



Variation in helminth infection prevalence, abundance, and co-infection in an intermediate host across a large spatial scale

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ABSTRACT: Parasites are often distributed heterogeneously across host populations, but the controls of this heterogeneity across regional scales often remain unclear. Here, we test the relative importance of natural and anthropogenic environmental factors and biological attributes of host populations on the large-scale variability in infection probability and parasite abundance. We quantified a larval acanthocephalan parasite (*Profilicollis altmani*), as well as the trematode *Maritrema* sp. and the nematode *Proleptus* sp., infection of mole crabs *Emerita analoga* using a hierarchical design at 8 sites spanning 500 km of the south-central shoreline of Chile. At each site, we measured the variables of beach size, morphodynamics, distance to nearest port, distance to tributaries, mole crab density, seagull density, and host body size. Using mixed-effects models, we analysed the associations of acanthocephalan infection probability and parasite abundance in mole crabs as functions of body size and the environmental site-level factors. Models accounted for 20 and 61 % of variation in acanthocephalan infection probability and abundance, respectively, with mole crab body size exclusively accounting for nearly all of the model fits. Also, acanthocephalan abundance decreased with increasing mole crab density, suggesting a possible encounter–dilution effect. Co-infection was strong, with the 2 other larval parasite species correlated positively with acanthocephalan parasites. The low influence of environmental variables on acanthocephalan infection could be because spatial variability in these factors is relatively low or their influences are quick to saturate. Therefore, in this system, parasite infection is apparently more strongly related to the duration of host exposure than spatially variable environmental factors, even across large spatial scales.

KEY WORDS: Likelihood ratio test · Parasite burden · Prevalence · Sandy beaches · Southeastern Pacific

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1. INTRODUCTION

Parasites are ubiquitous members of natural communities. They are generally distributed heterogeneously across space and time (Poulin 1998, Byers et al. 2008, 2016, Johnson & Hoverman 2014), which

has important consequences for host health, host–parasite dynamics, and community structure (Lafferty et al. 2006, Thieltges & Reise 2007, Byers et al. 2008, Mouritsen & Poulin 2010, Rodríguez & Valdivia 2017). In recent decades, interest in the drivers of parasite variability has increased (Koprivnikar &

Redfern 2012, Altman & Byers 2014, Taglioretti et al. 2018). At larger scales, variability would seemingly be high because influential factors have a large scope for variation (Smith 2001, Johnson & Hoverman 2014). However, few studies have assessed the relative importance of abiotic and biotic factors and their effects on parasite infection patterns, especially across large scales (Poulin & Mouritsen 2003, Altman & Byers 2014, Cohen et al. 2016, Gehman et al. 2017). Discerning how and why parasite patterns and their resultant influences change across spatial scales will improve our understanding of community dynamics as well as the development of epidemic and infectious processes.

Small-scale factors can also influence parasites, as strong gradients in physical and biological factors exist at these scales. Examples include microhabitat preferences of host species or desiccation gradients across elevation in the marine intertidal zone (Poulin & Mouritsen 2003, Byers et al. 2015). One of the reasons that biological variables can matter greatly to parasites at smaller spatial scales is that within-population biological attributes, such as host susceptibility (Keogh et al. 2016) and the body size of hosts, are typically important determinants of the infection patterns within populations (Smith 2007, Zambrano & George-Nascimento 2010, Byers et al. 2016). As long as infections are not strongly lethal, infection levels are typically higher in larger host individuals (e.g. Poulin 1998, Zambrano & George-Nascimento 2010). This is because as individuals age and become larger, an increase in cumulative parasite exposure can increase the host's infection probability and infection rate, leading to the higher levels often found among larger host individuals (Anderson & May 1978). For example, within subpopulations of mole crabs *Emerita analoga* Stimpson, 1857, along the southeastern Pacific coast, those composed of large body-sized individuals have higher infection intensity and population-level prevalence of infection compared to subpopulations composed of small individuals (Rodríguez & Valdivia 2017).

Another influential biological variable that varies at small and large scales is the abundance of other host species in a parasite's life cycle. Complex host–parasite systems include intermediate hosts that often accumulate parasites over their lifetime and highly mobile definitive hosts that disperse the parasites over broad spatial scales. For instance, migratory birds can disperse the infective stages of parasites over hundreds and thousands of kilometres (Smith 2007, Goulding & Cohen 2014, Gutiérrez et al. 2017, 2019). In this context, previous studies have shown similar results along the western

Pacific coast. For example, Smith (2007) surveyed seagulls and mole crabs in 2 contrasting seasons in different sandy beaches along the west coast of North America. Her results indicated a significant and positive relation between seagull abundance and the larvae of trematodes and acanthocephalans in one of the sampled seasons. Similarly, Rodríguez & Valdivia (2017) sampled several sites in the southern hemisphere and found that the prevalence of acanthocephalans increased with seagull density, a pattern that was stronger for small mole crabs than for large crabs. These studies show that for parasites with complex life cycles, the abundance of definitive hosts (as vectors of infection) often affects infection patterns (e.g. Latham & Poulin 2003, Smith 2007, Byers et al. 2008). Therefore, changes in bird abundances can affect the exposure of local intermediate hosts to parasite eggs and thus increase between-site heterogeneity in parasitism rates (Huspeni & Lafferty 2004, Fredensborg et al. 2006, Smith 2007, Byers et al. 2016, Rodríguez et al. 2017).

Host size and definitive host abundance often do not explain all of the variability in intermediate host infection patterns, suggesting there are other contributing factors that also influence infection rates (Altman & Byers 2014, Wood et al. 2014). The influence of these other factors can vary at any scale but may be especially pronounced at larger spatial scales which are increasingly likely to incorporate large environmental gradients, for example in temperature, humidity, disturbance, or habitat (Poulin & Mouritsen 2003, Thieltges & Reise 2007, Mouritsen & Poulin 2010). Thus, factors, both biological and physical, differ in their variability across scale, affecting scale-dependent and host demography-dependent patterns in host–parasite interactions. As previously mentioned, several studies have examined acanthocephalan parasitism in mole crabs (Smith 2007, Rodríguez & Valdivia 2017); however, they examined only the relationships of biological factors with mole crab infection and did not include any abiotic or environmental factors nor any examination of co-infection patterns.

The environmental drivers that alter host–parasite interactions, including parasite transmission, host susceptibility, and parasite propagule delivery, are diverse (Koprivnikar & Redfern 2012, Altman & Byers 2014, Byers et al. 2014, Sun et al. 2018). These drivers may act directly on parasites, as well as indirectly, through alteration of host abundance and behaviour (Balboa Figueroa et al. 2019). For example, diverse studies have demonstrated that human activities af-

fect habitat selection by gulls, which are forced to escape from severely impacted sites (Lafferty 2001, Whitney et al. 2007, Meager et al. 2012, Basso et al. 2018). Thus, the factors affecting gull abundance are indirectly influencing their input of parasite eggs (Huspeni & Lafferty 2004). In addition, water flow during high tide is another physical factor that may indirectly affect parasitosis in sandy shores. Wave-exposed sandy beaches are classified according to wave energy, sediment grain size, and sediment abundance (Short 1979, Wright & Short 1984). The combinations of these traits are collectively called morphodynamics. Reflective beaches have steep profiles, usually coarse grain size, and waves that break close to the base of the beach face. In contrast, dissipative beaches have flatter profiles with fine sand and waves that break far seaward of the beach face, dissipating most of their energy before they reach the beach (Short 1979, Wright & Short 1984). This leads to stronger water flows in reflective rather than dissipative beaches. Such differences in water flow and energy can be associated with different residence times of infective seagull faeces, which, in turn, can affect the infection probability of intermediate hosts. Similarly, other physical attributes of the habitat, such as distance from tributaries, and anthropogenic activities, including urban development, farm density, and forest cover, affect host abundances and thus patterns among host populations in coastal environments (Urban 2006, Smith 2007, Byers et al. 2008, Koprivnikar & Redfern 2012, Altman & Byers 2014, Wood et al. 2014, Taglioretti et al. 2018).

In this study, we analysed a complex host–parasite system within coastal sandy shores, in which several seagull species—kelp gull *Larus dominicanus*, brown-head gull *Chroicocephalus maculipennis*, Franklin's gull *Leucophaeus pipixcan*, and grey gull *L. modestus*—have been described as hosts of the adult stage of the acanthocephalan *Profilocollis altmani* Meyer, 1931. As definitive hosts, infected seagulls release acanthocephalan eggs within their faeces on the sandy substrate, which are infective to mole crabs. After the eggs are incidentally ingested by mole crabs, which are the intermediate hosts, the parasites develop into a series of acanthella larval stages, then finally into an infective cystacanth. The life cycle is completed after seagulls consume mole crabs containing cystacanth in the hemocoel (Goulding & Cohen 2014, Rodríguez et al. 2017). Previous studies on mole crabs have shown that parasitism increases with crab body size as well as with the abundance of

definitive hosts (Smith 2007, Zambrano & George-Nascimento 2010); nevertheless, this last relationship has not always been significant (Latham & Poulin 2003, Rodríguez & Valdivia 2017). Thus, we examined large-scale variability in *P. altmani* prevalence and abundance within intermediate host populations at multiple sites spanning 500 km along the shore of south-central Chile. In addition to biological factors, including the density and body size of the intermediate host and the abundance of definitive seagull hosts, we evaluated the influences of other diverse environmental attributes, including beach size, beach morphodynamics, and distance from port and from tributaries. Our analyses therefore considered both individual- (body size) and site-level variables (mole crab density, beach morphodynamics, beach size, seagull density, and the distances to nearest ports and freshwater inputs) influencing *P. altmani* infection.

Mole crabs also serve as an intermediate host for other larval helminth parasite species that reach their adult stage in seabirds (e.g. the trematode *Maritrema* sp., which uses mole crabs as a second intermediate host and a marine snail as a first intermediate host) and elasmobranchs (e.g. the nematode *Proleptus* sp.). Co-occurrence and positive associations among larval parasite species have been detected in mole crabs (Smith 2007, Violante-González et al. 2015, 2016, Bhaduri et al. 2018). Thus, we also examine patterns of co-infection of *P. altmani* with *Maritrema* sp. and *Proleptus* sp.

We predicted that mole crab host body size, definitive host (gull) abundance, and other parasite species would be associated positively with *P. altmani* infection probability and abundance. In addition, beach size, morphodynamics, and distance from tributaries are environmental variables that can directly affect the habitat of both intermediate and definitive hosts and their susceptibility to infection as well as the residence time and persistence of parasite infective stages (eggs) in the environment. A short distance to port could represent a proximate, profitable new feeding habitat for gulls, which in the short term might decrease their abundance at the beach but in the long term could alter their spatial distribution or boost local population size and thus the abundance of *P. altmani* eggs they deposit in proximity to mole crabs on the beaches. Lastly, because at least 3 larval parasite species share the same intermediate host, a positive co-infection pattern among them might result from parasites simply accumulating in older (larger) hosts or also possibly through their joint capitalisation on infected or compromised hosts.

2. MATERIALS AND METHODS

2.1. Study sites and sampling procedure

This study was conducted across 2 regions separated by ca. 500 km in south-central Chile. Both regions belong to the transitional area between the Peruvian and Magellan biogeographic provinces (Camus 2001). In each region, 4 beaches were haphazardly selected and sampled during April 2014. In the northern region (Biobío), the sites were Dichato (36.4°S, 72.9°W), Lengua (36.7°S, 73.1°W), Playa Blanca (37.0°S, 73.1°W), and Colcura (37.1°S, 73.1°W). In the southern region (Los Ríos), the sites were Cheuque (39.3°S, 73.2°W), Curiñanco (39.4°S, 73.2°W), Calfuco (39.7°S, 73.3°W), and Chaihuín (39.9°S, 73.5°W; Fig. 1). We sampled mole crabs at each site during low tide. At each site, we randomly designated 2 sampling patches separated by 5 m. In each patch, we randomly placed a set of 2 parallel 6 m transects that were perpendicular to the shoreline and separated by 2 m. Along each transect, we took 4 cores located ca. 2 m apart from each other starting at the effluent line (i.e. mid-low intertidal zone) and moving toward the swash line (low intertidal zone). Thus, we had a total of 4 cores per transect, 8 cores per patch, and 16 cores per site. The plastic corers (0.03 m²) were inserted to a depth of 20 cm (equating to a volume of 0.006 m³), and the sand was sieved through a 1 mm mesh sieve. Finally, mole crabs were collected from each core sample and transported to the laboratory, where they were frozen. Mole crab density was estimated for each beach as the number of individuals per square metre.

2.2. Dissection and parasite examination

In the laboratory, the mole crabs were defrosted, and the cephalothorax length (mm) and sex of each individual were recorded. Note, however, that sex and cephalothorax length are highly collinear variables because the

mole crab is a protandric hermaphrodite, meaning that all small individuals (<11 mm) are male, while all large individuals (>11 mm) are female (Subramoniam & Gunamalai 2003, Rodríguez et al. 2017). Therefore, cephalothorax length alone was used as an individual-level predictor variable in subsequent analyses. We dissected the body of each crab and placed it underneath a dissecting microscope (4×). We counted all *Profilicollis altmani* cystacanths (i.e. larval stage) from the hemocoel. The number of parasites was enumerated across all mole crabs regardless of infection status (i.e. abundance). For each beach, we calculated the prevalence (percentage of infected hosts) and mean abundance (arithmetic mean of the number of parasites per host examined;

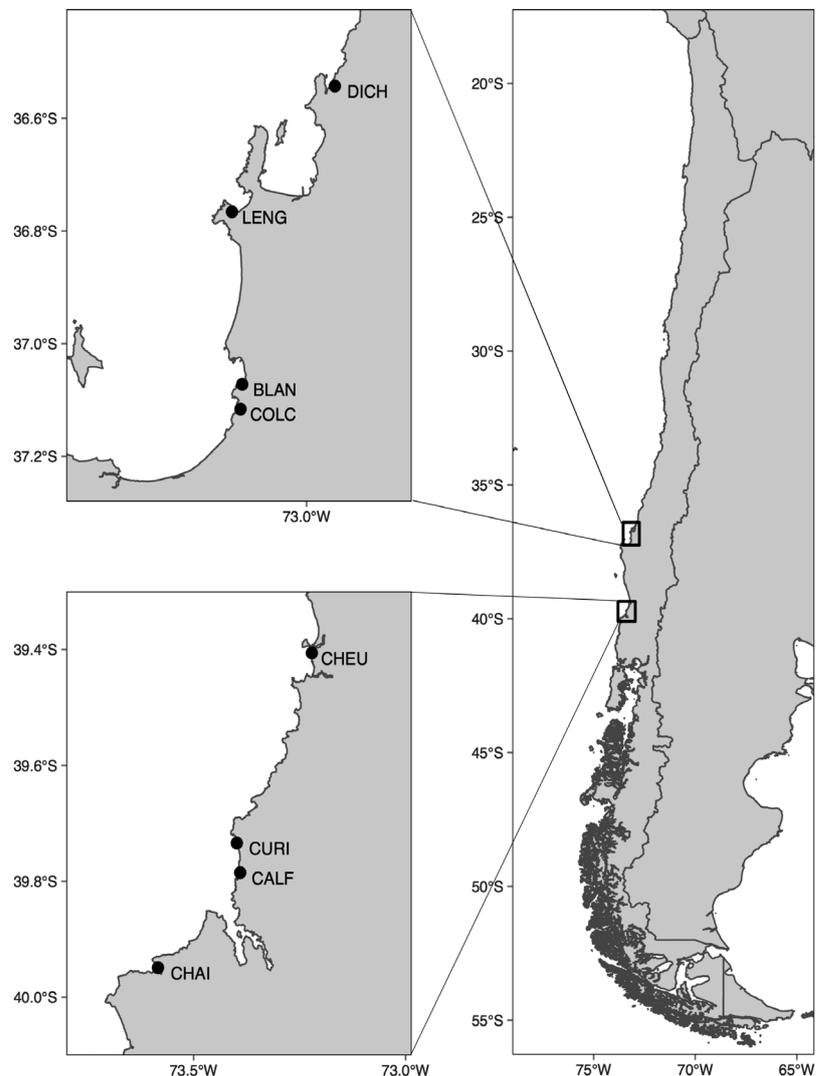


Fig. 1. Sampling sites across both study regions. Northern region (Biobío)—DICH: Dichato; LENG: Lengua; BLAN: Playa Blanca; COLC: Colcura. Southern region (Los Ríos)—CHEU: Cheuque; CURI: Curiñanco; CALF: Calfuco; CHAI: Chaihuín

Bush et al. 1997, Rózsa et al. 2000). The acanthellae (i.e. first larval stage of acanthocephalans) were not included in the study because their presence and abundance were low, and they were hard to detect in the mole crabs. We also recorded the prevalence and mean abundance of *Maritrema* sp. and *Proleptus* sp. for all sites with the exception of Colcura beach, which lacks these data.

2.3. Site-level attributes to predict infection probability and parasite abundance

To explore the potential influence of external biological and environmental factors on parasite infection, in addition to crab body size and crab density mentioned above, we selected 5 site-level biological and physical factors to quantify that previous literature analyses have shown to influence parasite transmission in the field (Skirnisson et al. 2004, Smith 2007, Koprivnikar & Redfern 2012, Altman & Byers 2014, Wood et al. 2014). For the biological variables, first we measured the density of the seagull species which are definitive hosts to *P. altmani* (kelp, brown-head, Franklin's, and grey gulls; Torres et al. 1993, Rodríguez et al. 2017). Immediately upon arrival at each beach and before collecting mole crabs, one observer counted only birds on the ground that were actively feeding along the swash zone from a blind for 45 min. Seagulls that were resting higher up on the beach (supralittoral zone; above the water line) were not included in bird counts, because their faeces would have almost no contact with mole crabs or the water—thus, resting seagulls are unlikely vectors for mole crab infection (McNeil et al. 1992, Byers et al. 2015). We converted the counts of the seagulls into densities by dividing by the linear kilometres of the whole beach. As a categorical physical variable, we determined the morphodynamics for each beach based on previous literature (Jaramillo et al. 1993). The beaches Dichato, Lengua, Curiñanco, and Chaihuín have reflective characteristics, and Blanca, Colcura, Cheuque, and Calfuco were characterised as dissipative beaches. Finally, using a geospatial approach, we calculated 3 environmental variables: distance to nearest port (km), size of beach (km²), and distance to closest freshwater discharge (km). To determine the distance of these variables, we used the GoogleEarthPro program. The variables distance to port and distance to freshwater discharge were measured along the coastline from the sampling point on the beach to the point where the closest port and freshwater input intersected the beach.

2.4. Statistical analyses

Mole crab infection status (i.e. infected or uninfected) and number of *P. altmani* cystacanths per host examined (mean abundance) were separately analysed with generalised linear mixed-effects models (GLMMs). We used 2 types of models: environmental and co-infection models. Environmental models allowed us to analyse the effects of both individual- (body size) and site-level predictors (mole crab density, beach size, beach morphodynamics, seagull density, and the distances to nearest ports and freshwater inputs) on individual-level *P. altmani* infection status and parasite abundance. Because the size and density of an organism can sometimes vary inversely, to expressly examine the independence of these 2 factors, we regressed mole crab mean size and density across the 8 sites. Co-infection models allowed us to analyse exclusively the effects of individual-level variables (body size, *Maritrema* sp., and *Proleptus* sp. infection status and abundances) on infection status and abundance in mole crabs. We performed these co-infection models separately, because Colcura beach lacks data on *Maritrema* sp. and *Proleptus* sp. infection.

Binomial and Poisson error structures were assumed for infection status and parasite abundance models, respectively. As explanatory variables for the environmental model, we used the individual mole crab body size and beach morphodynamics as fixed effects and the biological, physical, and anthropogenic variables of population density of mole crabs, density of seagulls, distance to nearest port and freshwater discharge, and beach size as random effects. Before the analyses, each record of each explanatory variable was centred and standardised by subtracting the variable's mean and dividing the variable's SD. Collinearity among the random variables was assessed by computing a correlation matrix. We verified that variables with Pearson product moment correlations between the predictor variables were less than |0.7|. Only the correlation between the length of the beach and the number of seagulls showed a moderate correlation, -0.686 (Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m681p103_supp.pdf; see also Dormann et al. 2013). Likelihood ratio tests (LRTs) were then used for both the environmental and co-infection models to assess the statistical significance of each explanatory variable in the global model. Specifically, each variable was individually removed one at a time from the global environmental and co-

infection models, and then each reduced model with this one variable removed was compared with the global model by means of a Chi-squared test. For both the parasite abundance and infection status global GLMMs, we calculated a coefficient of determination based on the LRT (R^2_{LR}), which represents the difference in log-likelihood between the global model and null (intercept only) model (Magee 1990, Nagelkerke 1991). The probability of infection and parasite abundance predicted by both global GLMMs were plotted against mole crab body size. These data were adjusted to the mean of every random variable in the model.

All statistical analyses were conducted in R 4.0.1 (R Core Team 2020). Linear mixed-effects models and pseudo- R^2 were computed with lme4 and MuMIn, respectively (Bates et al. 2015, Bartón, 2016).

3. RESULTS

A total of 849 mole crabs were captured across all sites. Overall, mole crab cephalothorax length varied from 4.8 to 29.5 mm. The cephalothorax length of the smallest mole crab infected with *Profilicollis altmani* was 9 mm (Fig. 2). Site-level prevalence of *P. altmani* ranged from 36 to 83% across the 8 sites, where Lenga had the lowest prevalence and Dichato the highest (Table 1). Cheuque beach also had a high prevalence at 74% (Table 1). *P. altmani* total abundance—i.e. the per capita number of parasites in all examined hosts—ranged between 0 and 22 cystacanths per mole crab (Figs. 3 & 4). Mean abundance varied from 0.59 (Lenga) to 3.96 (Dichato) cystacanths per host (Table 1). Similar to prevalence results, the mean abundance at Cheuque beach was high at ~2 cystacanths per host, while the mean abundance for other beaches was ~1 cystacanth per host (Table 1). The abundance of seagulls varied among sites, where Calfuco beach was the only site with the presence of all 4 seagull species. In contrast, at Dichato beach, only *Larus dominicanus* was reported (Table 1). Curiñanco beach harboured the greatest abundance of seagulls (848 ind. km⁻¹), even though it had only 2 seagull species, with *Chroicocephalus maculipennis* being the most abundant. In contrast, Lenga beach harboured the lowest abundance of gulls (14 ind. km⁻¹, Table 1).

The environmental model for *P. altmani* infection probability accounted for 20% of the variation ($R^2 = 0.20$). The LRT showed that mole crab size was the only variable that contributed significantly to the fit

of the global model (Table 2, $p < 0.001$). None of the analysed environmental explanatory variables significantly improved the statistical fit of the model for infection probability (Table 2). The probability of infection increased monotonically with increasing host body size (Fig. 4A). Dichato harboured the smallest infected mole crabs (Figs. 2 & 4). There was no relationship between mean mole crab size and density across the 8 sites ($F = 0.21$, $R^2 = 0.034$, $p = 0.66$).

For *P. altmani* abundance, the environmental model accounted for 61% of the variation ($R^2 = 0.61$). Mole crab size and density significantly contributed to the model fit (Table 2, LRT, $p < 0.0001$). On the other hand, no other site-level explanatory variables in the model accounted for a statistically significant proportion of the spatial variation in parasite abundance (Table 2, LRT, $p > 0.05$). Parasite abundance increased non-linearly with increasing mole crab body size (Fig. 4B). *P. altmani* abundance decreased with increasing mole crab density. Here, Lenga and Curiñanco beaches showed high densities of mole crabs, mainly of middle-sized individuals (12–17 mm), and low parasite abundance. In contrast, Blanca and Cheuque beaches harboured fewer densities of mole crabs and greater parasite abundance (Table 1). Compared to the overall pattern of infection, Dichato exhibited a steeper mole crab size–parasite abundance relationship (Fig. 4B).

In relation to other larval helminths that parasitise mole crabs, the metacercariae of *Maritrema* sp. in general had similar prevalences among beaches (30–36%), except for Dichato beach, which was 44% (Table 1). In turn, the mean abundance showed similar values among all beaches, ranging from 0.39 to 0.56 metacercaria per *Emerita* (Table 1). For the case of the nematode *Proleptus* sp., both its prevalence and mean abundance were far lower than *P. altmani* and *Maritrema* sp. Its lowest prevalence was 3.3% (Chaihuín), and its highest was 18.5% (Dichato); among the other beaches, prevalence was between 4.9 and 8.12% (Table 1). Mean abundance ranged from 0.03 (Chaihuín) to 0.26 (Dichato) nematodes per crab (Table 1).

The co-infection model for *P. altmani* infection probability explained 29% of the variation ($R^2 = 0.29$). All 3 variables—mole crab size and the presence of *Maritrema* sp. and *Proleptus* sp.—contributed significantly to the fit (Table 2, LRT, $p < 0.001$). The probability of infection of *P. altmani* increased with increasing host body size and presence of each parasite species, *Maritrema* sp. and *Proleptus* sp. (Fig. 5A).

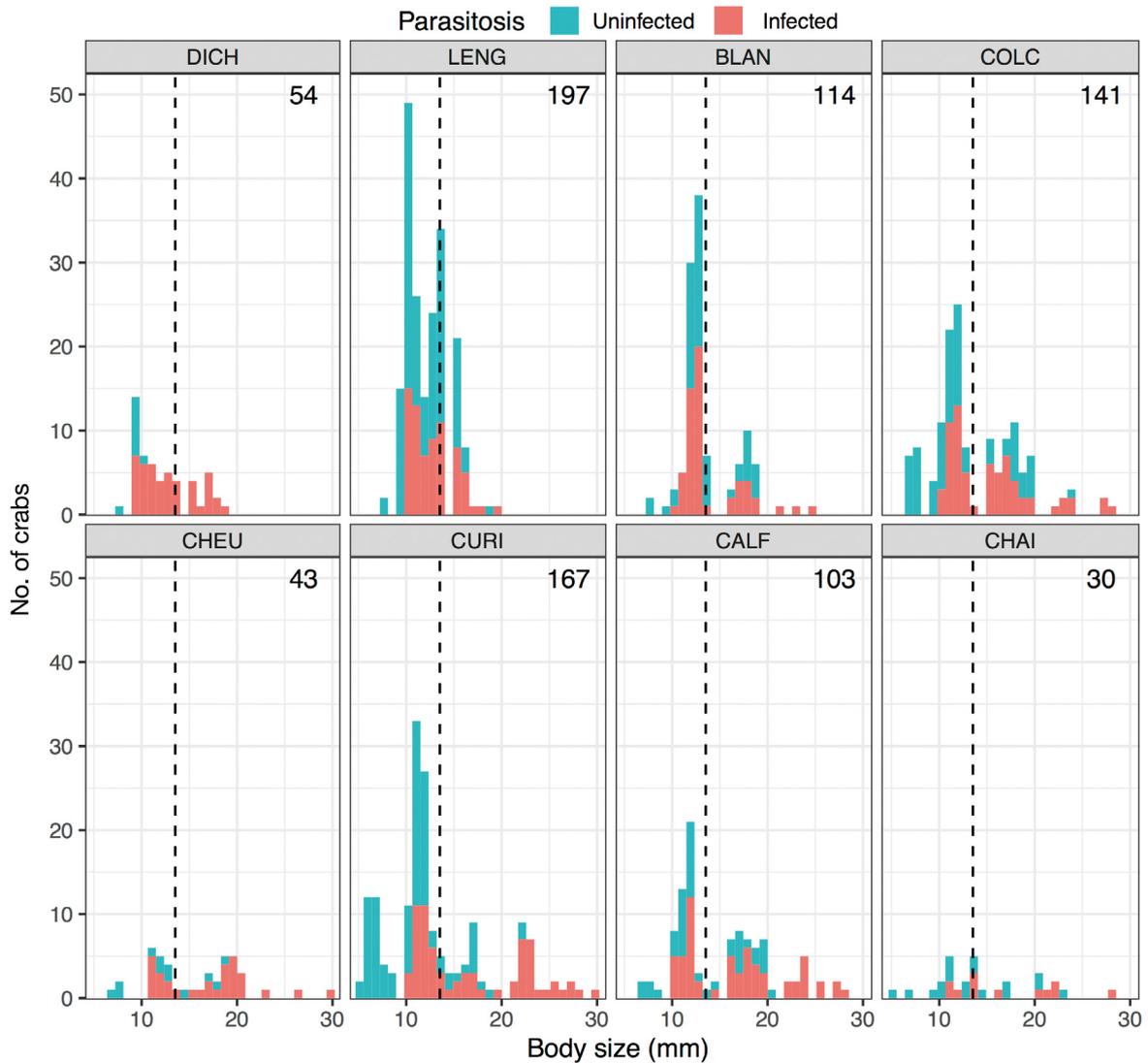


Fig. 2. Occurrence of *Profilicollis altmani* cystacanths in mole crabs sampled at each site (8 beaches) along the south-central Pacific coast of Chile as a function of host body size. Sites as defined in Fig. 1. Vertical dashed lines indicate the mean body size of all hosts sampled at each site. The number at the top right of each panel is the number of individuals sampled at each site

Table 1. Density of 4 species of seagulls (*Larus dominicanus*, *Chroicocephalus maculipennis*, *Leucophaeus pipixcan*, *L. modestus*) along the effluent line and the prevalence and mean abundance of 3 parasite species (*Profilicollis altmani*, *Maritrema* sp., *Proleptus* sp.) that parasitised mole crab at 8 study sites along the south-central Pacific coast of Chile. ND: no data available

Site	Density of gulls (ind. km ⁻¹)				Total gulls	Prevalence (%)			Mean abundance (parasites crab ⁻¹)		
	<i>L. domini-</i> <i>canus</i>	<i>C. maculi-</i> <i>pennis</i>	<i>L. pipix-</i> <i>can</i>	<i>L. modes-</i> <i>tus</i>		<i>P. alt-</i> <i>mani</i>	<i>Mari-</i> <i>trema</i> sp.	<i>Prolep-</i> <i>tus</i> sp.	<i>P. alt-</i> <i>mani</i>	<i>Maritre-</i> <i>ma</i> sp.	<i>Prolep-</i> <i>tus</i> sp.
Dichato	21	0	0	0	21	83.3	44.4	18.51	3.96	0.56	0.26
Lenga	2	12	0	0	14	36.0	30.9	8.12	0.59	0.39	0.10
Blanca	17	268	13	0	298	50.0	35.9	7.01	1.02	0.44	0.09
Colcura	63	0	25	0	88	47.5	ND	ND	1.04	ND	ND
Cheuque	14	86	0	1	101	74.4	37.2	11.6	1.91	0.44	0.14
Curiñanco	135	713	0	0	848	41.9	32.3	7.8	0.82	0.41	0.08
Calfuco	64	432	2	12	510	58.3	32.0	4.9	1.17	0.42	0.06
Chaihuín	3	92	0	0	95	40.0	36.7	3.3	0.77	0.50	0.03

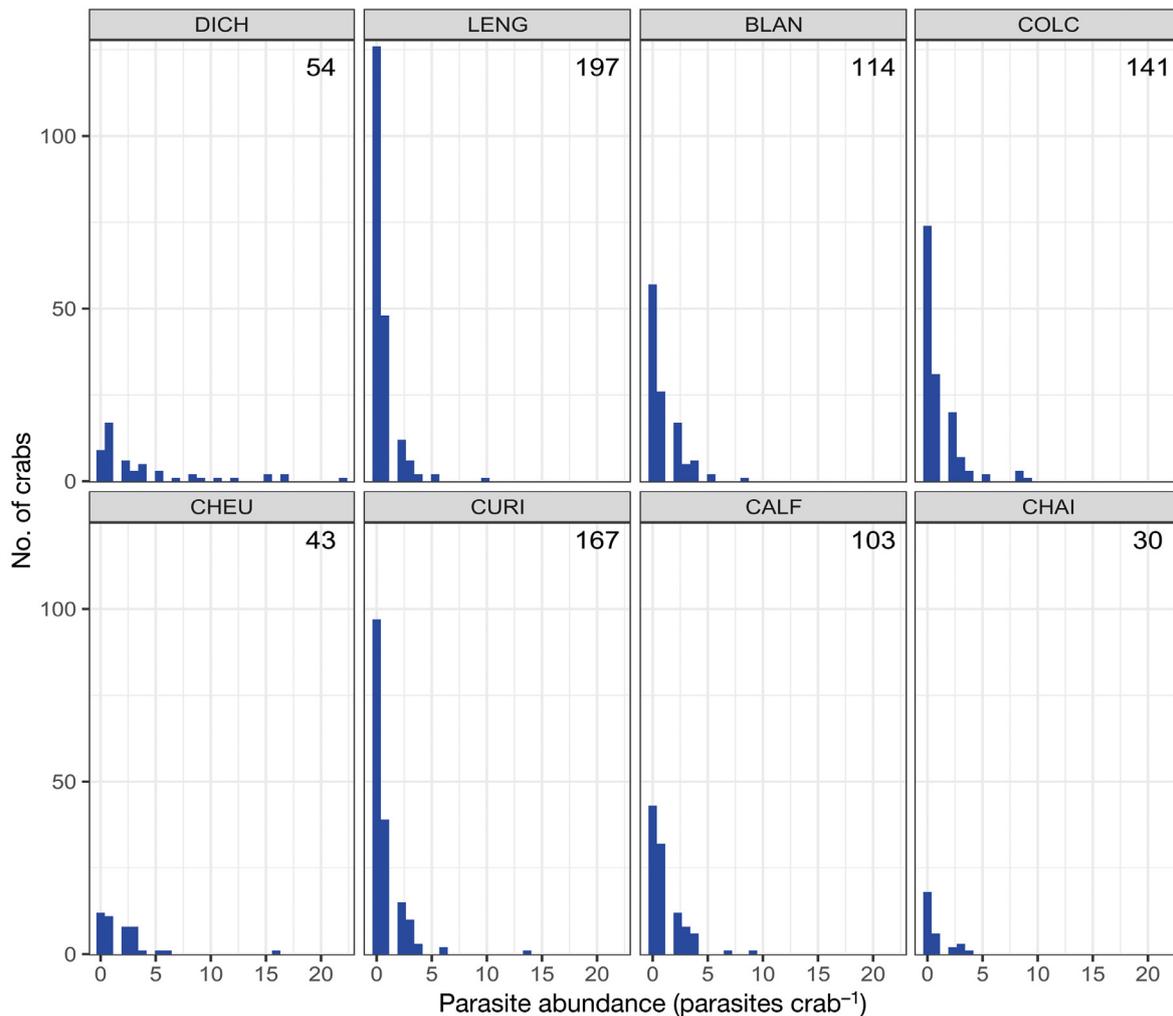


Fig. 3. Abundance of *Profilicollis altmani* cystacanths in mole crabs sampled at each site (8 beaches) along the south-central Pacific coast of Chile. Sites as defined in Fig. 1. The number at the top right of each panel is the number of individuals sampled at each site

The co-infection model for *P. altmani* abundance explained 67% of the variation ($R^2 = 0.67$). The LRT showed that mole crab size and the abundance of *Maritrema* sp. and *Proleptus* sp. significantly improved the statistical fit of the model for *P. altmani* abundance (Table 2, LRT, $p < 0.001$ for each). *P. altmani* abundance increased with increasing mole crab body size and the abundance of both other parasites species, especially *Proleptus* sp. (Fig. 5B).

4. DISCUSSION

Our study reveals a singular strong effect of host body size on *Profilicollis altmani* infection level and a high similarity in interspecific parasite patterns across large spatial scales. *P. altmani* had higher

prevalence and abundance in large crab hosts compared to those of smaller body size, as is commonly reported in many host–parasite systems (Smith 2007, Byers et al. 2008, 2016, Johnson & Hoverman 2014). Also, we found high co-occurrence of the larvae of *P. altmani*, *Maritrema* sp., and *Proleptus* sp. within hosts among all sites studied. In fact, the latter 2 helminth species are new geographical records for all beaches of this study. At the individual level, parasite abundance decreased when the density of mole crabs increased. Our results did not show a significant relationship between mole crab density and mean size, although mole crab populations can at times be dominated by high densities of small individuals (Dugan et al. 1994, Contreras et al. 1999). In our case, the negative effect of density on parasite loads may be caused by an encounter–dilution effect.

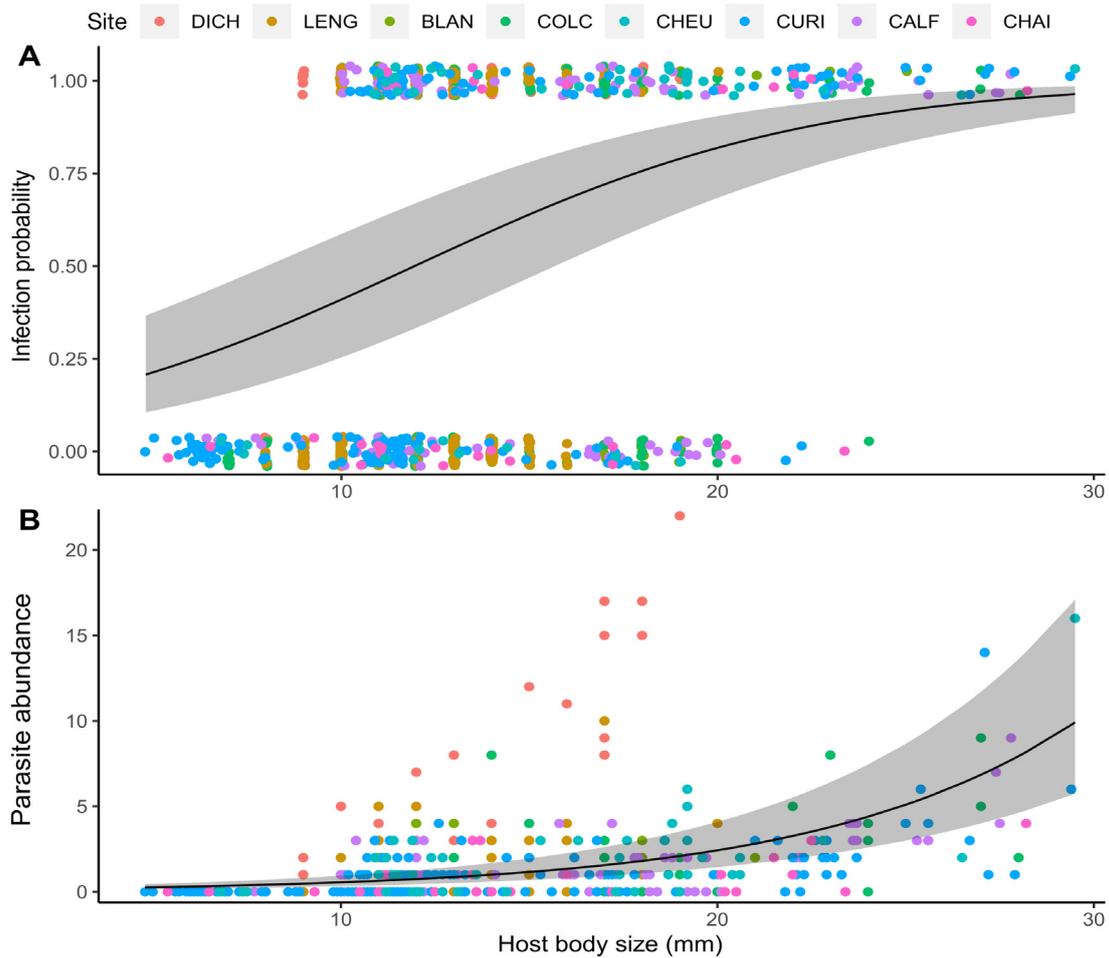


Fig. 4. Effects of mole crab body size on infection with *Profilicollis altmani* cystacanths. Black lines show the mean value (\pm 95% CI) predicted by the global models controlling for 6 site-level variables (Table 2). Predicted values were estimated for the mean of each standardised environmental variable. Each coloured symbol represents the observed *P. altmani* (A) infection status (0 = uninfected, 1 = infected) or (B) abundance (no. of parasites per examined host) of a single mole crab. A small random value was added to 0 and 1 in panel (A) to stagger the points and improve visualisation of site colours. See Fig. 1 for site abbreviations

Even though a dilution effect seems unlikely for parasites with complex life cycles, it has been posited as a logical possibility for certain more mobile stages in the life cycle (Zambrano & George-Nascimento 2010, Buck & Lutterschmidt 2017). Below, we discuss the roles of body size of intermediate hosts, identity and abundance of definitive hosts, and the co-infection of these larval parasite species in driving helminth parasitism along the southeastern Pacific coast.

The most important variable in our models was body size, which showed significant and positive relationships with infection probability and parasite abundance. This relationship was a consistent pattern independent of the distance among sites, which covered almost 500 km of coastline. At all sites, the smallest crab hosts harboured the lowest prevalence and abundance of parasites. This pattern has been

previously observed in other systems involving parasites of the genus *Profilicollis*. For example, on the New Zealand coast, Latham & Poulin (2002, 2003) showed a similar infection pattern in crabs of the families Grapsidae and Ocipodidae. Similarly, the low infection levels in small *P. altmani* individuals had been described in different subpopulations of mole crabs from the southern Pacific coast (Rodríguez & Valdivia 2017). In these host–parasite complex systems, usually the parasites are not lethal to the intermediate hosts; hence, these hosts accumulate parasites through their ontogeny, without expelling them (Latham & Poulin 2002, 2003, Rodríguez & Valdivia 2017). Consequently, parasite accumulation over time seems to be a widespread feature of second intermediate hosts of parasites with complex life cycles. Importantly, this implies that host body

Table 2. Likelihood ratio test for each explanatory variable in a generalised linear mixed-effects model for *Profilicollis altmani* infection probability and parasite abundance. For each response variable, there are 2 model types—the environmental model, which includes many site-level explanatory variables, and the co-infection model, which includes a smaller number of variables which are all individual level. The deviance of the global model is reported on the top line of each model's output. Each subsequent row reports the summary statistics of the global model minus the 1 named dropped variable. A significant p-value ($p < 0.05$, in **bold**) indicates that the dropped variable significantly increased the model's unexplained variation (deviance). Port dist.: distance to port; Freshwater dist.: distance to freshwater discharge; p/a: presence–absence of parasite species; ab: abundance of parasite species; -: not applicable

<i>P. altmani</i>	Model	Dropped variable	Deviance	Chi-square	p
Infection probability	Environmental model	–	1039.58	–	–
		Body size	1137.62	98.042	<0.001
		Morphodynamics	1040.12	0.541	0.461
		Crab density	1041.74	2.164	0.141
		Port dist.	1039.58	<0.001	0.998
		Beach size	1040.82	1.244	0.264
		Freshwater dist.	1039.58	<0.001	0.997
	Seagulls	1039.58	<0.001	0.997	
	Co-infection model	–	801.22	–	–
		Body size	839.27	38.055	<0.001
		<i>Maritrema</i> sp. (p/a)	836.95	35.732	<0.001
		<i>Proleptus</i> sp. (p/a)	817.62	16.402	<0.001
	Parasite abundance	Environmental model	–	2320.49	–
Body size			2738.12	417.633	<0.001
Morphodynamics			2320.54	0.049	0.824
Crab density			2340.63	20.147	<0.001
Port dist.			2320.49	<0.001	0.999
Beach size			2321.73	1.246	0.264
Freshwater dist.			2320.49	<0.001	0.999
Seagulls		2320.49	<0.001	0.999	
Co-infection model		–	1869.5	–	–
		Body size	2136.1	266.600	<0.001
		<i>Maritrema</i> sp. (ab)	1876.8	7.245	<0.001
		<i>Proleptus</i> sp. (ab)	1916.0	46.464	<0.001

size is a proxy for exposure duration to infective agents.

Surprisingly, the biological variable of density of definitive hosts (seagulls) did not show strong support in the final model. Parasite prevalence is often strongly related to definitive host abundance, due to the direct link between infection levels in the first intermediate host and definitive host exposure (Marcogliese et al. 2001, Byers et al. 2008). However, in some cases, authors have shown that these relationships are positive but not always significant (Smith 2001, 2007, Latham & Poulin 2003). Latham & Poulin (2003) found similar results in grapsid crabs parasitised by acanthocephalan larvae. In their study, the infection level in crabs trended positively both temporally and spatially with shorebird abundance, but these correlations were not statistically significant. In our study, the modest number of analysed sites supplies lower statistical power and may make it difficult to find a correlation if the link be-

tween definitive host abundance and infection level in crabs is weak. Another illustrative example is Smith (2007), who surveyed mole crabs distributed along 8 sites along the west coast of the USA. Smith (2007) collected crabs and counted seagulls in 2 seasons (spring and autumn) with the aim to detect temporal differences in the infection level. Even so, Smith (2007) found that the association between bird abundance and infection level of parasites in mole crabs was significant and positive for trematode and acanthocephalan larvae in only 1 (autumn) of the 2 seasons analysed. Our study sampled during early autumn, when the abundance of seagulls is less than that in the summer season (Smith 2007, Rodríguez & Valdivia 2017). Therefore, although the abundance of definitive hosts may be an important factor in the variability of the infection level, as shown by Smith (2007), it is far from being a general pattern (present study, Latham & Poulin 2003, Zambrano & George-Nascimento 2010). Looking across these studies, it

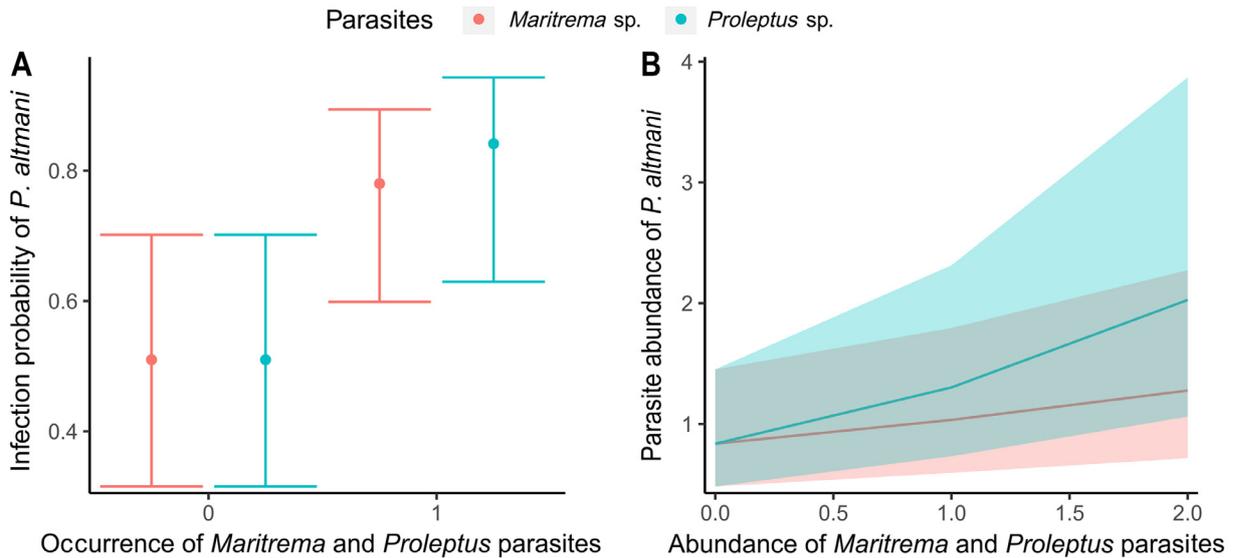


Fig. 5. (A) Infection probability of *Profilicollis altmani* in individual host crabs as a function of the presence–absence of the trematode *Maritrema* sp. and the nematode *Proleptus* sp. Values of infection probability indicate that 0 = uninfected, 1 = infected. Error bars indicate 95% CIs. (B) Parasite abundance of *P. altmani* in individual host crabs as a function of the abundance of the trematode *Maritrema* sp. and the nematode *Proleptus* sp. The coloured area indicates CIs predicted by the co-infection models. Data were collected at 7 of the 8 sites (excepting Colcura) along the south-central Pacific coast of Chile (see Fig. 1)

appears that sampling definitive gull hosts at peak season provides a more robust quantification of parasite propagule delivery. Thus, the weak correlation between gulls and parasites in our present study could be an artefact of choosing the season of the year to count the birds when they were in lower abundance.

Environmental effects often influence parasite distributions; however, we did not find any associations between site-level environmental variables and variation in crab parasites. This result contrasts with previous studies of parasites with complex life cycles. For example, infections of a trematode (*Alaria* sp.) in tadpoles positively correlate with distance to roads and forests (Koprivnikar & Redfern 2012). In addition, degree of urbanisation, pollutants, and fishing alter parasite abundance and richness (Altman & Byers 2014, Wood et al. 2014, Taglioretti et al. 2018). What accounts for the lack of effect of environmental variables in the present study? Perhaps considering other unmeasured factors would have improved the predictive power of our analysis (Poulin & Mouritsen 2003). One factor would be genetic similarity among hosts, which has been shown to influence host susceptibility (Vergara et al. 2013, Paczesniak et al. 2014). For example, Gibson et al. (2016), in a field survey and experimental work, showed that the prevalence of infection covaries with susceptibility between nearby sites, although these relationships

were not always consistent. This indicated that genetic differences among hosts could explain, in part, the host susceptibility to parasites (Paczesniak et al. 2014, Keogh et al. 2016). However, in our system, mole crabs have high gene flux across the southeastern Pacific coast (Haye et al. 2014). Thus, the observed variation in parasite prevalence and abundance suggests parasite susceptibility is not under strong genetic control. Another factor, such as disturbance, may also have an effect on parasite susceptibility. In this context, Dichato beach experienced an 8.8 Mw earthquake and subsequent tsunami in February 2010 (Jaramillo et al. 2012). This event produced massive mortality of planktonic and benthic organisms, severely affecting mole crab recruitment and population size (Jaramillo et al. 2012, Veas et al. 2013, Sepúlveda & Valdivia 2016). We saw these characteristics reflected in our study, where we observed a low mole crab population density, composed mainly of small individuals but almost all of them parasitised. Regardless of the reasons, the infection level at Dichato beach seems to be the exception, which suggests that disturbance could boost the prevalence and intensity of parasites in their hosts.

Positive associations among larval helminth species are common, especially among those that are phylogenetically distinct (Poulin 2001, Poulin et al. 2003, Smith 2007, Bhaduri et al. 2018). Similarly,

here, we found the acanthocephalan *P. altmani*, the trematode *Maritrema* sp., and the nematode *Proleptus* sp. commonly co-occurred in the same host individuals. However, the prevalence and abundance of *Maritrema* sp. and *Proleptus* sp. were lower than other helminths reported in different *Emerita* species, such as *E. rathbunae* (Violante-González et al. 2015, 2016). In our study, both *Maritrema* sp. and *Proleptus* sp. contributed significantly to the fit of the co-infection model, both for the probability and abundance of infection by *P. altmani*. Positive associations can result from various factors (Dezfuli et al. 2001, Poulin et al. 2003, Smith 2007, Bhaduri et al. 2018). First, infections by all parasites that are non-lethal may simply accumulate in larger crabs, causing high coincidence in crab hosts. Second, *P. altmani* and *Maritrema* sp. both share the same definitive host, i.e. gulls, and so they are being vectored to mole crabs in the same way. Interestingly, *Proleptus* sp. uses elasmobranchs as definitive hosts (Oliva et al. 1992, Alvitres et al. 1999). Third, the positive covariation among infection in mole crabs can be driven by processes other than shared definitive hosts, including especially intermediate host condition. Intermediate hosts that have weakened immunity or altered avoidance behaviour can be infected by other opportunistic parasites (Poulin et al. 2000, Dezfuli et al. 2001, Keogh et al. 2016, Bhaduri et al. 2018). The weakened immunity or altered behaviours could exist to begin with, or they could be accentuated by infection from an initial infection by 1 species. For example, Balboa Figueroa et al. (2019) showed that mole crabs infected with *P. altmani* have lower oxygen consumption compared to uninfected ones. Lowered respiratory abilities may decrease escape behaviours as well as overall host well-being or immunity.

5. CONCLUSIONS

In summary, we have shown that for *Profilicollis altmani*, infection of its intermediate mole crab host was heterogeneous across 500 km of coastline. Even though multiple environmental and anthropogenic variables were analysed, none of them explained patterns of spatial variability in infection level in mole crab populations. Two other helminth parasites that, along with *P. altmani*, share mole crabs as their intermediate host have strong and positive associations, evidencing similar accumulation in larger (older) hosts or possible facilitation or joint opportunism among them. Finally, host body size is the best predictor of the probability of infection and parasite abundance

across this large spatial scale. Overall, because of the typically tight association of body size and age, body size is a good proxy for a host's duration of parasite exposure, making it a highly relevant and easy to measure factor in systems where intermediate hosts accumulate parasites over time.

Acknowledgements. We thank all undergraduate interns (Marine Biology, UACH) who provided invaluable help during the fieldwork. We thank Daniela López for assistance in statistical analyses. S.M.R. acknowledges the FONDECYT Postdoctoral Program (grant no. 3190348). N.V. was supported by FONDAP (grant no. 15150003) and FONDECYT (grant nos. 1190529 and 1181300). All applicable institutional and/or national guidelines for the care and use of animals were followed.

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Editorial responsibility: Rochelle D. Seitz,
Gloucester Point, Virginia, USA
Reviewed by: 3 anonymous referees

Submitted: December 30, 2020

Accepted: September 8, 2021

Proofs received from author(s): November 22, 2021