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Transmission of *Corynosoma australe* (Acanthocephala: Polymorphidae) from fishes to South American sea lions *Otaria flavescens* in Patagonia, Argentina

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Abstract

Acanthocephalans display a two-host life cycle that involves arthropods as intermediate hosts and vertebrates as definitive hosts. Some species also use paratenic hosts to bridge the trophic gap between both obligatory hosts. However, the relative role of these paratenic hosts in the transmission to definitive hosts has seldom been assessed quantitatively. We report on infection patterns of cystacanths of *Corynosoma australe* Johnston, 1937 in 20 common teleost species and the Argentine shortfin squid *Illex argentinus* (Castellanos) from the Patagonian shelf of Argentina. We also explore the role of different fish species in the transmission of *C. australe* to the most important definitive host in the area, i.e. the South American sea lion *Otaria flavescens* Shaw. Cystacanths of *C. australe* were found in all host species except *Heliconus lahillei* Norman, *Merluccius hubbsi* Marini and *I. argentinus*. In eight fish species, the prevalence of *C. australe* was > 50% and mean intensity > 4, i.e. *Acanthistius patachonicus* (Jenyns), *Nemadactylus bergi* (Norman), *Paralichthys isosceles* Jordan, *Percophis brasiliensis* Quoy & Gaimard, *Prionotus nudigula* Ginsburg, *Scomber colias* Gmelin, *Raneya brasiliensis* (Kaup) and *Xystreurys rasile* (Jordan). Two surveys on the trophic ecology of South American sea lions in the study area consistently found a generalist diet dominated by *M. hubbsi*, and data on the frequency of occurrence and number of other fish and cephalopod species in stomach contents strongly suggest that only *R. brasiliensis* may play a prominent role in the transmission of *C. australe*. This result raises interesting questions on the costs of paratenicity.

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Introduction

Acanthocephalans display a two-host life cycle that involves arthropods as intermediate hosts and vertebrates as definitive hosts (Kennedy 2006). Some acanthocephalans also use paratenic hosts (usually teleosts, reptiles or small mammals) as complementary pathways to bridge the trophic gap between the arthropods and the vertebrate definitive hosts (Schmidt 1985). After being recruited into the paratenic host, cystacanths (the infective larval stage) pass from the intestinal wall to extra-intestinal sites, e.g. mesenteries, where they are encapsulated (Kennedy 2006; Taraschewski 2000).

Paratenic transmission seems to occur in 10–20% of the more than 1298 acanthocephalan species described (Parker et al. 2009; Amin 2013). However, little is known about the specific identity of paratenic hosts for most acanthocephalan species (Kennedy 2006). Available evidence suggests that

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paratenicity can be facultative in many cases (Schmidt 1985; Taraschewski 2000), but for species that reproduce in carnivorous mammals or birds (e.g. species of *Corynosoma* Lühe, 1904, *Centrorhynchus* Lühe, 1911 or *Oncicola* Travassos, 1916), transmission often depends on paratenic hosts to reach the definitive host (Taraschewski 2000).

Much of the research on acanthocephalans that use paratenic hosts has been carried out with species of *Corynosoma*, a group of cosmopolitan marine acanthocephalans that use pinnipeds as primary definitive hosts and, to a lesser extent, cetaceans, aquatic birds, sea otters and semi-aquatic rats (Aznar et al. 2006, 2012; Hernández-Orts et al. 2017 and references therein). The complete life cycle is relatively well-known only for few species of *Corynosoma*, and it involves benthic amphipods as intermediate hosts (e.g. Hoberg 1986; Sinisalo and Valtonen 2003) and a wide array of fish as potential paratenic hosts (e.g. Valtonen 1983; Laskowski and Zdzitowiecki 2005).

Studies on cystacanths of *Corynosoma* spp. in fish have provided valuable information about species records (e.g. Laskowski and Zdzitowiecki 2005), taxonomic issues (e.g. Sardella et al. 2005), host–parasite interactions (e.g. Skorobrechova and Nikishin 2011), development (e.g. Hernández-Orts et al. 2012) and ecology (e.g. Valtonen 1983; Sinisalo and Valtonen 2003). However, there is little quantitative research on the relative role of several paratenic fish hosts from a local community in the transmission to definitive hosts (Valtonen 1983). To assess such relative role in transmission, quantitative data on both prey composition in the definitive hosts and infection levels in both prey and non-prey fish hosts are required.

In Patagonia, Argentina, *Corynosoma australe* Johnston, 1937 is a common acanthocephalan that reproduces in the intestine of the South American sea lion *Otaria flavescens* (Shaw) and the South American fur seal *Arctocephalus australis* (Zimmermann) (Hernández-Orts et al. 2013). Gravid females of *C. australe* were recently found also in the intestine of the Magellanic penguin *Spheniscus magellanicus* (Forster) from Brazil (Hernández-Orts et al. 2017), but the parasite is generally unable to reproduce in non-pinniped predators such as elasmobranchs (Knoff et al. 2001), fish-eating birds (Hoberg and Ryan 1989) or cetaceans (Aznar et al. 2012). *Corynosoma australe* is known to use marine teleosts as paratenic hosts, and cystacanths have been commonly reported in many marine teleosts collected off the coast of Argentina (e.g. Timi et al. 2011; Vales et al. 2011; Soares et al. 2018 and references therein). However, to our knowledge, there have been not attempt to evaluate the role of these fish species in the transmission of *C. australe* to definitive hosts. In this study, we firstly report on infection parameters of *C. australe* in one species of cephalopod and 20 common teleost species inhabiting the Patagonian shelf of Argentina. Then, we use previous dietary data in the same area from one of the main definitive hosts, the South American sea lion (see Koen-Alonso et al. 2000; Romero et al. 2011), to investigate the role of different fish species in the transmission of *C. australe*.

Material and methods

Sample collection

A total of 27 Argentine shortfin squids *Illex argentinus* (Castellanos) and 542 individuals of 20 species of fish were examined (Table 1). Squids and fishes were caught by commercial bottom trawling vessels during 2006–2007 in two areas of the Patagonian shelf of Argentina: north (42° 45′–42° 59′ S, 61° 09′–62° 58′ W) and central Patagonia (47° 00′–47° 19′ S, 61° 59′–64° 25′ W). Hosts were selected based on their abundance in the sampling areas (Bezzi et al. 2000) and according to their body size, i.e. fish whose size was within the range of those reported in the diet of sea lions from the study area (Koen-Alonso et al. 2000; Marine Mammal Laboratory, CESIMAR – CCT CONICET – CENPAT, unpublished data). Collected specimens were kept on ice on board and, after arrival to the laboratory, were identified following Brunetti et al. (1999) for squids and Menni et al. (1984) for fishes. Scientific names for fish species were validated following Froese and Pauly (2018). Individual hosts were then either examined fresh or were frozen in plastic bags at − 20 °C for later examination. Fresh or thawed specimens were dissected, and internal organs were separated in Petri dishes and examined under a stereomicroscope (up to 40×) to detect encapsulated cystacanths. Worms were placed in physiological saline, removed from their capsule and fixed in 70% ethanol. All the cystacanths were examined using a stereomicroscope (up to 80×) and identified following Sardella et al. (2005).

Infection patterns

Ecological terms follow Bush et al. (1997) and Rózsa et al. (2000). The 95% confidence interval (CI) for prevalence was set with Sterne's exact method (Reiczigel 2003), whereas the 95% CIs for mean abundance and mean intensity were estimated with the bias-corrected and accelerated bootstrap using 20,000 replications (Reiczigel and Rózsa 2005). A preliminary analysis indicated that there were no significant differences in the abundance of cystacanths of *C. australe* between the two sampling localities for any fish species with a sample size ≥ 12 individuals (Mann–Whitney tests, $P > 0.05$). Therefore, infection parameters and statistical analyses were calculated for pooled data.

Table 1 Biological data of the squid and fish species examined for the presence of cystacanths of *Corynosoma australe* from the Patagonian shelf of Argentina. The length of squid (mantle length) and fish (total length) is given in centimetres as the mean ± standard deviation, followed by the range in parentheses

Family	Species	Common name	Number	Length
Cephalopods				
Ommastrephidae	*Illex argentinus* (Castellanos)	Argentine shortfin squid	27	23.4 ± 2.1 (20.2–27.5)
Teleosts				
Bramidae	*Brama brama* (Bonnaterre)	Atlantic pomfret	2	60.5 ± 2.1 (59.0–62.0)
Bovichtidae	*Cottoperca gobio* (Günther)	Channel bull blenny	8	30.2 ± 9.3 (22.0–52.0)
Centrolophidae	*Seriolella porosa* Guichenot	Choicy ruff	34	33.0 ± 5.6 (22.7–42.7)
Cheilodactylidae	*Nemadactylus bergi* (Norman)	Castaneta	32	25.6 ± 5.5 (11.4–34.6)
Congiopodidae	*Congiopodus peruvianus* (Cuvier)	Horsefish	15	23.9 ± 2.0 (21.0–28.0)
Merlucciidae	*Macruronus magellanicus* Lönnberg	Patagonian grenadier	3	56.7 ± 23.0 (40.1–83.0)
	Merluccius hubbsi Marini	Argentine hake	79	28.1 ± 4.2 (16.5–34.2)
Mullidae	*Mullus argentinae* Hubbs & Marini	Argentine goatfish	2	20.7 ± 0.4 (20.4–21.0)
Nototheniidae	*Patagonotothen ramsayi* (Regan)	Longtail southern cod	84	24.9 ± 3.5 (14.7–31.7)
Ophidiidae	*Genypterus blacodes* (Forster)	Pink cusk-eel	44	39.7 ± 9.4 (24.7–58.5)
	Raneya brasiliensis (Kaup)	Banded cusk-eel	16	21.2 ± 1.4 (18.2–23.3)
Paralichthyidae	*Paralichthys isosceles* Jordan	Flounder	15	27.2 ± 5.3 (17.9–34.4)
	Xystreurys rasile (Jordan)	Flounder	29	32.8 ± 5.8 (21.9–42.6)
Percophidae	*Percophis brasiliensis* Quoy & Gaimard	Brazilian flathead	8	45.3 ± 4.9 (37.1–51.8)
Pinguipedidae	*Pseudopercis semifasciata* (Cuvier)	Argentinian sandperch	31	26.5 ± 2.7 (22.3–32.2)
Scombridae	*Scomber colias* Gmelin	Atlantic chub mackerel	13	42.7 ± 5.0 (32.5–48.0)
Sebastidae	*Helicolenus lahillei* Norman	Rubio	6	28.8 ± 2.6 (25.9–32.5)
Serranidae	*Acanthistius patachonicus* (Jenyns)	Argentine seabass	16	30.0 ± 2.6 (24.1–34.2)
Stromateidae	*Stromateus brasiliensis* Fowler	Southwest Atlantic butterfish	73	27.5 ± 3.6 (13.7–36.4)
Triglidae	*Prionotus nudigula* Ginsburg	Red searobin	32	23.1 ± 2.8 (16.7–27.8)

Relationship between infection patterns and South American sea lion diet

To explore the relative importance of different fish species in the transmission of *C. australe* to South American sea lions, we used dietary data from sea lions obtained in the study area. Two independent data sets were dealt with, namely, that from Koen-Alonso et al. (2000), including additional data from Koen-Alonso (1999), which was based on stomach contents obtained from 59 sea lions (28 males, 31 females) in northern and central Patagonia between 1982 and 1998, and that from Romero et al. (2011), which was based on 33 sea lions (17 males, 16 females) collected in northern Patagonia (San Matías Gulf) between 2006 and 2009.

We used two parameters to measure the relative importance of each fish species in the diet, which were gathered from the dietary surveys mentioned above:

1) Percentage by number (*%N*), which is calculated as per cent of prey individuals of fish species *i* in the overall sample of individual prey regardless of prey species. This parameter is somehow analogous to a 'relative abundance' of fish species per sea lion and is relevant from a parasitological point of view because each individual fish represents a potential 'packet' of *C. australe* recruits.

2) Index of relative importance (*IRI*) (Hart et al. 2002), which is calculated as $(\%N_i + \%W_i) \times \%FO_i$, where *%N* is as defined above, *%W* is the percentage wet weight of fish species *i* in the overall sample (a measure of biomass) and *FO* is the frequency of occurrence of fish species *i* in the sample of sea lions (analogous to a 'prevalence'). The *IRI* reduces bias in the description of animal dietary data and it is also important as it combines at least two parameters that potentially have a direct positive relationship with the likelihood of infection, i.e. *%N* and *%FO*.

The association between '*%N*' or '*IRI*' and prevalence or mean abundance of *C. australe* were investigated with one-tailed Spearman's correlation tests. Note that precision of the mean abundance is more dependent on sample size because of the aggregated nature of parasite populations (Rózsa et al. 2000). We attempted to gather the most accurate estimation on infection levels of *C. australe*, and therefore, the parasitological data obtained in this study was completed with published information for five fish species, i.e. *Engraulis anchoita* Hubbs & Marini, *Merluccius hubbsi* Marini, *Pinguipes*

brasilianus Cuvier, *Pseudopercis semifasciata* (Cuvier) and *Raneya brasiliensis* (Kaup) from the same area (MacKenzie and Longshaw 1995; Timi and Poulin 2003; Sardella and Timi 2004; Timi et al. 2008; Timi and Lanfranchi 2009; Vales et al. 2011). For these fish species, weighted averages of mean or median abundance per survey based on fish sample size were used.

Statistical software

Confidence intervals for infection parameters and bootstrap replications were calculated with the free software Quantitative Parasitology 3.0 (Reiczigel and Rózsa 2005). Other statistical analyses were carried out with SPSS v19. Statistical significance was set at $p < 0.05$.

Results

Infection patterns

A total of 1367 cystacanths of *C. australe* were collected from 18 of 20 marine fish species examined (Table 2). None of the Argentine shortfin squids *I. argentinus* were infected with acanthocephalans. Eight fish species, i.e. *Acanthistius patachonicus* (Jenyns), *Brama brama* (Bonnaterre), *Congiopodus peruvianus* (Cuvier), *Cottoperca gobio* (Günther), *Genypterus blacodes* (Forster), *Patagonotothen ramsayi* (Regan), *Seriolella porosa* Guichenot and *Stromateus brasiliensis* Fowler represent new host records for *C. australe*. The smallest fish infected was an individual of *P. ramsayi* 14.7 cm long (intensity, 1), whereas the largest was an individual of *Macruronus magellanicus* Lönnberg 83.0 cm long (intensity, 1). A specimen of *Paralichthys isosceles* Jordan 33.2 cm long presented the highest infection level (intensity, 138).

Corynosoma australe showed notable differences in the prevalence and abundance between fish species from Patagonia (Table 2). Prevalence (*P*) values were high (> 75%) in three benthic fishes, i.e. *Raneya brasiliensis* (Kaup) (*P* = 100%), *Paralichthys isosceles* Jordan (*P* = 80.0%) and *Xystreurys rasile* (Jordan) (*P* = 79.3%). The highest mean abundance (MA) values of *C. australe* were also observed in benthic fishes, i.e. *P. isosceles* (MA = 26.5), *A. patachonicus* (MA = 13.9) and *X. rasile* (MA = 6.9). In contrast, *C. peruvianus* and *C. gobio* and *S. brasiliensis* harboured much less cystacanths, and *Helicolenus lahillei* Norman and *Merluccius hubbsi* Marini were uninfected (Table 2). The eight fish species for which the prevalence of *C. australe* was > 50%, and mean intensity > 3 (Table 2) accounted for 90.7% of total number of worms found in the sample.

In six of the 14 fish species with $n \geq 10$, there was a significant positive correlation between the abundance of

cystacanths of *C. australe* and host body size: *A. patachonicus* (Spearman rank correlation: $r_s = 0.668$, $n = 16$, one-tailed $p = 0.005$), *G. blacodes* ($r_s = 0.558$, $n = 44$, one-tailed $p < 0.001$), *Nemadactylus bergi* (Norman) ($r_s = 0.609$, $n = 32$, one-tailed $p < 0.001$), *P. isosceles* ($r_s = 0.817$, $n = 15$, one-tailed $p < 0.001$), *P. ramsayi* ($r_s = 0.259$, $n = 84$, one-tailed $p = 0.018$) and *P. semifasciata* ($r_s = 0.381$, $n = 31$, one-tailed $p = 0.034$).

Relationship between infection patterns and sea lion diet

In the studies of Koen-Alonso et al. (2000) and Romero et al. (2011), *M. hubbsi* was, by far, the most important prey of South American sea lions, in terms of number and biomass (%IRI were 39.7% and 44.4% in each study, respectively), even including non-fish prey such as cephalopods. However, infections of *C. australe* in *M. hubbsi* were rare in the study area (Fig. 1; Table 2). In the present study, of the eight fish for which the prevalence of *C. australe* was > 50% and mean intensity > 3 (Table 2), two, i.e. *A. patachonicus* and *S. colias*, were not reported as prey of South American sea lions in any survey, and five seldom occurred in stomach contents (%FO < 8%): *N. bergi*, *P. isosceles*, *P. brasiliensis*, *P. nudigula* and *X. rasile* (Koen-Alonso et al. 2000; Romero et al. 2011). However, *R. brasiliensis* was the second fish species in importance in the diet of sea lions (%IRI were 7.3% and 15.1%, respectively in these studies). The most important cephalopod species in the diet of sea lion was *I. argentinus* (%IRI were 13.9% and 4.6%, respectively); however, cystacanths of *C. australe* were not detected in this squid species.

None of the correlations between infection levels of *C. australe* in fish species and the relative importance of each fish in the diet of sea lions was statistically significant. Results using Koen-Alonso's et al. (2000) dietary data set were as follows (all *p* values are one-tailed): %N and prevalence: $r_s = 0.003$, $n = 13$, $p = 0.50$; %N and mean abundance: $r_s = 0.28$, $p = 0.536$; IRI and prevalence: $r_s = -0.094$, $p = 0.62$; IRI and mean abundance: $r_s = -0.171$, $p = 0.712$. Results for Romero's et al. (2011) dietary dataset were as follows: %N and prevalence: $r_s = -0.350$, $n = 9$, $p = 0.82$; %N and mean abundance: $r_s = -0.576$, $p = 0.95$; IRI and prevalence: $r_s = -0.267$, $p = 0.76$; IRI and mean abundance: $r_s = -0.559$, $p = 0.94$.

Discussion

Results from the present study showed that cystacanths of *C. australe* are widely distributed in teleosts from Patagonia and suggest that not all fish species consumed by sea lions are heavily infected with *C. australe*. At least over a period of 27 years (1982–2009), the diet of sea lions was dominated by three fish species, i.e. *E. anchoita*, *R. brasiliensis* and,

Table 2 Infection parameters of cystacanths of *Corynosoma australe* in Argentine shortfin squids *Illex argentinus* and in 20 fish species from the Patagonian shelf of Argentina. The 95% CI was estimated only for fish species with $n \geq 15$

Host	n	Prevalence (%) (95% CI)	Mean abundance (95% CI)	Mean intensity (95% CI)	Range
Cephalopoda					
Illex argentines	27	–	–	–	–
Actinopterygii					
Acanthistius patachonicus	16	75.0 (50.0–90.1)	13.9 (4.8–44.8)	18.6 (6.8–57.2)	1–131
Brama brama	2	50.0	0.5	1	1
Congiopodus peruvianus	15	6.7 (0.4–30.2)	0.1 (0.0–0.2)	1	1
Cottoperca gobio	8	12.5	0.9	7.0	7
Genypterus blacodes	44	45.5 (31.2–60.3)	1.1 (0.7–1.9)	2.4 (1.7–4.0)	1–11
Helicolenus lahillei	6	–	–	–	–
Macruronus magellanicus	3	33.3	0.3	1	1
Merluccius hubbsi	79	–	–	–	–
Mullus argentinae	2	50.0	1.5	3	3
Nemadactylus bergi	32	65.6 (47.3–80.0)	5.0 (3.2–7.7)	7.6 (5.5–11.3)	1–29
Patagonotothen ramsayi	84	22.6 (14.7–32.7)	0.3 (0.2–0.5)	1.4 (1.1–1.8.0)	1–4
Paralichthys isosceles	15	80.0 (53.4–94.3)	26.5 (13.6–53.0)	33.1 (18.3–64.0)	2–138
Percophis brasiliensis	8	75.0	3.5	4.7	1–12
Prionotus nudigula	32	75.0 (57.7–87.9)	3.3 (2.3–5.0)	4.4 (3.3–6.5)	1–18
Pseudopercis semifasciata	31	32.3 (17.2–50.0)	0.4 (0.2–0.6)	1.1 (1–1.3)	1–2
Raneya brasiliensis	16	100 (79.2–100)	4.4 (3.3–5.7)	4.4 (3.3–5.7)	2–9
Scomber colias	13	76.9	4.4	5.5	2–14
Seriolella porosa	34	20.6 (9.9–38.1)	0.8 (0.2–2.7)	4.0 (1.6–10.0)	1–16
Stromateus brasiliensis	73	1.4 (0.1–7.3)	0.0 (0.0–0.04)	1	1
Xystreurys rasile	29	79.3 (60.5–90.6)	6.9 (4.1–15.0)	8.7 (5.3–18.7)	1–67

*CI* confidence interval, *n* number of specimens analysed

especially, *M. hubbsi* (Koen-Alonso et al. 2000; Romero et al. 2011). Two fish species, *E. anchoita* and *M. hubbsi*, are incidental hosts for *C. australe* in the southwestern Atlantic (MacKenzie and Longshaw 1995; Timi and Poulin 2003; present study). Therefore, two key prey for sea lions seems to be of little importance and would hardly contribute in the transmission of *C. australe* in this region. In contrast, the intake of *R. brasiliensis* by sea lions would likely promote a continuous recruitment of *C. australe* (see Vales et al. 2011). Indeed, *R. brasiliensis* could play a primary link in the transmission of *C. australe* throughout the trophic web since it has also been reported as an important prey item in wide array of marine birds and fishes (Gosztonyi et al. 2007), including other pinniped species inhabiting the study area (Vales et al. 2011).

The fact that the bulk of the sea lions' diet is derived from only a few species agrees with previous studies on other pinniped species (Naya et al. 2002). However, sea lions are, above all, opportunistic and broad-spectrum feeders that can shift their food habits depending on prey availability and distribution (Koen-Alonso et al. 2000). Just in the study area alone, 23 fish species and 7 cephalopod species have been reported as prey (Koen-Alonso et al. 2000; Romero et al. 2011). Strong short-term dietary

plasticity has been reported in otariid species in response to changes in prey availability (e.g. Naya et al. 2002). Thus, the ecological ubiquity of *C. australe* in the trophic web would ensure the chances of transmission to sea lions regardless of potential dietary changes (Aznar et al. 2004) and would explain the heavy infections reported in sea lions in the study area (Hernández-Orts et al. 2013).

Our results also showed a significant correlation between the abundance of cystacanths of *C. australe* and the size of at list six species of marine fish. Cystacanths of *Corynosoma* spp. are likely to have long life spans, surviving encapsulated in fish paratenic hosts for several years (Valtonen 1983; Comiskey and Mackenzie 2000). Although larger fish, heavily parasitized, will significantly contribute to the transmission of *C. australe*, there are physical limits to the size of fish that sea lions can consume. In fact, sea lions apparently consume mainly small fish (< 35 cm TL), occasionally medium-sized fish (> 50 cm TL) and rarely large fish (> 65 cm TL) (Koen-Alonso et al. 2000; Marine Mammal Laboratory, CESIMAR – CCT CONICET – CENPAT, unpublished data). Accordingly, most infections in large fish will probably be dead ends in the life cycle of *C. australe*.

Fig. 1 Relationship between infection levels of cystacanths of *Corynosoma australe* obtained in the present study (open symbols) or from other fish parasitological surveys (solid symbols) and percentage by number (*%N*) or index of relative importance (*IRI*) of individual fish species in the diet of South American sea lions *Otaria flavescens*. Dietary data were obtained from Koen-Alonso et al. (2000) (squares) and Romero et al. (2011) (circles)
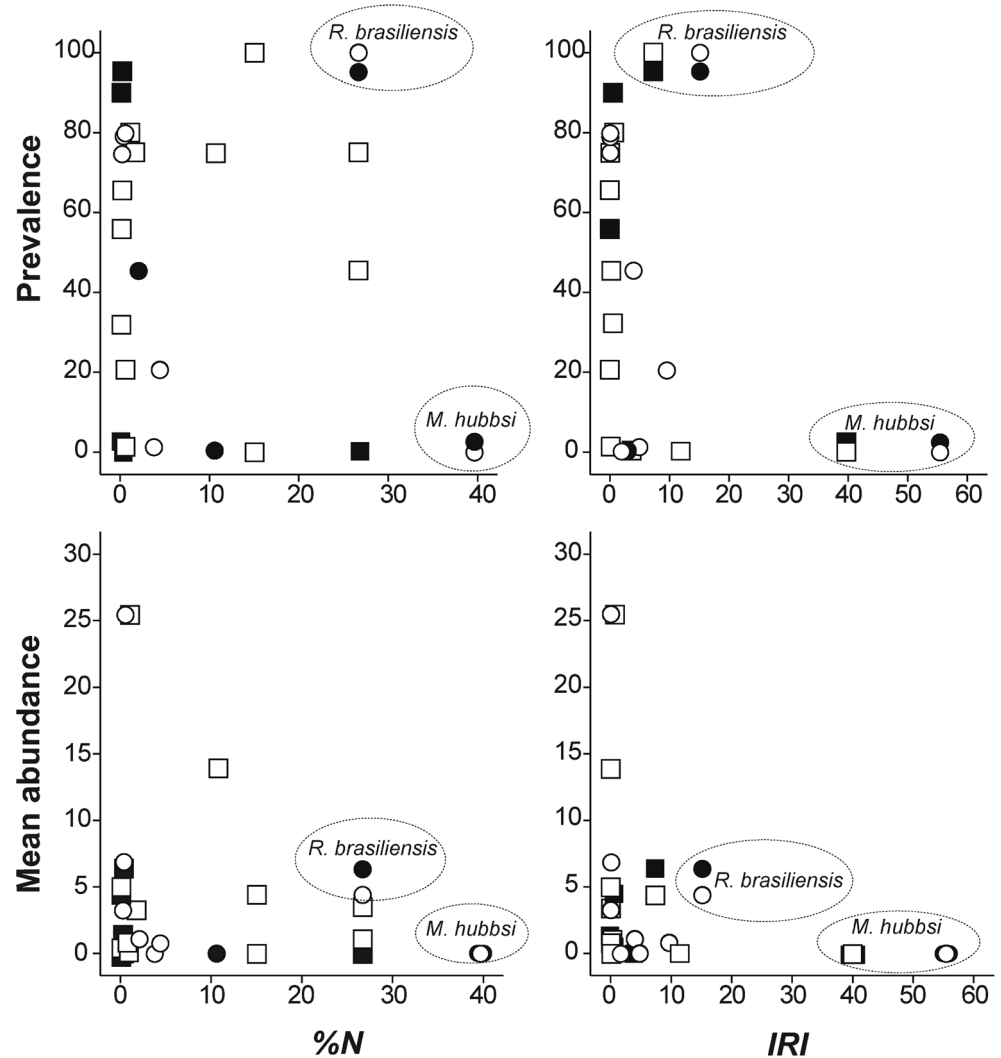
Cephalopods are other important preys of sea lions in Patagonia that were not included in our study except for a single species, i.e. the Argentine shortfin squid *I. argentinus*. However, this species seems to be unsuitable host for *C. australe* (Nigmatullin and Shukhgálter 1990; Sardella et al. 1990; González and Kroeck 2000; present study). Other species, like the red octopus *Enteroctopus megalocyathus* (Gould) and the Patagonian squid *Loligo gahi* (Orbigny), are important preys of sea lions, since they have *%IRI* ranging from 1.2 to 25.6 and 0.2 to 5.7, respectively (Koen-Alonso et al. 2000; Romero et al. 2011). Unfortunately, the helminth fauna of the red octopus and the Patagonian squid remains unknown. Available evidence suggests that acanthocephalan infections in cephalopods are infrequent and usually represent accidental or transitory infections (Pascual and Hochberg 1996).

In Patagonian waters, Magellanic penguins *S. magellanicus* and especially South American fur seals *A. australis* are also readily infected with *C. australe* and act as definitive host for this acanthocephalan (Hernández-Orts et al. 2013; Hernández-

Orts JS unpublished data). However, the diet of fur seals and penguins is dominated by small pelagic fishes (e.g. *M. hubbsi*, *R. brasiliensis*, *E. anchoita* or silverside *Odontesthes* spp.) and cephalopod (e.g. *Illex* spp. and *Loligo* spp.) (Scolaro et al. 1999; Vales et al. 2011; Marine Mammal Laboratory, CESIMAR – CCT CONICET – CENPAT, unpublished data). As noted above, most of these prey species are rarely infected with cystacanths of *C. australe* (MacKenzie and Longshaw 1995; González and Kroeck 2000; Timi and Poulin 2003; Carballo et al. 2011; present study). Future studies, addressing the role of fur seals and penguins as definitive hosts of *C. australe* are necessary to elucidate the transmission dynamics of this acanthocephalan in Patagonia.

The transmission patterns of *C. australe* in the study area underlie the potential trade-off between spreading infections through the trophic web, which would result in many paratenic host species being slightly infected, or infecting specific taxa that are likely consumed by definitive hosts, which would result in more reduced set of species but more heavily infected. In this context, the present study suggests that

significant potential losses of infective stages may occur through many infected fish that are non-prey for sea lions. Although paratenic fish hosts are an integral element in the life cycle of *C. australe*, it would be interesting to quantify losses due to infection of non-prey species and to explore the conditions that allow the long-term stability of transmission rates to definitive hosts.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed. Fish were collected under the collecting permit No. 24/06 and 23/07 issued by the Dirección de fauna y flora Silvestre, Gobierno del Chubut, Argentina, to EAC.

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