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The phylogeny and life cycle of two species of *Profilicollis* (Acanthocephala: Polymorphidae) in marine hosts off the Pacific coast of Chile

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Abstract

Resolving complex life cycles of parasites is a major goal of parasitological research. The aim of this study was to analyse the life cycle of two species of the genus *Profilicollis*, the taxonomy of which is still unstable and life cycles unclear. We extracted individuals of *Profilicollis* from two species of crustaceans (intermediate hosts) and four species of seagulls (definitive hosts) from sandy-shore and estuarine habitats along the south-east Pacific coast of Chile. Mitochondrial DNA analyses showed that two species of *Profilicollis* infected intermediate hosts from segregated habitats: while *P. altmani* larvae infected exclusively molecrabs of the genus *Emerita* from fully marine habitats, *P. antarcticus* larvae infected the crab *Hemigrapsus crenulatus* from estuarine habitats. Moreover, *P. altmani* completed its life cycle in four seagulls, *Chroicocephalus maculipennis*, *Leucopheus pipixcan*, *Larus modestus* and *L. dominicanus*, while *P. antarcticus*, on the other hand, completed its life cycle in the kelp gull *L. dominicanus*. Accordingly, our results show that two congeneric parasites use different and spatially segregated species as intermediate hosts, and both are capable of infecting one species of definitive hosts. As such, our analyses allow us to shed light on a complex interaction network.

Introduction

One of the major goals of parasitological research is to clarify the life cycles of parasites. Most of these parasites have complex life cycles, being trophically transmitted between intermediate and definitive hosts (Thomas *et al.*, 2009; Thieltges *et al.*, 2013). Although the evolution of parasites and that of hosts are not independent of each other, parasites can evolve far more rapidly than hosts (Kochin *et al.*, 2010). As a consequence, parasites can switch hosts in a given environment (Kochin *et al.*, 2010), and a single parasite species can have multiple intermediate and definitive host species (Near, 2002; Mayer *et al.*, 2003; Royal *et al.*, 2004; La Sala & Martorelli, 2007; Steinauer *et al.*, 2007; Kochin *et al.*, 2010; La Sala *et al.*, 2013).

Parasites of the genus *Profilicollis* (Polymorphidae: Acanthocephala) infect marine mammals, shorebirds and waterfowl as definitive hosts, and amphipods, decapods and euphausiids as intermediate hosts (Balboa *et al.*, 2009; García-Varela *et al.*, 2013). In the definitive predator host, the adult female worm develops and produces eggs (acanthors) that are released into the environment through the host faeces. Upon its intake by an arthropod host, the acanthor develops in the haemocoele

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into an acanthellae and then into a cystacanth. Finally, the cystacanth infects the definitive host when the latter predates upon an infected intermediate prey host (Zdzitowiecki, 1985).

Two *Profilicollis* species have been described from the shores of the south-east (SE) Pacific (Amin, 2013) – *P. altmani* (Perry, 1942; = *P. bullocki* Mateo, 1982) and *P. antarcticus* Zdzitowiecki, 1985 – which infect intermediate hosts from segregated habitats with little or no spatial overlap. While *P. altmani* infects the sandy-shore molecrab *Emerita analoga* (Stimpson, 1857) (Goulding & Cohen, 2014; Rodríguez & D'Elía, 2016), *P. antarcticus* infects the estuarine crab *Hemigrapsus crenulatus* (Varunidae; Milne-Edward, 1837) (Haye & Ojeda, 1998; Latham & Poulin, 2002a). However, recent work challenges the identification of the *Profilicollis* species that infects *H. crenulatus*, which has been ascribed either to *P. antarcticus* or another species, namely *P. chasmagnathi* (Balboa *et al.*, 2009). Therefore, it is still unclear which species actually infects the estuarine crab *H. crenulatus*.

In addition to the unclear parasite–intermediate host link described above, the identity of the species of *Profilicollis* infecting the definitive hosts is also unclear. While *P. antarcticus* has been registered only as a parasite of the kelp gull *Larus dominicanus* (Lichtenstein, 1823) (Torres *et al.*, 1991, Latham & Poulin, 2002b), *P. altmani* has been described in that seabird in addition to *Chroicocephalus maculipennis* Lichtenstein, 1823, *Leucopheus pipixcan* (Wagler, 1831), *Podiceps* sp. and *Numenius phaeopus* (Linnaeus, 1758). However, significant morphological differences between *P. altmani* individuals collected from different seabird species have been found (Riquelme *et al.*, 2006), suggesting that these individuals might belong to more than one species.

In order to answer the question of which parasite species (co-)occur in this parasitic system, we can suggest that, due to the differences in the prey item consumption and high mobility of seagulls (Smith, 2007; Yorio *et al.*, 2013), both *Profilicollis* species could be found co-occurring in any of the definite hosts. On the other hand, intermediate host species occur in specific habitats and with little spatial overlap (i.e. molecrabs inhabiting full marine habitats and crabs inhabiting estuaries), which can stimulate specific and strict parasite–intermediate host relationships (Near, 2002; Steinauer *et al.*, 2007). Thus, we might expect parasite co-occurrence in definitive, but not in intermediate, hosts. Testing this hypothesis requires the accurate identification of parasite species. Up to now, the identification of these species has been almost exclusively based on morphological characters. The analysis of this type of evidence has provided valuable contributions to our understanding of parasite–host interactions, but its reliability can be severely compromised by the high morphological similarity among acanthocephalan species (Near *et al.*, 1998, Balboa *et al.*, 2009) and the scarce knowledge of their geographic variation. Therefore, the assessment of molecular data provides an opportunity to identify cryptic species accurately (e.g. Goulding & Cohen, 2014; Rodríguez & D'Elía, 2016), and can well be used to shed light on the potentially complex *Profilicollis* interaction network in SE Pacific shores.

Here, we test whether multiple *Profilicollis* species are able to co-occur in definitive (seagulls) and intermediate (marine and estuarine crabs) hosts in SE Pacific shores. We analysed molecular data in order to identify accurately acanthocephalan specimens collected from intermediate and definitive hosts along 1200 km of the Chilean SE Pacific coast.

Materials and methods

Collection and examination of crab and avian hosts

The study area corresponded to marine and estuarine systems along the SE Pacific coast of Chile. Sandy-shore molecrabs, estuarine crabs and seagulls were captured at six sites located between 29.9 and 39.5°S, spanning 1200 km of the shore. The sandy beaches surveyed were 'Coquimbo' (29.9°S–71.2°W), 'Dichato' (36.4°S–72.9°W), 'Colcura' (37.1°S–73.1°W), 'Calfuco' (39.7°S–73.3°W) and 'Chaihuín' (39.9°S−73.5°W). The estuarine site corresponded to the mouth of the Valdivia River, 'Niebla' (39.8°S–73.4°W).

In the sandy-shore sites, 239 individuals of the molecrab *E. analoga* were captured during 2014 and 2015 in winter and summer seasons. At each site and sampling time, four transects were randomly deployed perpendicularly to the shoreline. Along each transect we placed six sampling stations located *c.* 2 m apart from each other, from the effluent line to the swash line. Plastic corers (0.03 m^2) were buried to a depth of 20 cm and the sand was sieved through a 1-mm-mesh sieve. Crabs were transferred to the laboratory for parasite identification and sorting. In the estuarine site, 30 individuals of *H. crenulatus* were sampled by hand between October 2015 and March 2016 along a 300-m transect on promontory rocks.

A total of 16 seagulls were captured around 40°S on the SE Pacific coast. Specimens were captured in resting areas by means of a 3 × 5 m Whosh net trap installed in the morning and activated after 2 h. After capture, the specimens were sedated with 40 $mg\,kg^{-1}$ of ketamine plus 7 $mg\,kg^{-1}$ of xylazine and transferred to the laboratory. In addition, we analysed nine seagulls found dead during March–April 2015 and summer of 2016 in the sampling region around 40°S. In summary, the analysed seagull sample was as follows: *C. maculipennis* ($n = 8$), *L. dominicanus* ($n = 8$), *L. modestus* ($n = 8$) and *L. pipixcan* ($n = 1$).

Each sampled crustacean was dissected, and the abundance of *Profilicollis* spp. in the haemocoele was determined under a stereomicroscope. Seagulls were euthanized using an overdose of 0.2–1 $ml\,kg^{-1}$ intracardiac thiopental. Afterwards, the birds were necropsied and each gastrointestinal tract was removed and opened in order to sort, identify and count the *Profilicollis* parasite specimens. Parasites were identified on the basis of published morphological characters (e.g. Riquelme *et al.*, 2006; Balboa *et al.*, 2009). A total of 749 *Profilicollis* specimens were extracted from the different hosts (see table 1) and were stored in 95% ethanol for subsequent DNA extraction. Prevalence and intensity of infection in each host species were calculated according to Bush *et al.* (1997).

Molecular and phylogenetic analyses

Genetic analyses were based on a fragment of 578 bp of the mitochondrial cytochrome oxidase I (COI) gene.

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Table 1. The prevalence (%), mean intensity (MI), range and number of sequences analysed (NS) of two species of *Profilicollis* in intermediate and definitive hosts from eight sites along the SE Pacific coast of Chile; *N* = number of hosts examined.

Host type	Location	*N*	%	MI	Range	NS
Intermediate						
E. analoga	Coquimbo	15	80.0	1.2	1–2	4
	Dichato	54	83.3	4.8	1–5	4
	Colcura	25	52.0	2.5	1–6	4
	Calfuco	71	66.2	2.2	1–9	10
	Chaihuín	75	62.1	2.1	1–7	10
H. crenulatus	Niebla	30	13.3	1.3	1–2	1
Definitive						
L. dominicanus	Pilolcura	3	33.3	9	9	6
	Curiñanco	5	40.0	37	1–73	5
L. modestus	Curiñanco	5	60.0	29	16–52	5
	Calfuco	3	66.7	19	12–26	4
C. maculipennis	Curiñanco	6	66.7	36.3	4–84	5
	Calfuco	2	100.0	4.5	4–5	5
L. pipixcan	Curiñanco	1	100	11	11	1

Sequences were gathered from 64 individuals of *Profilicollis* collected from both crustacean (*E. analoga*: 32; *H. crenulatus*: 1) and the four seagull species (*C. maculipennis*: 10; *L. dominicanus*: 11; *L. modestus*: 9; *L. pipixcan*: 1). Total DNA was isolated using a commercial extraction kit and the COI gene was amplified using the protocol and primers detailed by Folmer *et al*. (1994); amplicons were sequenced using an external sequencing service (Macrogen Inc., Seoul, South Korea). DNA sequences were edited using Codon-Code (Codon-Code, Dedham, Massachusetts, USA) and deposited in GenBank (KX646746–KX646796 and KX702242–KX702254). These sequences were integrated in a matrix, with one sequence for each haplotypic class of *Profilicollis* found by Goulding & Cohen (2014) and Rodríguez & D'Elía (2016); these sequences (*P. altmani*: 74; *P. antarcticus*: 3; *P. botulus*: 1) were downloaded from GenBank. Therefore, a total of 142 sequences of *Profilicollis* were analysed. Sequences of *Polymorphus minutus* and *Arhythmorhynchus brevis*, which are closely related to *Profilicollis* (García-Varela *et al*., 2013), were used to form the outgroups.

Sequences were aligned in Clustal as implemented in MEGA 7 (Tamura *et al*., 2013) using default parameter values. Observed genetic distances (*p*) between haplotype and sample pairs were calculated in MEGA 7. Phylogenetic relationships were inferred via Bayesian analysis (BA) implemented in MrBayes 3.1 (Ronquist & Huelsenbeck, 2003). BA consisted of two independent runs, each with five heated and one cooled Markov chains and the HKY + G model, selected by means of the jModel Test (Darriba *et al*., 2012). All model parameters were estimated in MrBayes. Uniform-interval priors were assumed for all parameters except for base composition and substitution model parameters, for which we assumed a Dirichlet prior. Runs were allowed to proceed for 20 million generations, with trees sampled every 1000 generations per chain. To check for convergence on a stable log-likelihood value, we plotted the log-likelihood values against generation time for each run. The first 25% of the trees were discarded as burn-in and the remaining trees were used to compute a 50% majority rule consensus tree and to obtain posterior probability (PP) estimates for each clade.

Results

The phylogenetic analysis indicated that haplotypes of *Profilicollis* fell into two main, highly supported clades (fig. 1) that, according to Goulding & Cohen (2014) and Rodríguez & D'Elía (2016), correspond to *P. altmani* (PP = 1) and *P. antarcticus* (PP = 1), respectively. As in Rodríguez & D'Elía (2016), the genus *Profilicollis* is not a monophyletic clade with the current taxonomic assignment of these outgroups. All sequences of cystacanths found in the marine molecrab *E. analoga* and all-but-one haplotypes of adult worms found in specimens of the four surveyed seagulls fell into the clade of *P. altmani*. On the other hand, all haplotypes of *Profilicollis* specimens from the estuarine crab *H. crenulatus* and one haplotype of an adult *Profilicollis* from a *L. dominicanus* seagull fell in the clade of *P. antarcticus*. The two sequences of cystacanths from *H. crenulatus* that were too short to be included in the phylogenetic analysis were indistinguishable from those of the *P. antarcticus* clade. Finally, the individuals of both species of *Profilicollis* found in *L. dominicanus* were extracted from two distinct gull individuals.

The sample of *P. altmani* showed a low level of genetic variation. On average, the analysed haplotypes of this species differed by 1% (range 0–2.5%). The haplotypes of *P. altmani* (of cystacanths and worms) from a given host species did not form a monophyletic group. In addition, the sample of *P. altmani* did not show a discernible geographic structure (see also Goulding & Cohen, 2014). For instance, a haplotype was found in worms extracted from three seagulls, namely *C. maculipennis* (02 in fig. 1), *L. modestus* (17) and *L. dominicanus* (06, 12), as well as from cystacanths found in *E. analoga* from Dichato (04) and Calfuco (14; SE Pacific coast; this study) and Bodega beach (KF835313; NE Pacific coast; Goulding & Cohen, 2014). Similarly, another haplotype was found in worms from *C. maculipennis* (04), *L. modestus* (05) and *L. dominicanus* (07). This haplotype was also found in cystacanths of *E. analoga* from Coquimbo (08), Colcura (01–03), Chaihuín (08) and Calfuco (15–17; SE Pacific coast; this study), in addition to San Francisco (KF835297; NE Pacific; Goulding & Cohen, 2014). In contrast, the most divergent haplotypes of *P. altmani* were found in individuals of *E. talpoidea* from North Carolina (KF835307; Goulding & Cohen, 2014) and a worm of *L. dominicanus* (01) from the SE Pacific (this study).

The clade of *P. antarcticus* was strongly supported (PP = 1) and showed low genetic variation (average = 0.3%, range 0–0.7%). Haplotypes from cystacanths found in the estuarine crab *H. crenulatus* and from mature worms found in *L. dominicanus* fell into this clade. *Profilicollis antarcticus* did not show geographic structure; a haplotype was obtained from a cystacanth found in *H. crenulatus* from Niebla (05; this study) and Lenga (JX442197; García-Varela *et al*., 2013). The observed genetic *p*-distance between the clades of *P. altmani* and *P. antarcticus* was 25%.

Prevalence and intensity of infection of *P. altmani* and *P. antarcticus* in their different hosts varied among sites (table 1). Prevalence of *P. altmani* in *E. analoga* fluctuated between 52 and 83.3% across sites. The intensity of the

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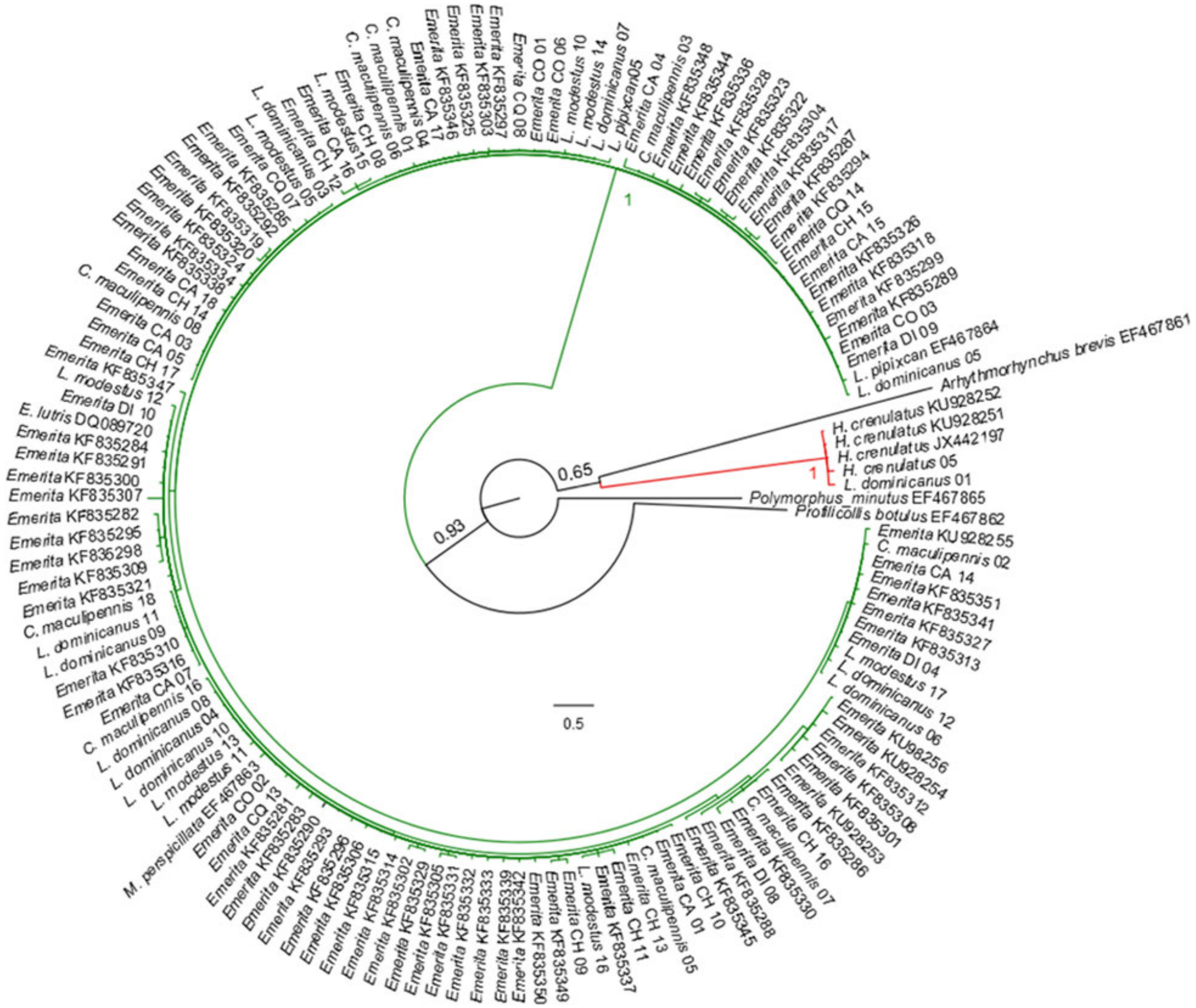

Fig. 1. Genealogical relationships of haplotypes of the COI gene of *Profilicollis altmani* (green) and *P. antarcticus* (red), as a result of Bayesian analysis. Support values correspond to posterior probability (only those for species and relationships among species are shown). GenBank accession numbers and host species are given at terminal labels. Sampling sites are indicated as CA = Calfuco, CH = Chaihuin, CO = Colcura, CQ = Coquimbo and DI = Dichato. Specimen numbers are also provided.

infection was similar between sites (between *c.* 1 and 3 parasites per host). Dichato did not conform to this pattern of low intensity of infection, showing *c.* 5 parasites per host. *Profilicollis antarcticus* had low prevalence in the *H. crenulatus* population, but it had an intensity of infection that was similar to that of *P. altmani* in molecrabs. Regarding the definitive hosts, prevalence and intensity of infection of both parasites were high in all seagull species (table 1). Infected seagulls showed a high degree of intestinal damage, with intestinal perforations mainly in the last two-thirds of the intestine.

Discussion

The results of this study suggest that cystacanths and adult worms sampled from crustaceans and seagulls along SE Pacific shores belong to two species of *Profilicollis*, *P. altmani* and *P. antarcticus*. Also, our results indicate that these two parasite species can both infect the same definitive host species from different intermediate host species. However, as these two species were found in different individual hosts, it is undetermined whether both species can co-occur in the same individual host or if competitive exclusion occurs, as has been described for some acanthocephalan species (Cezilly *et al.*, 2000; Dezfuli *et al.*, 2001; Sures, 2002). Juvenile *P. altmani* infected the sandy-shore molecrab *E. analoga* and the adult infected the seagulls *L. dominicanus*, *C. maculipennis*, *L. modestus* and *L. pipixcan*. Juvenile *P. antarcticus*, on the other hand, infected the estuarine crab *H. crenulatus* and the adult infected only the seagull *L. dominicanus*. Therefore, both species of *Profilicollis* co-occurred in only

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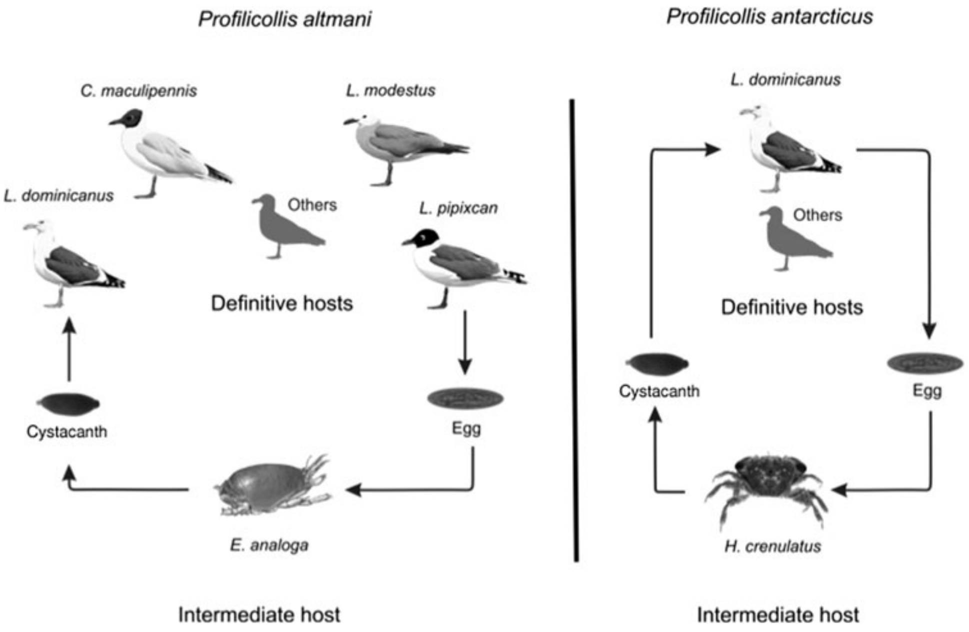

Fig. 2. Life cycle of *Profilicollis altmani* and *P. antarcticus* off the Chilean Pacific coasts. 'Others' are unknown definitive hosts.

one of the four definitive host species (fig. 2). Despite these differences in occurrence, both parasite species shared low levels of within-species haplotype variability. The present discussion therefore considers the influence of environmental variables on a specific host–parasite relationship. The role of host traits, such as foraging behaviour, diet selectivity and mobility, as determinants of predator–prey relationship and parasitosis, is also emphasized.

We observed that *P. altmani* infected only *E. analoga*, while *P. antarcticus* infected only *H. crenulatus* as intermediate hosts. These results are well in line with previous work showing a high fidelity of *P. altmani* to molecrabs on the SE Pacific shore (García-Varela *et al.*, 2013) and elsewhere (Hennessy & Morejohn, 1977; Goulding & Cohen, 2014; Rodríguez & D'Elía, 2016). Similarly, *P. antarcticus* has only been found in one intermediate host species (*H. crenulatus*) and has not been found in other grapsids along the SE Pacific shore. For instance, Leiva *et al.* (2015) described the parasite species composition of 15 decapod species from the central coast of Chile, and no species of *Profilicollis* were recorded. Therefore, alternative intermediate hosts in addition to those described here for *P. altmani* and *P. antarcticus* have not been reported.

Strict parasite–intermediate host relationships are often attributed to specific environmental conditions that vary among host types (Steinauer *et al.*, 2007). The coelomic cavity of invertebrates is exposed to 'external' environmental conditions, suggesting that the conditions in the coelom correlate with those in the environment (Near, 2002). If this holds for our model species, then we could speculate that coelomic environmental conditions of sandy-shore molecrabs and estuarine crabs differ significantly, as both environments differ in terms of water temperature, salinity and wave exposure, among other factors (Garcés-Vargas *et al.*, 2013). Therefore, environmental conditions may limit acanthocephalan species to particular arthropod hosts that are exposed to distinct environmental conditions.

Both parasite species analysed co-occurred in the kelp gull *L. dominicanus*, albeit in different individuals. This result can be a consequence of the generalist foraging behaviour of kelp gulls, which take advantage of the multiple trophic resources available along the coast from both marine and estuarine habitats (Bahamondes & Castilla, 1986; Yorio *et al.*, 2013). Accordingly, kelp gulls present a high diversity of endoparasites, including cestodes, nematodes, trematodes and acanthocephalans (Torres *et al.*, 1991; Riquelme *et al.*, 2006; González-Acuña *et al.*, 2009; Diaz *et al.*, 2011). In contrast, the degree of diet and habitat generalism of the other three seagulls analysed here – *L. modestus*, *L. pipixcan* and *C. maculipennis* – seems to be less clear. For instance, while *L. modestus* tends to specialize on molecrabs as its main foot item (Blokpoel *et al.*, 1992), *L. pipixcan* is a kleptoparasitic species that steals different kinds of food from other seabird species (Khatchikian *et al.*, 2002; pers. obs.). *Chroicocephalus maculipennis* can be found in freshwater marshes and intertidal sandy shores (Khatchikian *et al.*, 2002; Ghys & Favero, 2004; pers. obs.). During migratory periods, the diet of *C. maculipennis* is based mainly on crustaceans, including *E. analoga*, and other sandy-shore invertebrates (Khatchikian *et al.*, 2002; Bruschetti *et al.*, 2009). No *P. antarcticus* has been recorded infecting this species (Torres *et al.*, 1993). However, the low number of studies that analyse this host–parasite interaction biases the odds of finding *P. antarcticus* in *C. maculipennis*. Further field observations are needed to clarify the degree of diet specificity of these seagulls, in order to explain the occurrence patterns of their parasites.

We analysed and corroborated four definitive hosts of *P. altmani* and one of *P. antarcticus*, which raises the

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question of potential additional definitive hosts for these parasites in the study region. For example, along the Californian coast the surf scoter *Melanitta perspicillata* (Anatidae) was identified as a definitive host of *P. altmani* (Hennessy & Marejohn, 1977; Lafferty *et al*., 2013). In contrast, in ducks of the SE Pacific coast no species of *Profilicollis* have been recorded (Muñoz & Olmos, 2008; Hinojosa-Sáez *et al*., 2009). Other studies have mentioned that *Calidris* waders and the sea otter *Enhydra lutris* harbour *P. altmani* parasites (Hennessy & Marejohn, 1977; Margolis *et al*., 1997; Mayer *et al*., 2003; Riquelme *et al*., 2006; Buehler *et al*., 2010). However, these studies do not report the presence in these hosts of sexually mature *Profilicollis* parasites, which suggests that *Calidris* spp. and sea otters are not involved in the parasite life cycle (Mayer *et al*., 2003; Buehler *et al*., 2010). However, and since the SE Pacific coastal vertebrate fauna has been less explored than that of the northern Pacific, we cannot rule out that other bird species can serve as a definitive host of *P. altmani*. Likewise, it is worth noting that there is evidence that humans and domestic animals can be infected by *P. altmani* when eating molecrabs and accidently ingesting cystacanths (Tantaleán *et al*., 2002). Regarding *P. antarcticus*, morphology-based work suggests that *Phalacrocorax atriceps* is an additional definitive host in Chile (Torres *et al*., 1992). Since we did not analyse *P. atriceps* in the present study, we cannot confirm whether it is the same species infecting this host. Therefore, further research on other bird species is needed to determine whether *Profilicollis* spp. (co-)occur in other definitive hosts.

In summary, our molecular analysis of parasites collected from both intermediate and definite hosts along 1200 km of the SE Pacific shore allowed us to shed light on a complex interaction web in which two species of parasite, each infecting one particular intermediate host, co-occurred in the same species of definitive host. Nevertheless, it is still unknown if both species of *Profilicollis* can reside in the same individual or not. Also, both species of *Profilicollis* had low genetic variation and lacked geographical and host-related population structures. In agreement with previous evidence (Goulding & Cohen, 2014), and the fact that they share the same intermediate hosts, haplotypes of both *Profilicollis* spp. found in a given host species did not form a monophyletic group. In addition, the topology found in the phylogenetic analysis indicates that the limits of the genera of Polymorphidae need to be further evaluated. We suggest that environmental filtering results in strict parasite–intermediate host links, while trophic generalism leads to more free-to-vary parasite–definite host links. To test this novel hypothesis and to contrast it to alternative causes related to sampling bias and alternative host species, further field-based observations of diet and habitat specificity are needed. Overall, the results presented here contribute to improving our understanding of ecological and evolutionary mechanisms that allow the co-existence of parasites belonging to complex interaction webs.

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Conflict of interest

None.

Ethical standards

The Chilean authority Servicio Agrícola y Ganadero allowed the capture of seagulls; permit numbers 1412/2015 and 7916/2015.

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