Intestinal helminth fauna of the South American sea lion *Otaria flavescens* and fur seal *Arctocephalus australis* from northern Patagonia, Argentina

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Abstract

We report on the intestinal helminth fauna of 56 South American sea lions, *Otaria flavescens*, and 5 South American fur seals, *Arctocephalus australis*, from northern Patagonia, Argentina. A total of 97,325 helminth specimens were collected from sea lions. Gravid individuals were represented by 6 species of parasites: 1 digenean (*Ascocotyle* (*Ascocotyle*) *patagoniensis*), 1 cestode (*Diphyllobothrium* spp.), 3 nematodes (*Uncinaria hamiltoni*, *Contracaecum ogmorhini s.s.*, *Pseudoterranova cattani*) and 1 acanthocephalan (*Corynosoma australe*). In addition, third-stage larvae of 2 nematodes (*Contracaecum* sp. and *Anisakis* sp. type I) and 3 juvenile acanthocephalans (*Andracantha* sp., *Profilicollis chasmagnathi* and *Corynosoma cetaceum*) were also collected. *Andracantha* sp., *C. ogmorhini s.s.* and *P. chasmagnathi* represent new host records. A total of 1516 helminth specimens were collected from fur seals. Gravid individuals were represented by three species of parasites, namely, *Diphyllobothrium* spp., *C. ogmorhini s.s.* and *C. australe*. In addition, larvae of *Contracaecum* sp. and *P. cattani*, juveniles of *C. cetaceum* and immature cestodes (Tetrabothriidae gen. sp.) were also collected. *Corynosoma australe* was the most prevalent and abundant parasite in both hosts, accounting for >90% of all specimens. Sea lions and furs seals from northern Patagonia harbour the intestinal helminth communities that could be predicted for otariids, i.e. the combination of species of the genera *Corynosoma*, *Diphyllobothrium*, *Pseudoterranova*, *Contracaecum* and, in pups, *Uncinaria*. Additionally, both species of otariid are apparently unsuitable hosts (i.e. non-hosts) for as many as five parasite taxa. The inclusion or exclusion of these species affects estimation of species richness at both component community (11 versus 6 species in sea lions; 7 versus 3 species in fur seals) and infra-community (mean: 3.1 versus 2.6 in sea lions; 2.2 versus 1.7 species) levels. Information about the reproductive status of helminth species is often lacking in parasitological surveys on otariids and other marine vertebrates, but it is of significance to improve precision in parascript studies or ecological meta-analyses.

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Introduction

The South American sea lion, *Otaria flavescens*, and the South American fur seal, *Arctocephalus australis*, are common pinnipeds along the eastern and western coasts of South America. The South American sea lion and the South American fur seal are distributed from Peru to southern Brazil (Vaz-Ferreira, 1982; Crespo, 1988; Sanfelice *et al.*, 1999; Túnez *et al.*, 2008). Along only the Argentine coast, over 100 colonies of sea lion and 17 of fur seal have been reported to date (Crespo *et al.*, 1999; Dans *et al.*, 2004). Not surprisingly, there is a great deal of information about the feeding ecology, life history parameters and population dynamics for both species of otariid (Crespo *et al.*, 1997, 1999; Lima & Páez, 1997; Koen Alonso *et al.*, 2000; Naya *et al.*, 2002; Suarez *et al.*, 2005; Cappozzo & Perrin, 2009, and references therein).

Several studies have also addressed diverse aspects about the helminth fauna of South American sea lions and fur seals, including single-species records (Southwell & Walker, 1936; Dailey, 1975; Lauckner, 1985; Zdzitowiecki, 1991; Aznar *et al.*, 2012, and references therein), taxonomic issues (Zdzitowiecki, 1986; George-Nascimento & Urrutia, 2000; Timi *et al.*, 2003; Sardella *et al.*, 2005) and population studies of some parasite species (George-Nascimento & Marin, 1992; George-Nascimento *et al.*, 1992; Aznar *et al.*, 2004; Berón-Vera *et al.*, 2004). What is lacking, however, is a community perspective in the study of the helminth fauna from both species of pinnipeds. This integral, quantitative approach is fundamental to address key questions about the factors that determine the diversity and composition of parasite faunas in carnivores (Lindenfors *et al.*, 2007) or vertebrates in general (Poulin, 1995). To our knowledge, only the study by George-Nascimento & Carvajal (1981) has provided a partial quantitative account of the gastrointestinal helminth fauna of the South American sea lion based on a sample of seven male individuals collected on the coast of Chile.

In this study we report, for the first time, on the intestinal helminth communities of the South American sea lion and the South American fur seal from northern Patagonia, Argentina. In particular, we assess the importance of specificity in shaping community diversity. Recently, some authors (Mateu *et al.*, 2011; Aznar *et al.*, 2012) have pointed out that many putative hosts for trophically transmitted parasites from marine mammals could actually be non-hosts in which the parasite passes through the gut without further development (i.e. the parasite never establishes). This phenomenon may have important implications: (1) to assess the role of putative non-hosts in the population dynamics of helminths; and (2) to define the 'true' community of helminths of a given host species. This discussion provides the context to compare species richness and composition of the helminth communities of both species with those from other otariids.

Materials and methods

Collection and examination of sea lions and fur seals

A total of 56 South American sea lions and 5 South American fur seals were collected in northern Patagonia (40°43′–43°20′S, 63°04′–65°07′W), either stranded on the coast (48 sea lions and 4 fur seals) or as by-catch in fisheries (8 sea lions and 1 fur seal), between 1998 and 2009. For each specimen, the standard body length (SL) was measured to the nearest centimetre (Committee on Marine Mammals, 1967). The age has been estimated from counts of the incremental growth layers in the dentine of tooth sections or in the cementum growth layers (Grandi *et al.*, 2010). Thirty out of the 56 specimens of sea lion were males (SL, mean ± SD [range]: 168 ± 47.9 [90–239]; age (years), 6.4 ± 4.7 [0.3–15]) and 26 were females (SL: 159.4 ± 31.8 [109–228]; age, 10 ± 7.1 [0.4–21]). Four out of the 5 fur seals were males (SL: 139.3 ± 49.0 [68–176]; age, 6.6 ± 3.8 [1.0–10.5]) and 1 was a female (SL: 78; age, 1 year).

Following post-mortem examination, the intestine of each host was removed from the carcass and kept frozen at −20°C. After thawing, the intestine was opened following the procedure described in Aznar *et al.* (2004). Intestinal contents were washed with tap water through sieves of either 0.2 or 0.5 mm mesh. Additionally, the intestine wall was examined to collect attached worms. Intestinal contents were later examined under a stereomicroscope (40–80×). Parasites were fixed in 70% ethanol.

Parasitological procedures

For parasite identification, trematodes were stained with iron acetocarmine or alum carmine, dehydrated through an ethanol series, cleared in clove oil and mounted in Canada balsam. In the case of cestodes of the genus *Diphyllobothrium*, gravid proglottids ($n = 3$) were positioned in sagittal view alongside in cassettes, dehydrated and embedded in acrylic resin. Then, sections (2 μm) were obtained and stained with 1% toluidine blue. Also, gravid proglottids ($n = 5$) were stained in alum carmine and cut by hand using a microtome blade to obtain sagittal sections. Sections were then later dehydrated through an ethanol series, mounted in Canada balsam and examined in profile for species identification according to Rausch *et al.* (2010). Nematodes and acanthocephalans were cleared in glycerin or lactophenol. Additionally, some acanthocephalans were stained in Mayer's carmine, dehydrated through an ethanol series, cleared in methyl salicylate and mounted in Canada balsam. The stage of development of anisakids, i.e. third-stage, fourth-stage and adult, was determined according to Berland (1961), Kagei (1969), George-Nascimento & Urrutia (2000) and Timi *et al.* (2001, 2003). Mounted or cleared specimens were examined with a compound microscope using bright field and differential interference contrast optics (400–1000×). Drawings and morphometric measurements were taken with the aid of a drawing tube. All morphometric measurements are given in micrometres (μm) and expressed as the mean followed by SD, with the range in parentheses. Voucher specimens are deposited in the Natural History Museum, London, UK (accession numbers for parasites from *O. flavescens*: *Diphyllobothrium* spp. (2012.5.15.40–65), *Anisakis* sp. (2012.5.15.23–24), *Contracaecum* sp. (2012.5.15.25–34), *Contracaecum ogmorhini s.s.* (2012.5.15.77–92), *Pseudoterranova cattani* (2012.5.15.66–76), *Uncinaria hamiltoni* (2012.5.15.35–39), *Corynosoma australe* (2012.5.15.1–20)

and *Corynosoma cetaceum* (2012. 5.15.21–22); accession numbers for parasites from *A. australis*: *Diphyllobothrium* spp. (2012.5.15.140–141), Tetrabothriidae gen. sp. (2012.5.15.141–143), *Contracaecum* sp. (2012.5.15.125–139), *C. ogmorhini s.s.* (2012.5.15.173), *C. australe* (2012.5.15.93–122) and *C. cetaceum* (2012.5.15.123–124)) and the Collection of the Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Some cestode, nematode and acanthocephalan specimens were also examined using scanning electron microscopy. Specimens were dehydrated through an ethanol series, critical point dried and coated with gold–palladium alloy to a thickness of 250 nm. Specimens were then examined at the Central Service of the Support to the Experimental Research (SCSIE) of the University of Valencia with a Hitachi 4100 FE scanning electron microscope operating at 20 kV.

Infection parameters were estimated following Bush *et al.* (1997) and Rózsa *et al.* (2000). The 95% confidence intervals (CI) for prevalence were set with Sterne's exact method (Reiczigel, 2003); the 95% CIs of mean intensity and mean abundance were estimated with 20,000 bootstrap replications with the statistical software Quantitative Parasitology v.3 (Reiczigel & Rósza, 2005).

Results

All South American sea lions harboured intestinal helminths; infection parameters are shown in table 1. A total of 97,325 helminth specimens were collected; 88,998 were acanthocephalans, 3684 were nematodes, 4589 were digeneans and 54 were cestodes. Adult specimens were ascribed to six species, namely, *Ascocotyle* (*Ascocotyle*) *patagoniensis*, *Diphyllobothrium* spp., *Contracaecum ogmorhini s.s.*, *Pseudoterranova cattani*, *Uncinaria hamiltoni* and *Corynosoma australe*. In addition, five forms were found either as third-stage larvae (the nematodes

Contracaecum sp. and *Anisakis* sp. type I) or juvenile individuals (*Andracantha* sp., *Profilicollis chasmagnathi* and *Corynosoma cetaceum*).

In the South American fur seals, helminths were collected from the four males; the female was uninfected (table 2). From a total of 1516 helminth individuals, 1408 specimens were acanthocephalans, 99 were nematodes and 9 were cestodes. Adult specimens corresponded to three species, namely, *Diphyllobothrium* spp., *C. ogmorhini s.s.* and *C. australe*. In addition, four forms were found either as third-stage larvae (*Contracaecum* sp.), fourth-stage larvae (*P. cattani*), juvenile (*C. cetaceum*) or sexually immature individuals (Tetrabothriidae gen. sp.).

A single female specimen of an unidentified species of *Andracantha* was found in the rectum of one South American sea lion. The specimen, which was poorly preserved, had numerous ovarian balls. The pipe-shaped trunk was 2594 long and 1574 wide (disc diameter). The disc was covered with spines, except in a small circle on the anterior part where spines became scattered, or even disappeared in a small ventral area (fig. 1). A continuous field of faint spines was also observed along the hind trunk, but spines did not reach the vicinity of the genital pore (fig. 1). The proboscis was partly invaginated and its whole morphological features could only be ascertained by transparency. It had a conical shape, widest at its base, 670 long and 270 wide, with 12 hooks, the 4 basal ones being rootless.

Specimens of *Diphyllobothrium* spp. collected from the South American fur seal had a rounded–ellipsoidal scolex in lateral view (*n* = 2; fig. 2A). Gravid proglottids were 1944 ± 214 (1667–2292, *n* = 13 from two specimens) long and 3391 ± 274 (3042–3833) wide. Width–length ratio of mature proglottids was 1:1.8 (1:1.3–2.2). Transverse tegumentary recesses and pits were observed extending ventrally from the anterior margin of proglottid to the anterior margin of genital atrium on the midline of proglottid. Eggs were 56.9 ± 2.6 (52.1–59.6) long and

Table 1. Infection parameters of helminths found in 56 South American sea lions (*Otaria flavescens*) from northern Patagonia, Argentina.

Species	Prevalence (%) (95% CI)	Mean abundance (95% CI)	Mean intensity (95% CI)	Range
Trematoda				
Ascocotyle (*Ascocotyle*) *patagoniensis*[a]	–	–	–	48–4541
Cestoda				
Diphyllobothrium spp.	26.8 (17.8–41.9)	1.0 (0.5–2.6)	3.4 (1.8–7.9)	1–24
Nematoda				
Uncinaria hamiltoni	3.6 (0.6–12.2)	1.4 (0.0–4.9)	38.0	14–62
Contracaecum ogmorhini[b]	62.5 (49.1–74.2)	8.3 (5.5–12.8)	13.3 (9.3–19.6)	1–70
Pseudoterranova cattani	66.1 (54.7–77.9)	9.8 (3.5–34.5)	14.8 (5.5–55.8)	1–313
Contracaecum sp. (L3)	69.9 (56.3–80.5)	45.6 (21.9–121.1)	65.5 (32.0–169.1)	1–1022
Anisakis sp. (L3)	28.6 (17.6–41.9)	0.6 (0.4–1.2)	2.3 (1.5–3.8)	1–9
Acanthocephala				
Corynosoma australe	100 (93.3–100)	1589 (1177.4–2215.1)	1589 (1182.9–2233.9)	3–10,489
Corynosoma cetaceum	8.9 (3.6–19.4)	0.21 (0.1–0.7)	2.4 (1.0–4.8)	1–7
Profilicollis chasmagnathi[b]	0.2 (0.0–1.0)	0.02 (0.0–0.05)	1.0	1
Andracantha sp.[b]	0.2 (0.0–1.0)	0.02 (0.0–0.05)	1.0	1

CI, confidence interval; L3, third-stage larvae.
[a] Infection parameters could not be calculated for the entire sample (see Materials and methods). The range corresponds to two hosts for which a complete census of specimens was obtained.
[b] New host record.

Table 2. Infection parameters of helminths found in five South American fur seals (*Arctocephalus australis*) from northern Patagonia, Argentina.

Species	Prevalence (%) (95% CI)	Mean abundance (95% CI)	Mean intensity (95% CI)	Range
Cestoda				
Diphyllobothrium spp.	20 (0.0–71.7)	0.4 (0.0–0.8)	2	–
Tetrabothriidae gen. sp.	20 (0.0–71.7)	1.4 (0.0–2.8)	7	–
Nematoda				
Contracaecum ogmorhini	20 (0.0–71.7)	5.0 (0.0–10.0)	25	–
Pseudoterranova cattani	20 (0.0–71.7)	0.4 (0.0–0.8)	2	–
Contracaecum sp. (L3)	20 (0.0–71.7)	14.4 (0.0–28.8)	72	–
Acanthocephala				
Corynosoma australe	80 (28.4–99.5)	279.6 (100.0–459.2)	349.5 (162.3–523.5)	149–567
Corynosoma cetaceum	40 (5.3–85.4)	2 (0.0–5.6)	5 (1.0–5.0)	1–9

CI, confidence interval; L3, third-stage larvae.

39.6 ± 2.0 (36.2–43.3) wide ($n = 25$, from six proglottids of two specimens). No other structures were discernible.

Specimens of *Diphyllobothrium* spp. from the South American sea lion had a lanceolate scolex ($n = 54$; fig. 2B). Gravid proglottids were 2874 ± 763 (1750–4042, $n = 15$ from two specimens) long and 2056 ± 263 (1667–2500, $n = 15$) wide. Width–length ratio of mature proglottids was 1:0.78 (1:0.42–1.33). Transverse tegumentary recesses or pits could not be observed in these specimens, probably because the tegument was poorly preserved. Eggs were 55.8 ± 2.2 (54.0–60.4) long and 35.2 ± 2.0 (33.3–37.5) wide ($n = 18$, from five proglottids of three specimens). No other structures were discernible.

Specimens of Tetrabothriidae gen. sp. from the South American fur seal had a round scolex ($n = 7$; fig. 3A) with four round, sucker-like bothridia; 184 ± 51 (81–226, $n = 10$) long and 166 ± 36 (93–196) wide, each with a small appendage located in antero-lateral to anterio-medial position (fig. 3A and B). Remains of a sucker-like structure were observed at the apex of the scolex in two specimens (fig. 3A). Numerous fragments of strobili with non-mature proglottids were observed.

The intestinal component community of helminths from the South American sea lion was composed of 11 species. At infracommunity level, species richness ranged from 1 to 6 species (mean ± SD: 3.1 ± 1.1 species). A total of 3 hosts (5.4%) were infected with 1 helminth species; 14 (25.0%) with 2; 20 (35.7%) with 3; 14 (25.0%) with 4; 4 (7.1%) with 5, and a single host (1.8%) with 6. In contrast, the intestinal component helminth community of the South American fur seal was composed of seven species. At infracommunity level, species richness ranged from 1 to 5 species (2.2 ± 1.9). One host (20%) was infected with 1 helminth species, 1 (20%) with 2, 1 (20%) with 3, and 1 host (20%) with 5. A single host (a 1-year-old female) was uninfected. There were no significant differences of infracommunity richness between sea lions and fur seals (Mann–Witney test, $U = 91.5$, $P = 0.209$).

Values of helminth species richness are strongly influenced by the taxa that were found only as larvae or juvenile individuals. When these taxa are excluded, the component community of the South American sea lion dropped to six species, and mean infracommunity species richness to 2.6 ± 0.9 species (range 1–5). A total of 5 hosts (8.9%) were infected with 1 helminth species; 20 (35.7%)
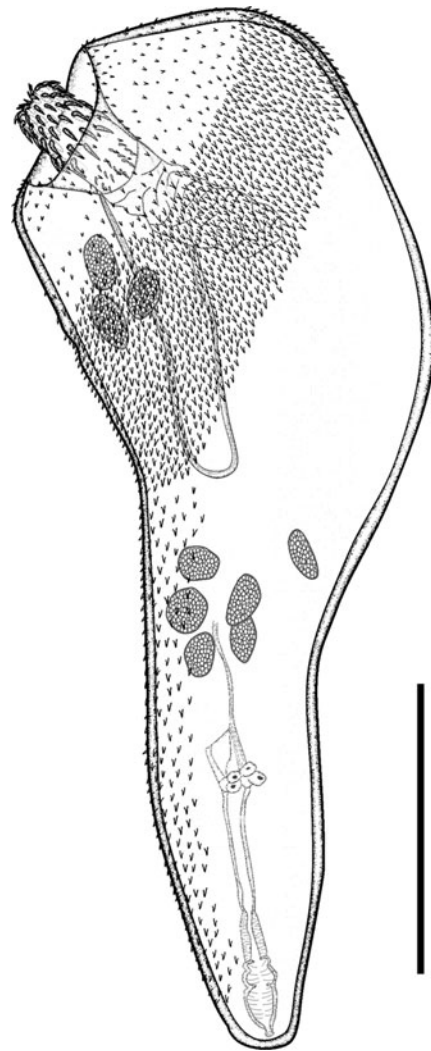

Fig. 1. *Andracantha* sp. from the intestine of the South American sea lion, *Otaria flavescens* from northern Patagonia, whole-mount lateral view. Scale bar: 1000 µm.
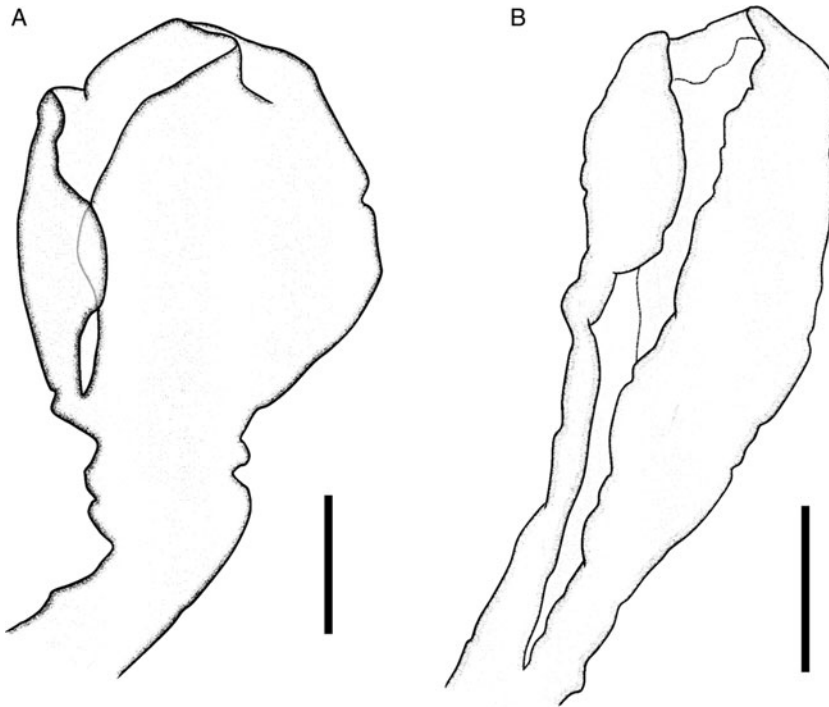
Fig. 2. Scolices of *Diphyllobothrium* spp. collected from the intestine of otariids from northern Patagonia, Argentina, lateral view. (A) *Diphyllobothrium* spp. from the South American fur seal, *Arctocephalus australis*. (B) *Diphyllobothrium* spp. from the South American sea lion, *Otaria flavescens*. Scale bars: 500 μm.

with 2; 22 (39.3%) with 3; 8 (14.3%) with 4 and 1 (1.8%) with 5. In the South American fur seal, the component community excluding larvae and juveniles was composed of four species (mean infracommunity species richness 1.75 ± 1.0). A single host (20%) harboured 4 helminth species and 3 (60%) harboured 1.

Discussion

Parasite composition

Ascocotyle (*A.*) *patagoniensis* was recently described from the South American sea lion (Hernández-Orts *et al.*, 2012). Species of the subgenus *Ascocotyle* infect birds and
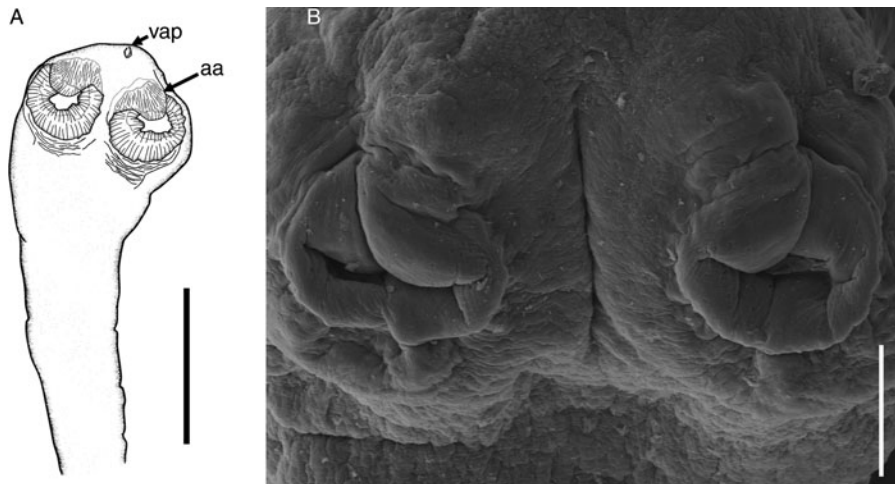

Fig. 3. Tetrabothriidae gen. sp. from the South American fur seal, *Arctocephalus australis*. (A) Scolex, lateral view. (B) Scanning electron micrographs of the round, sucker-like bothridia, lateral view. Scale bars: 400 μm (A) and 60 μm (B). vap, vestiges of apical sucker; aa, anterior appendage.

mammals of freshwater or brackish habitats (Font et al., 1984; Ostrowski de Nuñez, 2001). Therefore, this is the first record of a species from this subgenus in a marine habitat and in a marine mammal. However, the life cycle of A. (A.) patagoniensis is yet to be elucidated; no metacercariae of this species were found in 542 individuals from 20 marine teleost species (Hernández-Orts et al., 2012), nor have specimens of Ascocotyle spp. been reported in marine fish from Patagonia (Timi & Poulin, 2003; Sardella & Timi, 2004; Vales et al., 2011, and references therein). Although the high parasite burdens indicated that it was not an accidental parasite, infection parameters of A. (A.) patagoniensis could not be determined reliably because we could not rule out that an indeterminate number of specimens had been lost during sieving, due to the small size of the parasite. It is therefore advisable that sieves <0.2 mm mesh are used in future parasitological surveys of sea lions or other pinnipeds.

Species of Diphyllobothrium are common intestinal parasites of fur seals and sea lions (Rausch et al., 2010). Two species have been reported frequently in otariids from the southern hemisphere, i.e. D. pacificum and D. arctocephalinum, in the Pacific and Atlantic Oceans, respectively (Rausch et al., 2010). The specimens of Diphyllobothrium spp. collected in the present study were very poorly preserved, which prevents identification at the species level. Based on some morphological traits (e.g. scolex shape, proglottids and size of eggs) specimens of Diphyllobothrium spp. from South American fur seals resemble both D. pacificum and D. arctocephalinum (table 3). Similarities are less evident in specimens collected from South American sea lions (table 3). Molecular data and morphological examination based on suitable material will be necessary for a reliable identification of specimens of species of Diphyllobothrium infecting sea lions and fur seals in northern Patagonia.

Species of Tetrabothriidae occur as parasites of marine birds and marine mammals and are assigned to six genera based on features of the scolex and the reproductive system (Hoberg, 1994). No gravid proglottids were observed in any of the specimens collected from fur seals in our study. Nor did the structure of the scolex allow us to make a reliable generic allocation of our specimens. In tetrabothriids, the presence of vestiges of the larval apical sucker suggests that the ontogeny of the scolex is almost complete (Hoberg, 1987; Hoberg et al., 1991; Hoberg & Measures, 1995). Accordingly, our specimens probably represented a relatively recent infection and/or they could not progress development further. In any event, the structure of the scolex would preclude the assignation of our specimens to Tetrabothrius, which should exhibit clear, laterally directed auricular appendages at this stage of development (Hoberg, 1987). The type of anterior appendages that we observed is reminiscent of, but not similar to, those from species of Anophryocephalus or Trygonocotyle (Hoberg, 1994, and references therein). New material should therefore be made available to perform further morphological and molecular analyses in order to identify these cestodes.

Species of Uncinaria have been reported in fur seals and sea lions worldwide, including the South American sea lion in the study area (Berón-Vera et al., 2004). Adults

Table 3. Comparison of taxonomic data between Diphyllobothrium pacificum, D. arctocephalinum and unidentified species of Diphyllobothrium collected from sea lions and fur seals in northern Patagonia, Argentina. Measurements in micrometres.

	D. pacificum	D. arctocephalinum	Diphyllobothrium spp.	Diphyllobothrium spp.
Reference	Rausch et al. (2010)	Rausch et al. (2010)	Present study	Present study
Host	Otariids	Otariids	South American sea lion	South American fur seal
Distribution	Pacific Ocean (northern and southern hemispheres)	Pacific Ocean (southern hemisphere), southern Atlantic coast of South Africa	Southern Atlantic, coast of Argentina	Southern Atlantic, coast of Argentina
Scolex morphology (lateral view)	Rounded–ellipsoidal	Rather ellipsoidal	Lanceolate	Rounded–ellipsoidal
Pits anterior to genital atrium	Present	Present	Could not be observed	Present
Length/width ratio of gravid proglottids	1:4–5	1:1.5	1:0.42–1.33	1:1.3–2.2
Egg size (range)	48.7–56.0 × 38.9–48.7	41.4–56.0 × 36.5–43.8	54.0–60.4 × 33.3–37.5	52.1–59.6 × 36.2–43.3

reproduce in the intestine of pups, and evidence suggests that pups become infected through the milk of mothers carrying third-stage larvae (Lyons *et al.*, 2000 and references therein). In our sample, individuals of *U. hamiltoni* were collected from the two youngest pups, 5 and 7 months old, but were not found in any of ten pups aged 8–10 months. The latter were probably in the weaning process (Cappozzo & Perrin, 2009) and had no further opportunity of (re)infection. Therefore, these pups either had never been infected or had cleared previous infections. The latter possibility would confirm that most infections occurred soon after parturition, as has been suggested for species of *Uncinaria* infecting otariids in the northern hemisphere; in these species, the estimated life-span of the parasite in pups was 3–8 months (Lyons *et al.*, 2000).

Contracaecum ogmorhini s.s. and *P. cattani* have been reported in the stomach of pinnipeds in South America (George-Nascimento & Urrutia, 2000; Timi *et al.*, 2003). In this study, fourth-stage larvae and adult specimens of both species were frequently found in the intestine of sea lions, and in 1 out of 5 fur seals. Most specimens, especially those collected from the middle and posterior intestine, were degraded, suggesting that they likely were senescent worms from the stomach that were passing throughout the gut. However, whether or not the upper intestine could be a suitable microhabitat for these nematodes is an open question.

Third-stage larvae of *Contracaecum* sp. were the most abundant nematodes collected from the intestine (tables 1 and 2). Larvae of *Contracaecum* sp. cannot be identified to the species level based on morphological traits. We believe that our material probably contains not only third-stage larvae from *C. ogmorhini s.s.*, but also from sympatric species of *Contracaecum* that typically mature in marine birds or other pinnipeds, which come from digested fishes. Apart from *C. ogmorhini s.s.* at least four species of *Contracaecum* have been reported in northern Patagonia: *C. pelagicum*, from the Magellan penguin, *Spheniscus magellanicus*; *C. chubutensis* from the Imperial cormorant, *Phalacrocorax atriceps*; *C. osculatum s.l.* and *C. miroungae* from the elephant seal, *Mirounga leonina* (Mattiucci *et al.*, 2003; Garbin *et al.*, 2007, 2008).

Species of *Anisakis* are typical parasites of cetaceans (Mattiucci & Nascetti, 2008). The morphology of the third-stage larvae of *Anisakis* sp. collected from South American sea lions conforms to Berland's (1961) type I, which corresponds to the larvae of *A. simplex s.l.* (Nascetti *et al.*, 1986). These larvae are widespread in fishes from northern Patagonia (Timi & Poulin, 2003; Sardella & Timi, 2004; Timi & Lanfranchi, 2009, and references therein), whereas adults have been recorded from species of toothed whales from the same locality (Dans *et al.*, 1999; Berón-Vera *et al.*, 2007, 2008).

Corynosoma australe was the most prevalent and abundant parasite from the intestine of the South American sea lion and the South American fur seal, accounting for >90% of all individual parasites found in both species. This acanthocephalan is a common parasite of pinnipeds (principally otariids) from the southern hemisphere, including sea lions (George-Nascimento & Marin, 1992; Aznar *et al.*, 2012) and fur seals (Aznar *et al.*, 2004; Sardella *et al.*, 2005). In Uruguay, *C. australe* is known to readily infect the South American fur seal because the parasite seems to be ecologically ubiquitous, occurring in many species of both pelagic and demersal fish (Aznar *et al.*, 2004). The same situation appears to occur in northern Patagonia, where cystacanths of this species have been found in at least 17 pelagic, benthopelagic and benthic fish species (Hernández-Orts, unpublished data); there are additional records in other parasitological surveys (Timi & Poulin, 2003; Sardella & Timi, 2004; Vales *et al.*, 2011, and references therein). Not surprisingly, *C. australe* appeared in all sea lions analysed, even in pups aged 4, 5 or 7 months.

Juvenile specimens of three additional acanthocephalan species, i.e. *C. cetaceum, P. chasmagnathi* and *Andracantha* sp. were found in this study. It has been suggested that *C. cetaceum* is specific to cetaceans, but juvenile specimens also occur in different pinniped species, including both species of otariids from South America (Aznar *et al.*, 2001, 2012). Our data confirm that *C. cetaceum* is apparently unable to mature in sea lions and fur seals. Definitive hosts for species of *Profilicollis* are marine fish-eating birds (Zdzitowiecki, 1991). *Profilicollis chasmagnathi* is the only species from this genus that has been reported from the Atlantic coast of South America. There are records of cystacanths in grapsid crabs from Uruguay (Holcman-Spector *et al.*, 1977). Adult worms have been recorded in Olrog's gull, *Larus atlanticus,* from Bahía Blanca (La Sala & Martorelli, 2007) and in the kelp gull, *Larus dominicanus*, from northern Patagonia (Diaz *et al.*, 2011).

Species of *Andracantha* also reproduce in marine birds, especially cormorants, worldwide (García-Varela *et al.*, 2009). In Argentina, *Andracantha* sp. had only been reported from nototheniid fishes in the Beagle Channel (Laskowski & Zdzitowiecki, 2009). We assigned our specimen to this genus based on the observed pattern of trunk spination, which conforms to the generic concept as defined by Zdzitowiecki (1989), i.e. the possession of conspicuous spines arranged in two circular fields separated from each other by either a bare zone or a zone covered with smaller spines. Unfortunately, we were unable to make a reliable specific assignation of our immature specimen because it, too, was in poor condition and had a partly inverted proboscis. Interestingly, our specimen closely resembles immature specimens of an unidentified species of *Andracantha* that was recently found in a Franciscana dolphin, *Pontoporia blainvillei*, in Buenos Aires Province (Aznar *et al.*, 2012). Overall, specimens of *Andracantha* collected from marine mammals in Argentina are most similar to *A. phalacrocoracis*, but the combination of a singular pattern of trunk armature and proboscis traits does not preclude the possibility that they might represent a new species (see Schmidt, 1975; Zdzitowiecki, 1989).

Parasite diversity

Otariids from northern Patagonia seem to be suitable hosts for 6–7 species (depending on whether there are one or two species of *Diphyllobothrium*), five of which belong to genera whose species infect otariids worldwide (table 4), i.e. *Diphyllobothrium, Corynosoma, Pseudoterranova, Contracaecum* and *Uncinaria* (Dailey, 1975;

Table 4. Richness and composition of intestinal heminth fauna of otariid species obtained from surveys worldwide. N, host sample size; C, number of helminth taxa in the total sample (component community); I, number of taxa per individual host (infracommunity) calculated as the sum of prevalences expressed on a per unit basis.

Species	Locality[a]	N	C	I	Number of species				
					Diphyllobothrium	*Corynosoma*	*Contracaecum*	*Pseudoterranova*	Other species (genera)
Callorhinus ursinus	Northern Japan[1]	50	6	NA	1	1	1	1	1 (*Anisakis*)
	Komandor Islands[2]	109	12	NA	3	2	1	1	5 (*Anisakis, Phocascaris,* Anisakidae gen.)
	Okhotsk Sea[3]	38	6	1.2	2	–	–	1	3 (*Bolbosoma,* Anisakidae gen.)
Eumetopias jubatus	California[4]	9	3	0.4	1	1	–	–	1 (*Apophallus*)
	Oregon[5]	9	7	1.3	3	2	–	1	1 (*Apophallus*)
	Gulf of Alaska[6]	67	9	4.2	1	2	1	–	5 (*Diplogonoporus, Anophryocephalus, Apophallus, Phocitrema, Bolbosoma*)
	Bering Sea[6]	7	7	2.6	1	3	1	–	3 (*Diplogonoporus, Anophryocephalus*)
Zalophus californianus	California[4]	14	6	1.6	1	1	1	–	3 (*Apophallus, Stictodora, Uncinaria*)
	Oregon[5]	7	3	0.7	–	–	–	1	2 (*Apophallus, Nanophyetus*)
Arctocephalus philippii	Juan Fernández I.[7]	17	3	1.9	1	1	–	–	1 (*Ogmogaster*)
Arctocephalus pusillus	Namibia[8]	8	3	NA	1	1	–	–	1 (Tetrabothriidae gen.)
Otaria flavescens	Chile[9]	7	3	NA	1	1	–	–	1 (*Ogmogaster*)
	Argentina[10]	56	11	3.1	1	2	2	1	5 (*Ascocotyle, Anisakis, Profilicollis, Andracantha, Uncinaria*)
Arctocephalus australis	Argentina[10]	5	7	2.2	1	2	2	1	1 (Tetrabothriidae gen. sp.)

NA, Not available.
[a] Source: [1]Machida (1969); [2]Delyamure & Skrjabin (1960); [3]Krotov & Delyamure (1952); [4]Dailey & Hill (1970); [5]Stroud (1978); [6]Shults (1986); [7]Sepulveda & Alcaino (1993); [8]Delyamure & Parukhin (1968); [9]George-Nascimento & Carvajal (1981); [10]Present study.

Lauckner, 1985; Nascetti *et al.*, 1986; Aznar *et al.*, 2006; Castinel *et al.*, 2006; Rausch *et al.*, 2010, and references therein). The global occurrence of this predictable group of species in pinnipeds suggests that associations might have been established prior to the splitting of the three major pinniped clades (Hoberg & Adams, 2000); nevertheless, *Uncinaria* is almost exclusively associated with otariids (George-Nascimento *et al.*, 1992). However, the coevolutionary history between these five parasite taxa and otariids may be complex, including independent associations of the parasites with fur seals and sea lions during the expansion to the southern hemisphere (Hoberg & Adams, 2000).

There are additional taxa that appear to have become associated with otariids at a more regional geographical scale. This might be the case of species of *Anophryocephalus*, *Phocitrema* and *Stictodora* in the northern hemisphere, and species of *Ogmogaster* and *Ascocotyle* in the southern hemisphere (see references in table 4). These associations are probably linked to a history of host-switching, with geographical restriction resulting, at least in part, from the temporal limits of the initial colonization event (Hoberg & Adams, 2000; see also Hoberg, 1995, for a detailed account of the history of *Anophryocephalus* spp.). Finally, there is another group of species whose consideration as actual community members is more doubtful. As many as six parasite taxa found in this study have cetaceans, marine birds and even fish as definitive hosts, pinnipeds being apparently unsuitable hosts for these taxa. This might also be the case at least for species of *Anisakis*, Tetrabothriidae, *Bolbosoma* and *Nanophyetus* reported in other otariids (table 4).

The exchange of parasites species is not particularly surprising in hosts that belong to the same trophic level, because many infective stages of parasites can end up in the 'wrong' hosts (Hoberg, 1987, 1996; Hoberg & Adams, 2000; Raga *et al.*, 2009). This process is apparent in guilds of hosts with close phylogenetic affiliation; for instance, Antarctic pinnipeds share several species of *Corynosoma*, but not all species are able to mature in all pinniped species (Zdzitowiecki, 1991). The point is, however, the extent to which species that do not reproduce in a given host can be qualified as members of its helminth community or assemblage with regard to taxonomic composition or diversity (e.g. species richness) of the assemblage, or the potential for interspecific interactions. For instance, the helminth component community of the South American sea lion is close to the upper limit of values reported for otariids worldwide (table 4). However, this does not result just from an artefact due to a high sampling effort, but also from the inclusion of parasites for which sea lions are putative non-hosts. Obviously, the category 'non-host' is based on the assumption that the absence of sexually mature worms is related to their inability to reproduce in sea lions and/ or fur seals, rather than to the fact that these infections are recent (Mateu *et al.*, 2011; Aznar *et al.*, 2012). This assumption appears to be reasonably supported in parasite taxa that are typical in other definitive hosts, i.e. *Andracantha* sp. and *P. chasmagnathi* from birds, *C. cetaceum* and *Anisakis* sp. from cetaceans. However, the caveat remains that larger host sample sizes collected over longer time frames could be necessary to confirm categorization of sea lions and fur seals as 'non-hosts' for specific parasites.

Omitting the parasite taxa for which sea lion and fur seals are putative non-hosts can have a significant impact on the estimation of species richness, particularly at component community level, and can lead to more accurate comparisons among otariid species (table 4). Unfortunately, information about the reproductive status of helminths is frequently lacking from parasitological surveys of otariids, or it is merely assumed that any parasite found in a host is part of their helminth fauna (see references in table 4). However, data from our study highlight the quantitative difference of including or excluding parasites obtained from non-hosts (see Aznar *et al.*, 2012). We urge researchers to always provide appropriate information on maturity status of the parasites, if they are to be informative for parascript studies (e.g. Hoberg & Adams, 2000) or meta-analyses (e.g. Poulin, 1995; Lindenfors *et al.*, 2007).

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