne
- Muzaffar SB, Jones IL (2004) Parasites and diseases of the auks (Alcidae) of the world and their ecology. Mar Ornithol 32:121–146
- Olsen B, Duffy DC, Jaenson TGT, Gylfe A, Bonnedahl J, Berström S (1995) Transhemispheric exchange of Lyme disease spirochetes by seabirds. J Clin Microbiol 33:3270–3274
- Palacios MJ, Valera F, Barbosa A (2012) Experimental assessment of the effects of gastrointestinal parasites on offspring quality in chinstrap penguins (*Pygoscelis antarctica*). Parasitology 139:819–824
- Palma RL, Horning DS (2002) The lice (Insecta:Phthiraptera) from Macquarie island. ANARE Res Notes 105:1–27
- Perrot-Minnot M-J, Cézilly F (2009) Parasites and behaviour. In: Thomas F, Guégan J-F, Renaud F (eds) Ecology and evolution of parasitism. Oxford University Press, Oxford, pp 49–67
- Poulin R, Morand S (2004) Parasite biodiversity. Smithsonian Books, Washington, DC, p 216
- Price PW (1980) Evolutionary biology of parasites. Monogr Popul Biol 15:1–237
- Prudhoe S (1969) Cestodes from fish, birds and whales. BANZARE Rep Ser B VIII (Part 9)
- Pütz K (1995) The post-moult diet of Emperor Penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea. Antarct Polar Biol 15:457–463
- Rocka A (2003) Cestodes of the Antarctic fishes. Polar Res 24:261–276
- Rocka A (2004) Nematodes of the Antarctic fishes. Polar Res 25:135–152
- Schmidt H (1965) *Tetrameres (G.) wetzeli* sp. n. (Nematoda, Spirurida), eine neue Tetrameresart aus dem Felsenpinguin, *Eudyptes (=Catarrhactes) chrysocome* Forst (Aves, Sphenisciformes). Z f Parasitenkunde 26:71–81
- Schramm F, Gauthier-Clerc M, Fournier JC, McCoy KD, Barthel C, Postic D, Handrich Y, Le Maho Y, Jaulhac B (2014) First detection of *Borrelia burgdorferi* sensu lato DNA in king penguins (*Aptenodytes patagonicus halli*). Ticks Tick Borne Dis 5:939–942. doi:10.1016/j.ttbdis.2014.07.013
- Schultz A, Petersen SL (2003) Absence of haematozoa in breeding Macaroni Eudyptes chrysocome and Rockhopper E. chrysocome Penguins at Marion Island. African Journal of Marine Science 25:499–502
- Siers S, Merkel JF, Bataille A, Vargas FH, Parker PG (2010) Ecological correlates of microfilarial prevalence in endangered Galapagos birds. J Parasitol 96:259–272
- Sutherst RW (2001) The vulnerability of animal and human health to parasites under global change. Int J Parasitol 31:933–948
- Stammerjohn S, Martinson D, Smith R, Yuan X, Rind DH (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño-Southern Oscillation and Southern Annular Mode variability. J Geophys Res 113:C03S90

- Tragardh (1908) The Acari of the Swedish South Polar Expedition. *Wissensch. Ergebn. Schwed. Südpolar Expedition* 5:1–34
- Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc Natl Acad Sci U S A* 108:7625–7628
- Vidal V, Ortiz J, Diaz JI et al (2012) Gastrointestinal parasites in chinstrap penguins from Deception Island, South Shetlands, Antarctica. *Parasitol Res* 111:723–727. doi:[10.1007/s00436-012-2892-z1](https://doi.org/10.1007/s00436-012-2892-z1)
- Vidal V et al (2016) Morphological, molecular and phylogenetic analyses of the spirurid nematode *Stegophorus macronectes* (Johnston & Mawson, 1942). *J Helminthol.* doi:[10.1017/S0022149X15000218](https://doi.org/10.1017/S0022149X15000218)
- Williams TD (1995) The penguins. Spheniscidae. (Birds Families of the Word, No 2). Oxford University Press, p 328
- Wilson N (1967) Acarina: Mesostigmata: Halarachnidae, Rhynonisidae of South Georgia, Heard and Kerguelen. *Pacific Insect Monogr* 23:71–77
- Windsor DA (1998) Controversies in parasitology. Most of the species on Earth are parasites. *Int J Parasitol* 28:1939–1941
- Yabsley MJ, Parsons NJ, Horne EC, Shock BC, Purdee M (2012) Novel relapsing fever *Borrelia* detected in African penguins (*Spheniscus demersus*) admitted to two rehabilitation centers in South Africa. *Parasitol Res* 110:1125–1130
- Zdzitowiecki K (1991) Synopses of the Antarctic benthos koenigstein koeltz scientific books. Antarctic Acanthocephala, Koenigstein, p 116
- Zdzitowiecki K, Drózd J (1980) Redescription of *Stegophorus macronectes* (Johnston et Mawson, 1942) and description of *Stegophorus arctowskii* sp. n. (Nematoda, Spirurida) from birds of South Shetlands (the Antarctic). *Acta Parasitol* 26:205–212