

## RESEARCH/REVIEW ARTICLE

## Gastrointestinal helminths of Adélie penguins (*Pygoscelis adeliae*) from Antarctica

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### Keywords

*Parorchites zederi*; *Stegophorus macronectes*; *Tetrameres* sp.; parasites; ecosystem health.

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### Abstract

Knowledge about parasitic organisms in Antarctica is scarce and fragmentary. The study reported here adds to the knowledge of gastrointestinal parasites of the Adélie penguin (*Pygoscelis adeliae*) (Sphenisciformes), from 25 de Mayo/King George Island (South Shetlands), Bahía Esperanza (Hope Bay) and Avian Island (Antarctica). Thirty-five freshly dead specimens (20 chicks and 15 adults) were collected from December 2007 to December 2014 and examined for internal macroparasites. Three adult parasite species were found: one Cestoda, *Parorchites zederi*, and two Nematoda, *Stegophorus macronectes* and *Tetrameres* sp. Immature *Tetrabothrius* sp. were found in hosts from Avian Island. Helminth communities are known to be related to host feeding behaviours. Low parasite richness observed in Adélie penguins could be related to the stenophagic and pelagic diet of this host species, which feeds almost exclusively on krill.

Almost all animals are affected by some kind of parasites at some time during their life (Bush et al. 2001). By affecting the assimilation of nutrients, reproduction and behaviour parasites can be an important factor modulating host populations (Fonteneau et al. 2011). Examples of the impacts of parasites include the die-offs involving several ring-billed gulls (*Larus delawarensis*) in the St. Lawrence River and the mortality of some wild-caught in Brant that were maintained in captivity on a freshwater pond (Dellaire 2006). An unidentified species of schistosome and a mixed infection with *Trichobilharzia* and *Dendrotobilharzia* were considered the primary causes of death in these two populations, respectively (Huffman & Fried 2008). Impacts of parasites at the scale of host populations have been both extensively modelled and experimentally demonstrated for *Trichostrongylus tenuis* in red grouse in northern England (Tompkins 2008).

In marine ecosystems, the parasite community of a host species reflects the presence of other organisms (intermediate hosts) that are involved in their life cycle through

trophic interactions, making parasites natural markers of changes in biodiversity (Marcogliese 2005). Also, environmental changes, including climate change, can result in a variation in the distribution, abundance or virulence of parasites and pathogens (Daszak et al. 2000; Harvell et al. 2002; Epstein et al. 2003). As excellent indicators of ecosystem health, parasites are also potentially useful as early-warning indicators of environmental perturbations. Therefore, baseline information on the parasitofauna is very important to understand possible modifications in a changing world.

Knowledge about the parasites and diseases of Antarctic birds is limited and fragmentary (Barbosa & Palacios 2009), even in the case of penguins, which represent around 80% of the vertebrate biomass and are the most studied birds in Antarctica (Barbraud & Weimerskirch 2006). Recent studies have expanded our knowledge about parasites of some Antarctic penguin species, providing taxonomic information but also data on prevalence and intensities (Fonteneau et al. 2011; Vidal et al. 2012;

**Abbreviations in this article**

P: prevalence, i.e., the number of hosts infected with at least one parasite species divided by the number of hosts examined

MI: mean intensity, i.e., the total number of individuals of a parasite species found in a sample divided by the number of hosts infected

S: richness, i.e., the number of total parasite species in the sample

Diaz et al. 2013; González-Acuña et al. 2013). However, despite the fact that the Adélie penguins (*Pygoscelis adeliae* [Hombron & Jacquinot]) (Aves, Spheniscidae) are probably the best studied of all penguin species, data on their parasites remain fragmentary (Kerry et al. 1999; Barbosa & Palacios 2009).

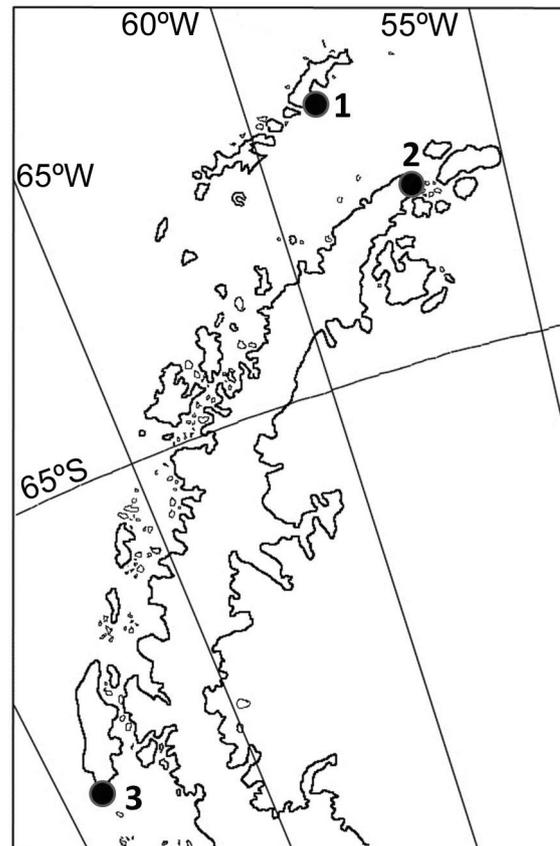
The Adélie penguin is one of more abundant marine birds in the Antarctic ecosystem (Croxall & Prince 1980), with an estimated population of approximately 3.8 million breeding pairs (Lynch & LaRue 2014). The species has a circumpolar distribution, between 46° and 77°S (Woehler 1993). Adults begin to arrive on the coast in late September or early October and the breeding season lasts until February. Adélie penguins feed along the marginal ice zone, which extends for approximately 100 km from the edge of the pack ice (Croxall et al. 2002), and are susceptible to changes in the distribution and abundance of krill and fish (Schofield et al. 2010; Saillely et al. 2013), which are their main prey species (Coria et al. 1995; Libertelli et al. 2003). During the winter, Adélie penguins are obligate inhabitants of the pack ice (Trivelpiece et al. 1987).

In this paper, we describe the gastrointestinal helminth community of the Adélie penguin, analysing specimens from three reproductive populations established in the Antarctic Peninsula and islands around it. Given that any change in parasite diversity may be a sign of “ecosystem distress syndrome” (Rapport 2007), this information will be an important baseline in terms of ecosystem health.

**Materials and methods**

A total of 35 Adélie penguins freshly dead from natural causes were collected from different locations along the Antarctic Peninsula and associated islands (Stranger Point, 25 de Mayo/King George Island, South Shetland Islands during summers from 2007 to 2012; Bahia Esperanza/Hope Bay during the summers of 2013/14 and 2014/15; and Avian Island during the summer of 2009/10 [Fig. 1, Table 1]). Causes of death were unknown although we can exclude predation.

Digestive tracts were immediately removed, placed in plastic bags and frozen at  $-20^{\circ}\text{C}$  or fixed in 10% formalin



**Fig. 1** Localities sampled: (1) Stranger Point, Isla 25 de Mayo/King George Island, (2) Bahia Esperanza/Hope Bay, (3) Avian Island.

until parasitological examination could be carried out. Viscera were separated into oesophagus, stomach (glandular proventriculus and muscular gizzard), intestine and cloaca. Gastrointestinal helminths were removed under a stereomicroscope, fixed in 5% formalin and preserved in 70% ethanol. Cestodes were stained in Semichon’s carmine, dehydrated in a graded ethanol series, cleared in methyl salicylate and mounted in Canada balsam. Nematodes were cleared in 25% glycerine ethanol. All specimens were studied using an optical microscope. Some specimens were dehydrated, dried by the critical point method, gold coated, observed and photographed using a scanning electron microscope (JSMT 6360 LV, JEOL). The terms P, MI and S were interpreted according to Bush et al. (1997). The MI and S are followed by the range. Specimens were identified following keys and specific bibliography (Johnston & Mawson 1945; Delymure 1955; Petter 1959; Yamaguti 1959, 1961; Chabaud 1974; Cielecka et al. 1992; Khalil et al. 1994) and deposited in the Helminthological Collection of the Museo de La Plata, La Plata, Argentina (MLP He 7032, 7033, 7034). Tests were carried out using Quantitative

**Table 1** Parasite composition and ecological parameters of *Pygoscelis adeliae* by locality and age group.

	Stranger Point 62°14' S; 58°39' W			Bahia Esperanza 63°24' S; 56°59' W			Avian Island 67°46' S; 68°64' W		
	Adults	Chicks	Total	Adults	Chicks	Total	Adults	Chicks	Adults
Host analysed [n <sup>a</sup> (P; MI)]	15 (73; 21)	20 (35; 35)	26 (35; 30)	7 (57; 6)	19 (26; 48)	7 (71; 40)	6 (83; 40)	1	2 (100; 1.5)
<i>Parorchites zederi</i> (P; MI)	20; 5	15; 5	19; 6	29; 6	16; 5				100; 1
<i>Stegophorus macronectes</i> (P; MI)	27; 49	30; 38	27; 34	14; 9	21; 56	43; 63	50; 63		
<i>Tetrameres</i> sp. (P; MI)	20; 5		4; 2	14; 2		29; 7	33; 7		
<i>Tetrabothrius</i> sp. (P; MI)	13; 1								50; 1

<sup>a</sup>Number of analysed hosts.

Parasitology 3.0 Budapest software (Rózsa et al. 2000). Chi-square test and unconditional test were applied to test differences in *P* between species of penguins, age groups and localities. MI differences were estimated by bootstrap test. *P* values <0.05 were considered significant. Data from chinstrap and gentoo penguins were taken from Vidal et al. (2012) and Diaz et al. (2013), respectively.

## Results

A total of 471 helminths were recovered from all hosts analysed, belonging to three adult parasite species: the cestode *Parorchites zederi* (Baird 1853) (Dilepididae) from the intestine, and two nematode species, *Stegophorus macronectes* (Johnston & Mawson 1942) (Acuariidae) in the oesophagus and stomach and *Tetrameres* sp. (Tetrameriidae) in the glandular stomach. Also, immature specimens identified as *Tetrabothrius* sp. were recovered from the intestine of penguins from Avian Island.

Of the total penguins examined, 51.4% were parasitized by at least one of the species identified (MI = 26, 1–151). *Parorchites zederi* were found free in the lumen or profoundly fixed in the mucosa forming nodular lesions (*P* = 17.1%; MI = 4.8, 1–12). Specimens were identified on the basis of features of the scolex and proglottids and the presence of a pseudoscolex. *Stegophorus macronectes* (*P* = 28.6%; MI = 42.3, 1–150) were identified based on the morphology of ornamental cephalic structures, cephalic collar and deirids, position of the vulva in females, papillae distribution and spicules in males (see Vidal et al. 2016). *Tetrameres* sp. were found in three adult host (*P* = 8.6%; MI = 5.3, 1–13) and were identified by features of the buccal capsule and spination of the body surface. Two immature *Tetrabothrius* sp. specimens were found only in two hosts. Specific identification was not possible since specimens were immature.

Most infracommunities were composed of only one parasite species, *S* = 1 (1–2). Some 83% of infections were monospecific (53% with *S. macronectes*, 20% with *P. zederi*, 20% with *Tetrameres* sp. and 7% with *Tetrabothrius* sp.),

whereas 17% of infected penguins were parasitized by two different species (66% with *S. macronectes* and *P. zederi*, 33% with *P. zederi* and *Tetrabothrius* sp.). There were no specimens parasitized by more than two species. Composition and ecological parameters by locality and age group are shown in Table 1.

The richness of the component community was greater in adults than chicks (*S* = 4 versus *S* = 2). *P* was greater in adults than chicks (*P* = 0.02). No other significant difference was observed between groups.

## Discussion

Penguins are pelagic and stenophagic birds that are characterized by a low helminth richness (Hoberg 2005; Fonteneau et al. 2011). Two of the parasite species registered in this work are widely distributed among Antarctic penguins. *Parorchites zederi* is a very common parasite in the three pygoscelid species: Adélie penguin, chinstrap and gentoo penguins (Cielecka et al. 1992; Hoberg 2005; Barbosa & Palacios 2009; Vidal et al. 2012; Diaz et al. 2013). It is the only member of the order Cyclophyllidea in pelagic systems (Hoberg 2005). These cestodes penetrate the intestinal mucosa reaching the serosa, where they generate large nodules associated with lesions (Ippen et al. 1981; Tzvetkov et al. 1999; Martin 2015; Martin et al. in press).

The other common parasite is the nematode *Stegophorus macronectes*, which has a wide host and geographical distribution (Barbosa & Palacios 2009). Among penguins, this species has been reported to inhabit the oesophagus and stomach in the three pygoscelid species, and in the rockhopper penguin (*Eudyptes chrysocome* [Forster]) and macaroni penguin (*Eudyptes crysolophus* [Brandt]) (Johnston & Mawson 1945; Mawson 1953; Zdzitowiecki & Drózd 1980; Vidal et al. 2012; Diaz et al. 2013; Vidal et al. 2016).

Euphausiid species have been recorded as suitable intermediate/paratenic hosts of both of the dominant parasite species found in this study (Anderson 2000; Hoberg 2005). The Adélie penguin diet in the South Shetlands Islands area is composed mainly of the pelagic

crustacean *Euphausia superba* (krill), representing 98.5% by weight of the total prey items in the stomach contents (Coria et al. 1995). It is highly likely that *E. superba* acts as the intermediate host of the dominant parasitic species, *P. zederi* and *S. macronectes*, which use food webs to infect definitive hosts.

Species of *Tetrameres* parasitize different orders of birds, but because the specimens typically are hidden in the proventricular glands, their presence is often underreported. *Tetrameres wetzeli* (Schmidt 1965) is the only species of this genus parasitizing penguin hosts (Fonteneau et al. 2011; Diaz et al. 2013). Life cycles of *Tetrameres* species also include crustaceans as intermediate hosts (Hoberg 2005).

Finally, species of *Tetrabothrius* are widely distributed among penguins, for example, *T. lutzi* from the Magellanic penguin (*Spheniscus magellanicus* [Forster]), *T. pauliani* and *T. joubini* from chinstrap penguin and *T. wrighti* from the emperor penguin (*Aptenodytes forsteri* Gray) (Barbosa & Palacios 2009; Diaz et al. 2010; Fonteneau et al. 2011; Vidal et al. 2012). Life cycles of *Tetrabothrius* species includes mainly fish as paratenic hosts (Hoberg 2005).

Although the low sample size of penguins analysed from each age group and from the locations of Esperanza/ Hope Bay and Avian Island precludes making robust conclusions, it is possible to state that adults and chicks share the same parasitofauna because they feed on the same prey items. However, the higher S and P observed in adults are in agreement with what is expected considering that older hosts have more time to be exposed to parasites because transmission does not decrease with age, transmission rates are low and/or parasite mortality does not increase with age (Hudson & Dobson 1997; Morand & Deter 2009).

*Tetrabothrius* sp. was found in Avian Island, but not in the other two localities. This could be associated with a differentiation in the diet related with geographical distribution. In fact, it is known that in the most southern colonies the diet of Adélie penguin includes a higher proportion of fish than in northern populations (Coria et al. 1995; Libertelli et al. 2003; Tierney et al. 2008). This may explain the finding of *Tetrabothrius* sp. in hosts from Avian Island. Other species of this genus were reported in Adélie penguins inhabiting the South Shetlands, with authors considering these records as rare findings at this latitude (Cielecka et al. 1992).

The present study reports the genus *Tetrameres* for first time in the Adélie penguin, and adds to those already recorded previously in other penguins.

Previous authors reported other helminth species in the Adélie penguin in different areas of Antarctica

(e.g., *Corynosoma* spp., *Contraecaecum* spp., *Streptocara* sp.) (Mawson 1953; Fredes et al. 2008; Barbosa & Palacios 2009; Brandao et al. 2014). However, it could be assumed that many of these species might represent occasional and/or accidental findings because almost all of them consisted of a few immature parasite specimens (Cielecka et al. 1992).

Taking into account that phylogeny is an important factor that modulates the host–parasite relationship (Poulin & Morand 2004), it is common to find the same parasite species among hosts of the same genus. The Adélie penguin shares the dominant helminth species (i.e., *P. zederi* and *S. macronectes*) with their two congeneric species, gentoo and chinstrap penguins (Vidal et al. 2012; Diaz et al. 2013). The parasite community of the Adélie penguin shows a low richness similar to the other pygoscelid species, probably as a result of the narrow diet spectrum based mainly on krill (see Vidal et al. 2012; Diaz et al. 2013; D'Amico et al. 2014).

Finally, the presence of *P. zederi* and *S. macronectes* as dominant species (i.e., high P and MI) in all groups of host analysed is indicative of a strong intake of crustaceans in all localities and age classes. The presence of *Tetrabothrius* in those hosts from Avian Island could be associated with an increase of fish in the diet in the southern areas.

## Conclusions

Knowledge about parasites and diseases in Antarctic fauna is important in assessing potential changes due to diet shifts in relation to climate. Here we report baseline data about the gastrointestinal parasite fauna of the Adélie penguin in different localities along the Antarctic Peninsula. This information, together with that arising from previous and future studies of different species of penguins, will be useful for the study of ecosystem health in a changing world.

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## References

- Anderson R.C. 2000. *Nematode parasite of vertebrates: their development and transmission*. 2nd edn. Wallingford: CAB International.
- Barbosa A. & Palacios M.J. 2009. Health of Antarctic birds: a revision of their parasites, pathogens and diseases. *Polar Biology* 32, 1095–1115.
- Barbraud C. & Weimerskirch H. 2006. Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences of the United States of America* 103, 6248–6251.
- Brandao M.L., Moreira J. & Luque J.L. 2014. Checklist of Platyhelminthes, Acanthocephala, Nematoda and Arthropoda parasitizing penguins of the world. *Check List* 10, 562–573.
- Bush A.O., Fernández J.C., Esch G.W. & Seed J.R. 2001. *Parasitism. The diversity and ecology of animal parasites*. Cambridge: Cambridge University Press.
- Bush A.O., Lafferty K.D., Lotz J.M. & Shostak A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* 83, 575–583.
- Chabaud A.G. 1974. Keys to genera of the order Spirurida. In R.C. Anderson et al. (eds.): *Keys to the nematode parasites of vertebrates*. Pp. 29–58. Farnham Royal: Commonwealth Agricultural Bureaux.
- Cielecka D., Wojciechowska A. & Zdzitowiecki K. 1992. Cestodes from penguins on King George Island (South Shetlands, Antarctic). *Acta Parasitologica* 37, 65–72.
- Coria N.R., Fontana R., Vivequin S. & Spairani H. 1995. Diet of Adélie penguins *Pygoscelis adeliae* during the post-hatching period at Stranger Point, King George Island, South Shetland Island, Antarctica. *Museo Regionale di Scienze Naturali Bollettino* 132, 377–383.
- Croxall J.P. & Prince E.D. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society* 14, 103–131.
- Croxall J.P., Trathan P.N. & Murphy E.J. 2002. Environmental change and Antarctic seabird populations. *Science* 297, 1510–1514.
- D'Amico V.L., Bertelotti M., Diaz J.I., Coria N., Vidal V. & Barbosa A. 2014. Leucocyte levels in some Antarctic and non-Antarctic penguins. *Ardeola* 61, 145–162.
- Daszak P., Cunningham A.A. & Hyatt A.D. 2000. Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* 287, 443–449.
- Dellaire A.D. 2006. Schistosomiasis-related mortality in ring billed ducks. *Wildlife Health Center Newsletter* 12, 9.
- Delymure S.L. 1955. *Helminthofauna of marine mammals (ecology and phylogeny)*. Jerusalem: Israel Program for Scientific Translations.
- Diaz J.I., Cremonte F. & Navone G.T. 2010. Helminths of the Magellanic penguin, *Spheniscus magellanicus* (Sphenisciformes), during the breeding season in Patagonian Coast, Chubut, Argentina. *Comparative Parasitology* 77, 172–177.
- Diaz J.I., Fusaro B., Longarzo L., Coria N.R., 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. *Parasitology Research* 112, 1877–1881.
- Epstein P.R., Chivian E. & Frith K. 2003. Emerging diseases threaten conservation. *Environmental Health Perspectives* 111, A506–A507.
- Fonteneau F., Geiger S., Marion L., Le Maho Y., Robin J.P. & Kinsella J.M. 2011. Gastrointestinal helminths of king penguins (*Aptenodytes patagonicus*) at Crozet Archipelago. *Polar Biology* 34, 1249–1252.
- Fredes F., Raffo E., Muñoz P., Herrera M. & Godoy C. 2008. Fauna parasitaria gastrointestinal en el pingüino Adelia (*Pygoscelis adeliae*) de zona antártica especialmente protegida (ZAEPN 150). (Gastrointestinal fauna in an Adélie penguin [*Pygoscelis adeliae*] in Antarctic Specially Protected Area 150.) *Parasitología Latinoamericana* 63, 64–68.
- González-Acuña D., Hernández J., Moreno L., Herrmann B., Palma R., Latorre A., Medina-Vogel G., Kinsella J.M., Martín N., Araya K., Torres I., Fernandez N. & Olsen B. 2013. Health evaluation of wild gentoo penguins (*Pygoscelis papua*) in the Antarctic Peninsula. *Polar Biology* 36, 1749–1760.
- Harvell C.D., Mitchell C.E., Ward J.R., Altizer S., Dobson A.P., Ostfeld R.S. & Samuel M.D. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296, 2158–2163.
- Hoberg E.P. 2005. Economic, environmental and medical importance: marine birds and their helminth parasites. In K. Rohde (ed.): *Marine parasitology*. Pp. 414–421. Sydney: Scientific and Industrial Research Organisation.
- Hudson P.J. & Dobson A.P. 1997. Host-parasite processes and demographic consequences. In D.H. Clayton & J. Moore (eds.): *Host-parasite evolution. General principles and avian models*. Pp. 128–154. Oxford: Oxford University Press.
- Huffman J. & Fried B. 2008. Schistosomes. In C.T. Atkinson et al. (eds.): *Parasitic diseases of wild birds*. Pp. 246–260. Ames, IA: Wiley-Blackwell.
- Ippen R., Odening K. & Henne D. 1981. Cestoden (*Parorchites zederi*) und Sarkosporidienbefall (*Sarcocystis* sp.) bei Pinguinen der Slid-Shetland Inseln (*Cestodes* (*Parorchites zederi*) and sarcosporidia infestation (*Sarcocystis* sp.) in penguins at South Shetland Island). In R. Ippen & H.-D. Schröder (eds.): *Verhandlung des XXIII Internationalen Symposiums über die Erkrankungen der Zootiere vom 24. Juni bis 28. Juni 1981 in Halle/Saale*. Pp. 203–210. Berlin: Akademischer Verlag.

- Johnston T.H. & Mawson P.M. 1945. Parasitic nematodes. *BANZARE Reports Series B 2*, 73–160.
- Kerry K., Riddle M. & Clarke K. 1999. *Diseases of Antarctic wildlife. Report to the Scientific Committee on Antarctic Research (SCAR) and the Council of Managers of National Antarctic Programs (COMNAP)*. Hobart: Australian Antarctic Division.
- Khalil L.F., Jones A. & Bray R.A. 1994. *Key to the cestode parasite of vertebrates*. Albans: CABI Publishing.
- Libertelli M.M., Coria N. & Marateo G. 2003. Diet of the Adélie penguin during three consecutive chick rearing periods at Laurie Island. *Polar Research 24*, 133–142.
- Lynch H.J. & LaRue M.A. 2014. First global census of the Adélie penguin. *The Auk 131*, 457–466.
- Marcogliese D.J. 2005. Parasites of the superorganism: are they indicators of ecosystems health? *International Journal for Parasitology 35*, 705–716.
- Martin M.A., Ortiz J.M., Seva J., Vidal V., Valera F., Benzal J., Cuervo J.J., De La Cruz C., Belliure J., Martínez A.M., Diaz J.I., Motas M., Jerez S., D'Amico V. & Barbosa A. In press. 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*. doi: <http://dx.doi.org/10.7589/2015-07-200>
- Martin M.A. 2015. *Alteraciones morfológicas asociadas a macroparásitos digestivos en los pingüinos pigoscélidos. (Digestive macroparasites associated with morphological alterations in pygoscelid penguins.)* PhD thesis, University of Murcia.
- Mawson P. 1953. Parasitic Nematoda collected by the Australian National Antarctic Research Expedition: Heard Island and Macquarie Island, 1948–1951. *Parasitology 43*, 291–297.
- Morand S. & Deter J. 2009. Parasitism and regulation of the host population. In F. Thomas et al. (eds.): *Ecology and evolution of parasitism*. Pp. 83–105. Oxford: Oxford University Press.
- Petter A.J. 1959. Redescription de *Paryseria adeliae* Johnston, 1938. Remarques sur le genre *Paryseria* et les genres voisins *Rusguniella*, *Aviculariella*, *Proyseria* (Gen. nov.), *Seuratia*. (Notes on *Paryseria* and related genera *Rusguniella*, *Aviculariella*, *Proyseria* (Gen. nov.), *Seuratia*.) *Annales de Parasitologie Humaine et Comparée 34*, 322–330.
- Poulin R. & Morand S. 2004. *Parasite biodiversity*. Washington, DC: Smithsonian Books.
- Rapport D.J. 2007. Sustainability science: an ecohealth perspective. *Sustain Science 2*, 77–84.
- Rózsa L., Reiczigel J. & Majoros G. 2000. Quantifying parasites in samples of hosts. *Journal of Parasitology 86*, 228–232.
- Sailey S.F., Ducklow H.W., Moeller H.V., Fraser W.F., Schofield O.M., Steinberg D.K., Garzio L.M. & Doney S.C. 2013. Carbon fluxes and pelagic ecosystem dynamics near two western Antarctic Peninsula Adélie penguin colonies: an inverse model approach. *Marine Ecology Progress Series 492*, 253–272.
- Schofield O., Ducklow H.W., Martinson D.G., Meredith M.P., Moline M.A. & Fraser W.R. 2010. How do polar marine ecosystems respond to rapid climate change? *Science 328*, 1520–1523.
- Tierney J.E., Russell J.M., Huang Y., Sinninghe Damsté J.S., Hopmans E.C. & Cohen A.S. 2008. Northern Hemisphere controls on tropical southeast African climate during the past 60,000 years. *Science 322*, 252–255.
- Tompkins D.M. 2008. *Trichostrongylus*. In C.T. Atkinson et al. (eds.): *Parasitic diseases of wild birds*. Pp. 316–325. Ames, IA: Wiley-Blackwell.
- Trivelpiece W.Z., Trivelpiece S.G. & Volkman N.J. 1987. Ecological segregation of Adélie, gentoo and chinstrap penguins at King George Island, Antarctica. *Ecology 68*, 351–361.
- Tzvetkov Y., Kril A., Georgiev B.B. & Chipev N.H. 1999. Morphology of lesions in the intestinal wall of the gentoo penguin, *Pygoscelis papua*, caused by *Parorchites zederi* (Cestoda: Dilepididae). In V. Golemansky & N. Chipev (eds.): (eds.): *Bulgarian Antarctic research. Vol. 2*. Pp. 62–67. Sofia: Pensoft Publishers.
- Vidal V., Ortiz J., Diaz J.I., de Ybañez M.R., Amat M.T., Palacios M.J., Benzal J., Valera F., de la Cruz C., Motas M. & Barbosa A. 2012. Gastrointestinal parasites in chinstrap penguins from Deception Island, South Shetlands, Antarctica. *Parasitology Research 111*, 723–727.
- Vidal V., Ortiz J., Diaz J.I., Zafrilla B., Bonete M.J., de Ybañez M.R., Palacios M.J., Benzal J., Valera F., de la Cruz C., Motas M., Bautista V., Machordom A. & Barbosa A. 2016. Morphological, molecular and phylogenetic analyses of the spirurid nematode *Stegophorus macronectes* (Johnston & Mawson, 1942). *Journal of Helminthology 90*, 214–222.
- Woehler E.J. 1993. *The distribution and abundance of Antarctic and Subantarctic penguins*. Cambridge: Scientific Committee on Antarctic Research.
- Yamaguti S. 1959. *Systema helminthum. Vol. 2. The cestodes of vertebrates*. New York: Interscience Publishers.
- Yamaguti S. 1961. *Systema Helminthum. Vol. 3. The nematodes of vertebrates*. New York: Interscience Publishers.
- 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 Parasitologica 26*, 205–212.