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Research Article

Infestation of *Pseudione tuberculata* (Isopoda: Bopyridae) on juveniles of *Lithodes santolla* (Magellan region, Chile): a spatial mesoscale analysis

Juan I. Cañete[1], Javier A. Díaz-Ochoa[1], Tania Figueroa[1] & Alvaro Medina[1]
[1]Departamento Ciencias y Recursos Naturales, Facultad de Ciencias
Universidad de Magallanes, Punta Arenas, Chile
Corresponding author: Javier Díaz (javier.diaz@umag.cl)

ABSTRACT. We document latitudinal patterns of infestation of the bopyrid parasite isopod *Pseudione tuberculata* on southern king crab *Lithodes santolla* juveniles (20-77 mm carapace length) recruited to fishing grounds in the southern Chilean fjord system. Seven hundred and fifty individuals were collected by semi-autonomous diving in 11 of 21 sampling locations in the study area, along the western margin of the Magellan region between August and October 2013.The prevalence of *P. tuberculata* varied between 0 and ~22%, and displayed a spatial pattern associated with three areas: i) northern Beagle Channel (10 to ~22%; lengths between 37 and 47 mm), ii) northwestern Navarino Island without infestations (0%; 26-55 mm), and iii) Piazzi Island-Capitán Aracena Island (0-12%; 50-77 mm). Infestations were independent of host sex, while parasite prevalence decreased with host length. No parasites were observed on crabs longer than 60 mm. A comparison of slopes between linearized length-weight regressions suggests that parasitized individuals had lower weight growth than uninfested individuals. Both southern king crab juvenile density and *P. tuberculata* prevalence were higher in fishing areas towards Beagle Channel where previous research reported lower average surface water temperatures (<6.5°C) and higher surface water salinity (>30). The study area covers five zones relevant for the conservation and protection of sub Antarctic biodiversity, and provides opportunities for large-scale geographic studies of the host-parasite relationship.

Keywords: *Pseudione tuberculata*, *Lithodes santolla*, southern king crab, parasitism, estuaries, recruitment, spatial mesoscale.

INTRODUCTION

Parasites play an important role in the evolution of organisms and their association with hosts can affect their geographic distribution, and the abundance and age distributions of both populations (Thieltges *et al.*, 2009; Froeschke & Von der Heyden, 2014). Spatial variability of parasite prevalence and abundance depend on key factors like host specificity, latitudinal and depth distribution and marine current dynamics (MacKenzie & Abaunza, 1998; Pérez del Olmo *et al.*, 2011). Moreover, parasites can be considered biological markers and are frequently used as indicators of zoogeographic regions and barriers for dispersion of parasites and hosts (Rohde, 2002). The prevalence of parasites depends on local conditions, and it has been observed that infection/infestation levels can be much less variable geographically than would be expected from purely random distributions (Thieltges *et al.*, 2009). Such observations are especially remarkable considering the migratory potential of host populations. For instance, large crustaceans and aquatic birds act as intermediaries for parasite dispersion at scales of several kilometers (Thieltges *et al.*, 2009). This could be the case for parasite-host associations of the southern king crab *Lithodes santolla* at the spatial mesoscale considered in our study (~700 km long coast; Mann & Lazier, 1991). Additionally, the distributional patterns of bopyrids are influenced by a combination of their definitive (both benthic and pelagic species) and intermediate host distributions. The dispersal of these parasites can be efficiently developed throughout of a definitive as well as by an intermediate host (pelagic copepod) (Williams & Boyko, 2012).

The southern king crab is one of the main crab resources caught in the channels and fjords of southern Chile (SERNAPESCA, 2013) and fishing grounds that stretch ~1500 km along the Chilean Austral Fjord

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System (CAFS) between 42.5º and 55ºS (Sievers *et al.*, 2002; Silva & Palma, 2008). Factors such as a wide geographic extension, high variations in salinity, the formation of different sub-basins (each with its own bathymetric characteristics) as well as insular fragmentation, suggest the existence of several subpopulations, each with its own composition and a diversity of parasites potentially useful for stock identification purposes (*e.g.*, Campodonico *et al.*, 1974; Lovrich, 1997; Petriella & Boschi, 1997).

The study of parasites of *L. santolla* could also be important considering many possible factors regulating the abundance of exploited lithodid crab populations like i) embryonic mortality during egg carrying due to microscopic (*e.g.*, protozoa of the phylum *Microsporidia*) and macroscopic parasites, ii) environmental and hydrographic variability at local and regional scales, iii) biased stock assessment, iv) increased predatory populations (Morado *et al.*, 2014) and reductions of optimum settling areas (Blaum, 1986; Epelbaum & Borisov, 2007; Cañete *et al.*, 2008; Daly *et al.*, 2009).

Among the metazoan parasites associated with the family Lithodidae are bopyrid isopods. These organisms sterilize their hosts, and produce alterations during gametogenesis and modify several secondary sexual characters; usually the hosts of these parasites belong to different decapod crustacean taxa (Dall *et al.*, 1990; Thatje, 2003; Cañete *et al.*, 2008; Morado *et al.*, 2014). The bopyrid isopod of the genus *Pseudione* is a recurrent parasite of several benthonic crustaceans along the Chilean coast and to date five species have been identified: *P. tuberculata* (Miranda-Vargas & Roccatagliata, 2004; Cañete *et al.*, 2008), *P. brattstroemi*, parasitizing *Neotrypaea uncinata* (Stuardo *et al.*, 1986), *P. humboldtensis* parasitizing squat lobsters *Cervimunida johni* and *Pleuroncodes monodon* (Pardo *et al.*, 1998), *P. chiloensis* parasitizing *Nauticaris magellanica* (Román-Contreras & Werthmann, 1997) and *P. galacanthae*, recently reported parasitizing the squat lobster *Munida subrugosa* in the Strait of Magellan off Punta Arenas (J.I. Cañete, unpublished data).

Parasitic isopods of the superfamilies Bopyroidea and Cryptoniscoidea (commonly referred to as epicarideans) are unique in that they use crustaceans as intermediate and definitive hosts. In total, 795 epicarideans are known, representing ~7.7% of described isopods. Among epicarideans, nearly all species of Bopyroidea are ectoparasitic on decapod hosts. Bopyrids are the most diverse taxon (605 species), with the greatest diversity in the North West Pacific (139 species), East Asian Sea (120 species), and Central Indian Ocean (44 species). Most epicarideans are known from relatively shallow waters, although some bopyrids are known from depths below 4000 m (Williams & Boyko, 2012).

For southernmost Chile and Argentina *Pseudione tuberculata* has been found parasitizing the lithodid crabs *L. santolla* and *Paralomis granulosa* (Lovrich, 1991; Roccatagliata & Lovrich, 1999; Cañete *et al.*, 2008; Vinuesa & Balzi, 2010). However, these studies did not consider simultaneous latitudinal variations of infestation (*i.e.*, spatial mesoscale; ~700 km) or else they simply described such variability using samples collected exclusively in processing plants.

In this work we describe the spatial dynamics of recruitment to fishing grounds of the southern king crab *L. santolla* along the western margin of the Magellan region (Fig. 1; Cañete *et al.*, 2016) between August and October 2013. A substantial number of the collected individuals were infested with the isopod *P. tuberculata* and the opportunity was taken to analyze potential latitudinal variations in the prevalence of this parasite. This work complements and considerably expands the spatial range analyzed by previous works that only analyzed a small area in the middle of Paso Ancho in the Magellan Strait (Cárdenas *et al.*, 2007; Cañete *et al.*, 2008). Consequently this research had as objectives: i) to determine possible spatial differences (*i.e.*, latitudinal mesoscale gradient; *sensu* Mann & Lazier, 1991; ~700 km) experienced by infestation levels, ii) to know the size range of infested southern king crabs, and iii) to identify environmental and oceanographic factors forcing such variability.

MATERIALS AND METHODS

Sampling was conducted between August and October 2013 aboard the chartered vessel "Mary Paz II" at 21 locations in the Magellan region (Chile) covering a spatial range of *ca.* 700 km (spatial mesoscale; Mann & Lazier, 1991; Miller & Wheeler, 2007; Fig. 1). We describe the spatial dynamics of recruitment to fishing grounds of the southern king crab *L. santolla* along the western margin of the Magellan region (Fig. 1; Cañete *et al.*, 2016), an area that has sustained the fishery in recent decades (*e.g.*, mean landing was 3276 ± 921 ton year^{-1} between 2000 and 2013) (SERNAPESCA, 2013; Humberto Camelio, *pers. comm.*). Given the lack of knowledge on juvenile spatial distribution, types of habitats frequented by recruits and seasonal and spatial changes in migration in the study area; sampling was carried out based on information provided by experienced crews working in the southern king crab fishery. Another criterion for sampling allocation was the presence of protected bays and *Macrocystis pyrifera* kelp beds (depths <20 m), which some authors have suggested favors juvenile recruitment (Cárdenas *et al.*,

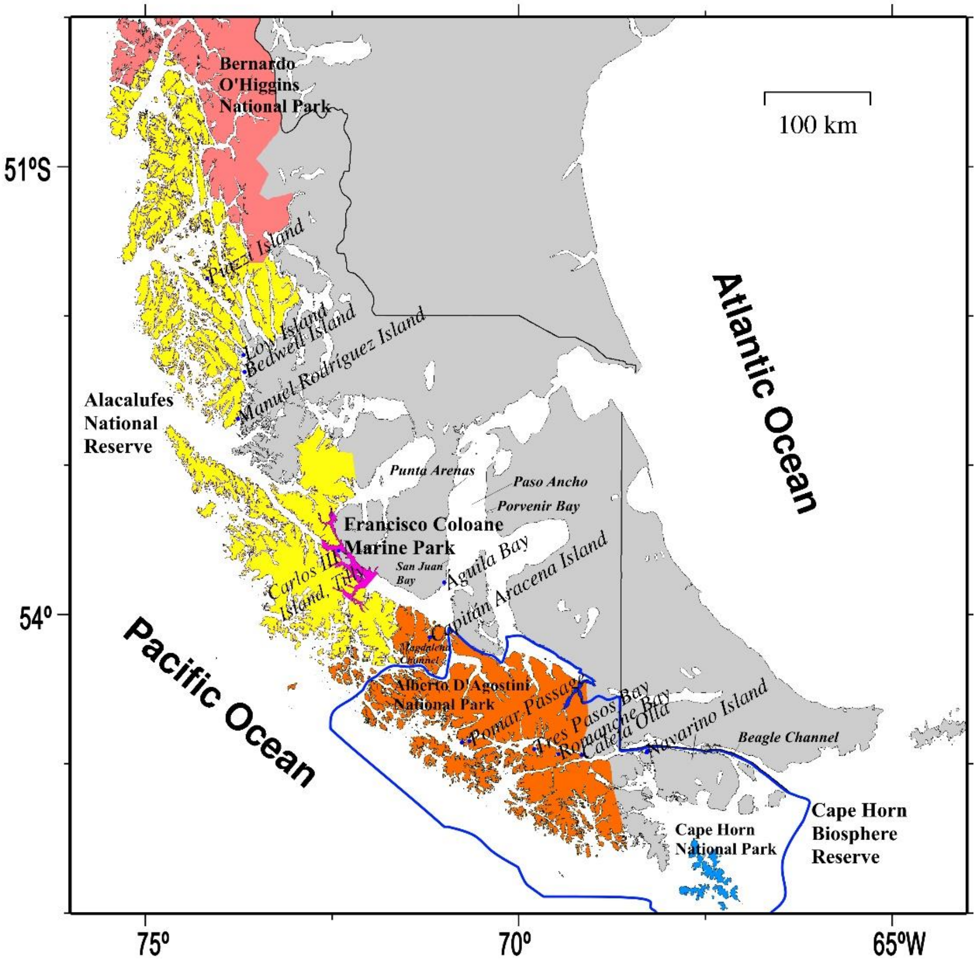

Figure 1. Sampling areas of southern king crab (*Lithodes santolla*) recruits along the western sector of Magellan region (Chile) between August and October 2013 (blue dots correspond to sampling locations). National and marine parks as well as reserves are also shown (drawn according to data from the Chilean National System of Wildlife Protected Areas; SNASPE; http://www.bienesnacionales.cl).

2007; Cañete *et al.*, 2008), and the presence of biogenic substrate (*i.e.*, Mytilidae shell debris; Tapella *et al.*, 2012). Additionally, the western part of the Magellan region can be divided into two subareas according to latitude: i) a northern section known as Patagonian channels and fjords, and ii) a southern section known as channels and fjords of Tierra del Fuego. These two subareas present different oceanographic and glaciological features and generate different micro-basins (Antezana, 1999) likely with different juvenile abundance and latitudinal infestation patterns. Given the scarcity of information about the spatial distribution of recruitment we adopted an adaptive sampling scheme in which sample allocation was random once the areas of interest were detected (Thompson, 2012), while taking into account safety restrictions for diving depths.

Specimen searches and sample collections were done by semi-autonomous diving and geographic positions were recorded with a portable GPS device. We report the presence or absence of recruits and parasites for every sampling location. In addition, the following environmental information was recorded to aid infestation level interpretations: a) salinity/temperature (from a secondary source, see below), b) fresh water input from small creeks draining glaciers, c) presence of kelp (*M. pyrifera*) beds, d) presence of subtidal mussel (Mytilidae) beds, e) presence of cliffs and vertical rock walls, f) spatial orientation of water bodies, g) local bathymetry, h) presence of biogenic sediments (*e.g.*, shell remains), i) presence of gravel in the sediment, j) presence of mountains providing shelter from the wind and k) presence of other green and/or brown seaweed beds (*e.g.*, *Ulva* sp., *Lessonia* spp., *Gigartina* sp.).

For each crab specimen we recorded the sex, carapace hardness and infestation with *P. tuberculata* by observing the presence of an abnormal bulge on the left posterolateral part of the cephalothorax (Roccatagliata & Lovrich, 1999; Miranda-Vargas & Roccatagliata, 2004; Cañete *et al*., 2008). Carapace length (CL) was measured with a caliper from the posterior margin of the carapace to the base of the right eye socket (Roccatagliata & Lovrich, 1999; Lovrich *et al*., 2004; Cárdenas *et al*., 2007; Cañete *et al*., 2008). Wet body weight was measured with a standard electronic balance with a capacity of 200 g and a precision of ±0.1 g. Once this information was recorded, the majority of crabs were returned to the sea. Only a few of the individuals were retained for dissection and taxonomical identification of parasite species of the genus *Pseudione* as reported for Chile by Benedict (1894), Stuardo *et al*. (1986), Pardo *et al*. (1998), Román-Contreras & Werthmann (1997) and Miranda-Vargas & Roccatagliata (2004). Previous confirmation of the identity of several specimens of *P. tuberculata* collected in Punta Santa Ana (50 km south of Punta Arenas) was requested from Dr. D. Roccatagliata (Universidad de Buenos Aires, Argentina) (Cañete *et al*., 2008).

Oceanography of the study area

We used secondary information to characterize several features of the study area, mainly from data obtained during two cruises, CIMAR Fiordos 15 (2009) and CIMAR Fiordos 16 (2010), both carried out between October and November (austral spring) by the Chilean Servicio Hidrográfico y Oceanográfico de la Armada (SHOA) and available from the Oceanographic Documentation Center-CENDOC of the Chilean Navy.

Statistical analysis

We assembled contingency tables to compare infestation percentages (prevalence) of *P. tuberculata* in males and females and checked the statistical significance ($P < 0.05$) with a chi-square (X^2) test (Zar, 2010). We then determined the effect of infestation on average individual growth by comparing the slopes (Zar, 2010) of two linearized length-weight regressions (Eq. 1) fitted to data of infested and uninfested individuals, respectively.

$$log\,(W) = log\,(a) + b \times log\,(CL) \qquad (1)$$

where: W: body mass (g), CL: carapace length (mm), a and b are constants (King, 2007).

RESULTS

We found *L. santolla* juveniles infested with *P. tuberculata* in 11 of 21 locations visited during the study period. The percentage of infested animals varied between 0 and 22.2% and had lengths between 25.8 and 76.8 mm CL (Table 1). About 98% of all the individuals observed had hard carapaces so molting had probably occurred well before the sampling period. No significant differences in parasite prevalence were found between males and females ($X^2 = 2.74$; $P > 0.05$). However, we found that parasite prevalence decreased linearly as crabs length increased (Fig. 2; $r = -0.62$; $P < 0.05$).

Latitudinal variability of infestation

The highest levels of infestation were detected in bays in the northern branch of Beagle Channel (10-22%, mean size between 37 and 59 mm CL), while no infested animals were found around Navarino Island (0%; mean size between 26 and 55 mm CL). In central and northern locations (Piazzi Island to Capitán Aracena Island) prevalence fluctuated between 0 and 12% (mean size between 50 and 77 mm CL) (Fig. 2). To the north and south of the sampling locations, on three locations (Piazzi Island, Low Island and Caleta Olla) we observed four animals infested by two kinds of parasites; the rhizocephalan cirriped *Briarosaccus callosus* (1-2 parasites per crab) and the isopod *P. tuberculata*. Mean size of these animals affected by "double parasitism" (with *Pseudione* and *Briarosaccus*) ranged between 32.0 and 53.5 mm CL.

Main common features of submarine landscape and oceanographic conditions important for southern king crab recruitment were: slightly estuarine conditions (Salinity 24.4-31.3), water temperature between 6 and 8.4°C, presence of freshwater input, kelp forests, Mytilidae beds and shell debris and gravel and boulders on shallow bottoms (<20 m water depth) (Table 2).

There are at least five zones in the study area that are considered natural reserves or zones with great value for conserving sub Antarctic natural resources, namely: i) the Alacalufes Natural Reserve, ii) the AMPC Francisco Coloane Marine Park, iii) the Alberto D'Agostini National Park in the Beagle sector, iv) Cape Horn National Park, and v) the Cape Horn Biosphere Reserve, the later including parts of the Alberto D'Agostini National Park and the Cape Horn National Park. We consider that the most relevant areas for the conservation of environmental services like southern king crab recruitment are in the western sector of the Alberto D'Agostini National Park, where we collected 75% of the recruits during our study, and in the inner channels of Alacalufes National Reserve, where we collected 10% of the specimens. Alberto D'Agostini National Park is located to the south of the Magellan region and comprises all the islands to the south of the Magellan Strait and to the west of Navarino Island, as well as part of the Tierra del Fuego Island south of

Table 1. Statistics of infestation of southern king crab (*L. santolla*) juveniles with the parasitic isopod *Pseudione tuberculata* in the Magellan region, collected between August and October 2013. CPUE: catch per unit effort (number of crabs collected by a diver in an hour; Nº/man-hour), CL: mean carapace length, W: mean wet weight, nd: no data available. Averages are presented ±1 standard deviation.

Location	Date	CPUE (Nº/man-h)	CL (mm)	W (g)	% Infestation
Northern and central locations					
Piazzi Island	25-08-2013	60	55.8	74.3	5.7
Low Island	27-08-2013	63	54 ± 5.9	64.4 ± 23	12
Bedwell Island	27-08-2013	6	50.3	53.5	0
Manuel Rodríguez Island	28-08-2013	7	76.8 ± 16.4	217 ± 100	0
Central and northern branch of Beagle Channel locations					
Águila Bay	30-08-2013	160	49.6 ± 7.0	49 ± 21	7.5
Carlos III Island, Tilly Bay	29-08-2013	nd	nd	nd	nd
Capitán Aracena Island 1	26-09-2013	120	54.6 ± 11.5	96 ± 50	3.3
Capitán Aracena Island 2	26-09-2013	125	52.08 ± 12.0	79.6 ± 41	4
Pomar Passage 1	29-09-2013	54	56.5 ± 16.0	86 ± 53	7.4
Pomar Passage 2	29-09-2013	70	58.9 ± 13.8	12 ± 84	0
Tres Brazos Bay	30-09-2013	160	47.6 ± 9.7	72.4 ± 41	1.25
Romanche Bay 1	01-10-2013	101	46.9 ± 10.1	64 ± 48	18.92
Romanche Bay 2	01-10-2013	120	39.8 ± 13.1	46 ± 37	10.7
Caleta Olla 1	02-10-2013	216	36.6. ± .4.9	33.±.12	22.22
Caleta Olla 2	02-10-2013	530	37.4 ± 7.3	37 ± 28	12.5
Caleta Olla 3	01-10-2013	nd	nd	nd	nd
Navarino Island locations					
Navarino Island, Caleta Honda	03-10-2013	4	27 ± 1.2	nd	nd
Navarino Island 1	03-10-2013	129	25.8 ± 4.1	12.6 ± 5	0
Navarino Island 2	03-10-2013	0	nd	nd	nd
Navarino Island 3	03-10-2013	12	55 ± 29.7	129 ± 148	0
Navarino Island, Caleta Navarino	03-10-2013	86	25.8 ± 12.5	18.7 ± 27	0

Almirantazgo Sound (Fig. 1). This National Park, with an area of 12,699 km^2, also includes the Darwin Mountain Range.

Length-weight relationship of infested and uninfested specimens

The lengths of the animals analyzed in this study ranged between 14 and 89 mm CL, with body masses between 2 and ~360 g. No significant differences were found between males and females for this relationship (t = 1.74; $P > 0.05$). In addition, the confidence intervals estimated for parameter b of the length-weight relationship indicated allometric growth ($b \neq 3$; $P < 0.05$) and it was established that infested animals had lower weight growth than uninfested animals (t = 12.34; $P < 0.001$; Fig. 3).

Parasite prevalence and environment relations

Multiple factors potentially affect the recruitment of *L. santolla* in shallow protected environments like channels, bays and small sounds. In all sampling locations we observed significant fresh water inputs from rivers and small creeks from glacier or snow melting in high mountains. In general, the western part of the Magellan region, an area where there is significant pressure from fishing and where we caught southern king crab juveniles, presents surface salinity levels between 25.4 and 31.3 (Fig. 4).

As a consequence, recruitment to fishing grounds in the western part of the Magellan region occurs in areas characterized by relatively low surface salinity like Smith Channel, between Low Island and Piazzi Island (25.4 to 27.7). However, higher density levels and shorter recruits were observed to the south of Capitán Aracena Island, where previous surface salinity measurements have ranged between 30.6 and 31.3 (Beagle Channel and Navarino Island; Fig. 4). With reference to temperatures the information available suggests that areas with high concentrations of recruits are characterized by comparatively low water surface temperatures (<6.5°C; Fig. 5).

It is worth noting the presence of a significant area of shallow grounds (<10 m) covered with biogenic sediments like shell debris from intertidal and subtidal

Table 2. A list of habitats analyzed during the study of recruitment to fishing areas of southern king crab in the Magellan region between August and October 2013. Salinity/temperature in °C (data from SHOA-CENDOC, Chilean Navy) a); freshwater input from creeks b); presence of *Macrosystis pyrifera* beds c); presence of Mytilidae beds (cholga *Aulacomya ater* and chorito *Mytilus chilensis*) d); presence of cliffs and vertical walls on the shoreline e); orientation of water bodies (N: north, S: south, E: east, W: west) f); water depth (m) g); presence of biogenic sediments (shell debris) h); gravel sediments i); presence of mountains higher than 400 m j); presence of seaweed beds other than kelp (*e.g.*, *Ulva* sp., *Lessonia* spp., *Gigartina* sp.) k.

Location	a	b	c	d	e	f	g	h	i	j	k
Northern and central locations											
Piazzi Island	27/8.4	No	Yes	Yes	No	NW-SE	<5	Yes	No	No	No
Low Island	25.4/6.0	Yes	Yes	No	No	SW-NE	<5	Yes	No	No	No
Bedwell Island	27.3/6.0	No	Yes	No	Yes	N-S	<25	No	No	No	No
Manuel Rodríguez Island	26.0/6.1	Yes	Yes	Yes	No	E-W	<5	Yes	No	No	No
Central and northern branch of Beagle Channel locations											
Águila Bay	30.5/7.2	Yes	Yes	Yes	No	NE-SW	<20	Yes	Yes	Yes	No
Carlos III Island, Tilly Bay	30.7/7.2	No	Yes	No	Yes	E	<80	Yes	Yes	Yes	No
Capitán Aracena Island 1 & 2	30.6/7.0	Yes	Yes	Yes	No	N-S	<10	Yes	Yes	Yes	No
Paso Pomar Passage 1 &2	30.5/7.3	Yes	Yes	No	No	E-W	<10	Yes	No	No	No
Tres Pasos Bay	30.2/7.5	Yes	Yes	Yes	No	NE-SW	<15	Yes	No	Yes	No
Romanche Bay	30.2/7.6	Yes	Yes	Yes	Yes	N-S	<15	No	No	Yes	No
Caleta Olla	30.2/7.4	Yes	Yes	Yes	Yes	NW-SE	<20	No	Yes	Yes	No
Navarino Island locations											
Navarino Island 1 & 4	31.3/7.4	No	Yes	No	No	E-W	<20	No	Yes	No	Yes

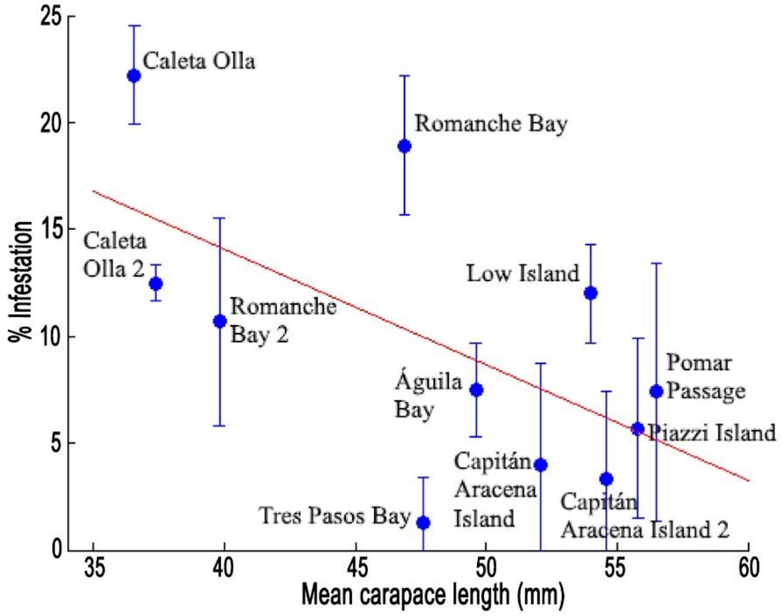

Figure 2. Infestation percent as a function of mean carapace length of juvenile southern king crabs *Lithodes santolla* along the western margin of the Magellan region (Chile) between August and October 2013 ($r = -0.61$; $P < 0.05$). Note that no infestation was detected in sampling locations to the north of Navarino Island (data not shown). The error bars correspond to 95% confidence intervals.

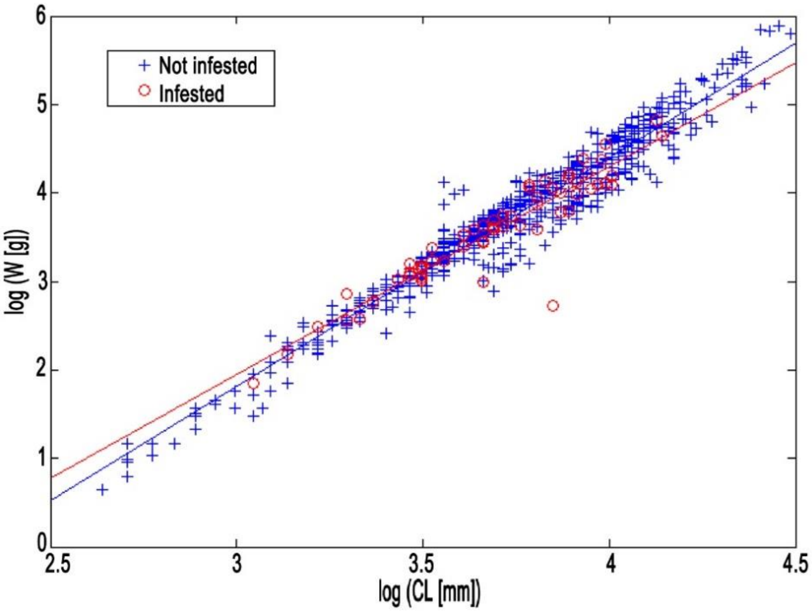

Figure 3. Length-weight relationship for juvenile southern king crabs *Lithodes santolla* collected in the western sector of the Magellan region (Chile) between August and October 2013. The slope of this relationship is significantly lower for infested individuals ($t = 12.34$; $P < 0.001$). CL: carapace length; W: wet weight. Note the logarithmic (natural logarithm) scale of both axes.

Mytilidae (*Mytilus chilensis*) and subtidal banks of *Aulacomya ater*. There is significant kelp cover (*M. pyrifera*) in these areas, although southern king crab juveniles were not always found there. A significant proportion of specimens were collected around boulders. However, we did not find recruits in open areas in Smith Channel, the Strait of Magellan or Beagle Channel, characterized by the presence of cliffs and despite the presence of thin vertical bands of kelp near the shoreline.

In Caleta Olla, where we found the highest abundance of recruits, there were unique conditions such as a bay opening to the southwest and parallel to Beagle Channel, significant fresh water input from nearby glaciers and the presence of sediments predominantly covered with gravel and shell debris. In addition, in this area we observed an important cover of *Macrocystis* and relatively high mountains that provide protection from wind action. All these factors may contribute to making Caleta Olla a particularly suitable area for southern king crab recruitment. The abundance of recruits in this area was so high that in only a couple of occasions we collected several juvenile specimens in the intertidal zone.

DISCUSSION

Fisheries of large crustaceans such as lobsters and king crabs are usually regulated so that fishing efforts are aimed at the male adult fraction of stocks. However, many diseases affect the productivity of such resources well before the exploited phase during juvenile stages and independently of the sex. Another aspect to consider is that these resources normally have wide geographic ranges and migrations, making surveillance difficult (Morado *et al.*, 2014). Environmental factors can exacerbate the levels of parasitic infestation. Kuris & Lafferty (1992) examined the impact of infestations on crustaceans that are recruited in closed systems like fjords, and verified an increased possibility of massive infestations (see also Shields, 2012). Previous works conducted in the study area on the prevalence of the isopod *P. tuberculata* on *L. santolla* were characterized by low spatial coverage, mostly centering sampling on Beagle Channel and San Jorge Gulf in Argentina (Roccatagliata & Lovrich, 1999; Miranda-Vargas & Roccatagliatta, 2004; Vinuesa & Balzi, 2010) and an isolated location in the Magellan Strait in Chile (Cañete *et al*., 2008). To the best of our knowledge, our work is the first to analyze southern king crab recruitment to fishing grounds at the spatial scale of *ca.* 700 km. At this spatial scale we suggest that higher recruitment occurs in areas combining relatively high levels of salinity (>30) and low temperatures (<6.5°C) between Tres Pasos Bay and Navarino Island (Tables 1-2; Figs. 4-5). This finding is consistent with previous studies reporting that juvenile stages of *L. santolla* are well adapted to temperatures of 5-10°C, a range typical of

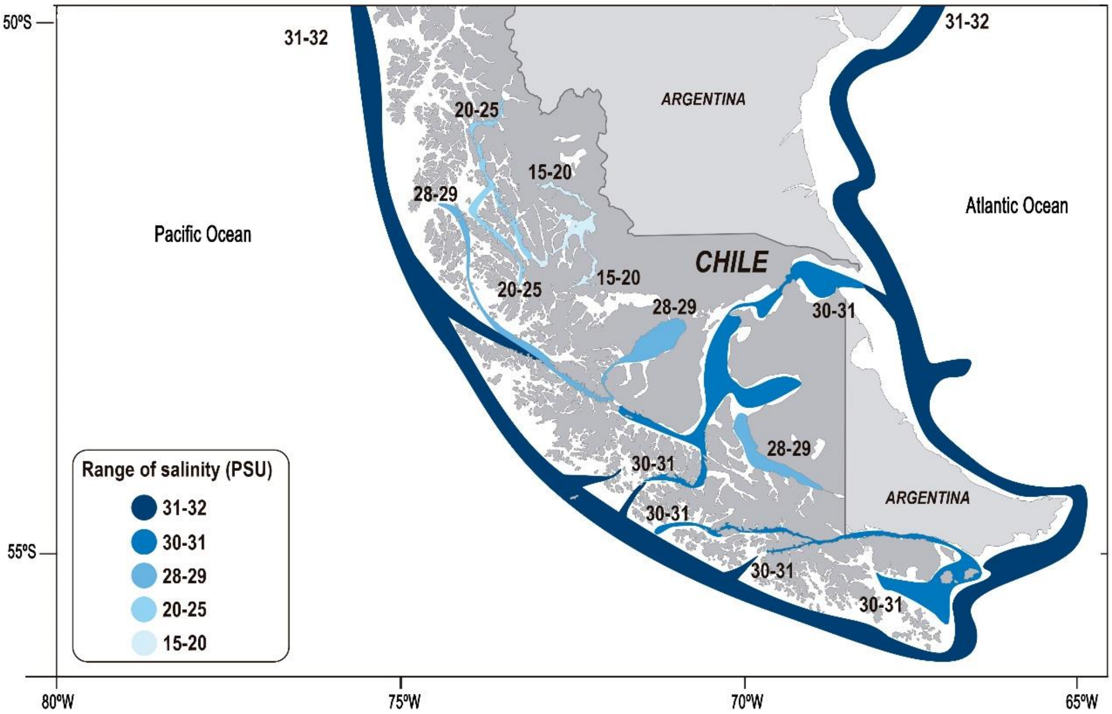

Figure 4. Horizontal distribution of surface water salinity in the study area derived from CTD measurements from the CIMAR Fiordos 15 and 16 cruises (2009-2010; Chilean Navy).

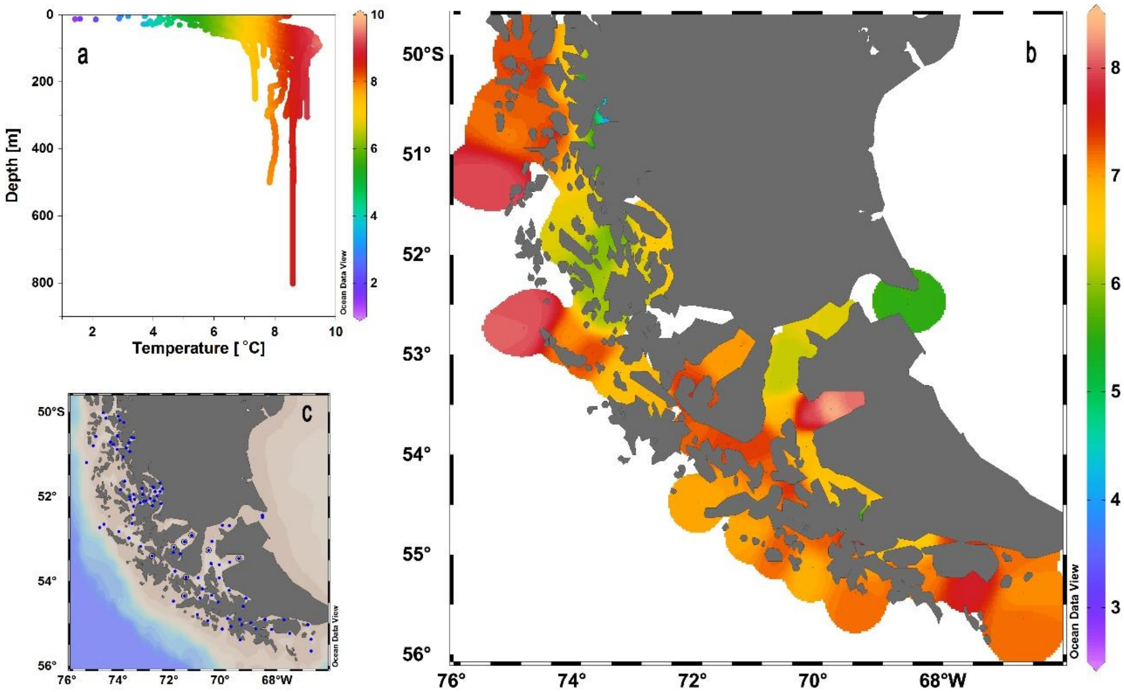

Figure 5. Water temperature in the study area derived from CTD measurements from the CIMAR Fiordos 15 and 16 cruises (October-November, 2009 and 2010; Chilean Navy). Profiles as a function of a) water depth; b) spatial distribution of surface temperature; c) location of sampling stations. The color scale represents water temperature (°C).

subantarctic marine environments (Anger *et al*., 2004; Calcagno *et al*., 2005; Cañete *et al*., 2012). Moreover, we found maximum abundance of recruits near Beagle Channel and Navarino Island, areas typified by low freshwater inputs and high salinity under the influence of the Pacific Ocean (Fig. 4) (Antezana, 1999).

The results presented in this work lead us to hypothesize that larval development and recruitment in the study area are favored by high salinity, which is consistent with laboratory experiments indicating that growth and survival of early development stages of *L. santolla* are optimal in marine and slightly estuarine waters (Vinuesa *et al*., 1985; Tapella & Lovrich, 2006). These authors observed maximum survival percentages when salinity increased, while at salinity levels as low as 26, the zoeae did not survive to the post-larvae stage at culture temperatures. The best combination of temperature and salinity under culture conditions was 7.5°C and 35, respectively (Vinuesa *et al*., 1985). Another laboratory study showed that red king crab zoeae (*Paralithodes camtschatica*) passively sank through low salinity water until reaching higher salinity and then resumed and maintained swimming activities (Shirley & Shirley, 1989). A preference for higher salinity by stage II zoeae (29.4) in comparison to stage I zoeae (27.5) agrees well with tolerance experiments and supports ontogenetic changes in salinity tolerance (Shirley & Shirley, 1989). In marine waters (salinity 27.6 and 9.4°C at surface, and 31.1 and 4.7°C at 30 m depth), the vertical distribution of zoeae in the plankton was closely aligned with laboratory determinations (Shirley & Shirley, 1989).

The spatial distribution of subantarctic aquatic organisms seems more affected by salinity than temperature. For instance, based on the spatial distribution of siphonophores and neustonic communities off Northern and Southern Ice Field channels in southern Chile, Palma *et al.* (2014) and Cañete *et al.* (2016) found biota from very low salinity environments in areas with surface salinities between 27 and 28 near river mouths. The same trend seems to be followed by seaweed species like the kelp *M. pyrifera* (Buschmann *et al.*, 2004).

Infestations with *P. tubertculata*

Prevalence values reported in this study were higher in areas with maximum abundance of juvenile crabs (Table 1), and smaller individuals were the most affected (CL <50 mm, Table 1, Fig. 2). A previous study established that the infestation levels in the middle of the Magellan Strait were higher than 21% (Cañete *et al*., 2008), whereas other authors have reported that the prevalence of infestations of *P. tuberculata* on *P. granulosa* decreases with crab size, from 45.6% at 10 to 20 mm CL to 0% at 90 to 100 mm CL (Roccatagliata & Lovrich, 1999; Cañete *et al*., 2008). These results are consistent with our observations of *P. tuberculata* infestation on *L. santolla*, with values >20% at lengths <50 mm CL and an inferred reduction to 0% at lengths >65 mm CL (Fig. 2). Parasite prevalence was high considering the low number of juveniles analyzed. The prevalence values of this study are high when compared to those reported by González & Acuña (2004) for the galatheid crustaceans *Cervimunida johni* and *Pleuroncodes monodon* off northern Chile, which varied between 6.8 and 13.6% for the former species and between 0.6 to 18.2% for the latter.

With respect to the effects of parasites on the infested crabs, we found that there was a significant increase in weight-at-size of crabs not infested by *Pseudione* (Fig. 3), suggesting a negative effect on growth. Thus, when the parasite leaves its host the latter should have higher growth performance. Alternatively, if parasitized crabs die, the surviving population is formed exclusively by specimens that were never parasitized by *Pseudione* and therefore the parasite plays an important role in regulating the population dynamics of juvenile southern king crabs.

Epidemiological description

Some epidemiological features that could be considered typical of the *L. santolla* and *P. tuberculata* parasitic relationship are: i) *P. tuberculata* is an ectoparasite; ii) there is always a female and male parasite per infested juvenile; iii) the parasite seems to produce only sublethal effects on the host and possibly it dies after juveniles migrate to deeper waters; iv) according to previous studies (Lovrich & Tapella, 2014) this seems to be an obligate host-parasite relationship only affecting juvenile stages between 20 to 50 mm CL, and v) based on previous age estimations, parasitized specimens observed in our study are between 3 and 4 years old (Guzmán *et al*., 2004; Calcagno *et al*., 2005; Stevens & Jewett, 2014).

Around 11 lithodid species inhabit Patagonian waters, providing an amazing opportunity to conduct comparative analyses of the parasite-host relationship between the Atlantic and Pacific sides of the Magellan Strait and between southern king crab populations inhabiting South America and those recently colonizing Antarctic waters (Lovrich & Tapella, 2014). Other interesting aspects to investigate are i) the abilities of parasite larvae to find their hosts considering the great migratory capacity of the latter, ii) their capacity to cope with crab molting process, and iii) the influence of factors like complex geography, current dynamics, wind and tidal regimes, thermal and haline stratification, freshwater inputs and the existence of microbasins with different bathymetry.

Effects of kelp forests on infestation levels

Higher recruitment has been detected in protected shallow water bodies with the presence of kelp beds and sediments covered with abundant shell debris of Mytilidae that could act as refuges (Cárdenas *et al*., 2007). In this study we did not find any early megalopae (LC < 10 mm) of *L. santolla* near kelp beds. However, we did find larger juveniles near the beds under boulders and shell debris (Table 2). Kelp beds are important habitats for a variety of marine organisms and provide protection from water motion (Ekman *et al.*, 1989; Balch & Scheibling, 2000). These features could increase retention of larval stages of parasitic isopods, as has been postulated for larval stages of other invertebrates, as well as for detritus and organic matter (Eckman *et al*., 1989; Duggins *et al*., 1990; Pakhomov *et al.*, 2002). One or more of these characteristics of kelp beds may explain the high levels of infestation of *P. tuberculata* on *L. santolla* recruits that settle in kelp beds. As well, because the studied locations are typically shallow and have homogeneous oceanographic characteristics, larval retention, *Pseudione* survival, and infestation rates may be higher than in stratified areas (Sulkin *et al.*, 1980; Roegner, 2000). Therefore, aggregations of organisms in shallow areas could explain high parasite prevalence.

Our study shows that the levels of prevalence and abundance of parasite communities display a certain degree of spatial heterogeneity that could be useful to identify potential stocks of crustaceans with a wide geographic distribution (mesoscale) like the southern king crab. Moreover, it was observed that in the north of the study area juveniles were larger than the individuals collected in central and southwestern margins of the Magellan region (Table 1).

In synthesis, our research proposes that *L. santolla* and its parasites represent biomodels that provide opportunities for large-scale geographic studies of host-parasite relationships associated with larval strategies, dispersal capacities, and latitudinal patterns. New challenges for the study of parasitism on large crustaceans could be related to trends in the coevolution between host and parasites in marine/estuarine systems at different spatial, temporal and taxonomic scales. The longevity of *L. santolla* can provide evidence of successional changes of its parasites during its life span and differential effects on reproductive fitness.

Coastal zones to the south of Bay San Juan (53°38'S, 70°56'W; 50 km south of Punta Arenas) were expected to be important for southern king crab recruitment considering the presence of two micro-basins (Panella *et al*., 1991; Antezana, 1999). However, benthos sampling during a study conducted between 2010 and 2012 in Porvenir Bay (Tierra del Fuego) did not detect southern king crab juveniles (Cañete *et al.*, 2014), a result that was confirmed by a project carried out between 2013 and 2014 addressed to study benthonic macrofauna in the area influenced by Las Minas River (Punta Arenas) (Cañete, unpublished data). Future investigations should shed light on this apparent contradiction.

Implications for fishery management

An implication of this study is that the southern king crab habitat along the western margin of the Magellan region could be divided into two stocks: one to the north of Carlos III Island, a habitat characterized by lower salinity (<30), less recruitment and the presence of rocky shores, and another stock to the south of Magdalena Channel, a habitat with higher salinity (>30) and higher levels of recruitment (Figs. 1, 4, 5). However, with the data at hand this implication should be considered preliminary and should be tested in future studies.

The hypothetical southern stock includes three important areas for conserving biodiversity (Alberto D'Agostini National Park, Cape Horn National Park and Cape Horn Biosphere Reserve) (Rovira *et al.*, 2008). Currently there are plans to create a new conservation area in Yendegaia Bay (54°52'S, 68°45'W). Moreover, traditional fishing grounds in Magallanes region includes the following biodiversity conservation and protected areas established by SNASPE (Chilean National Service for Protected Wildlife Areas), from north to south: O'Higgins National Park; Isla Madre de Dios Protected National Asset; Alacalufes National Reserve; Coastal and Marine Protected Area and Francisco Coloane Marine Park; Islote Rupert Protected National Assets, Batchelor River, Carlos III Island, Cape Froward, Diego Ramírez Island, San Ildefonso Islands and Caleta Róbalo; Alberto D'Agostini National Park; Cape Horn National Park and Cape Horn Biosphere Reserve. These protected areas have an extension of more than 10.5×10^6 ha. The protection of these natural heritage areas is vital for the preservation and sustainable exploitation of southern king crab in Chile and Argentina. The overlapping of fishing areas and natural heritage areas constitutes an opportunity to achieve the sustainability and conservation of southern king crab fisheries, taking into account the need to protect habitats important for the recruitment of this species and preserve the connectivity of its metapopulations (Moilanen & Hanski, 2006; PNUD/CONAMA, 2007; Kininmonth *et al*., 2011).

The prevalence of *P. tuberculata* on juvenile *L. santolla* in the western margin of the Magellan region seems to be higher than on other benthic crustaceans affected by the genus *Pseudione* along the Chilean coast. We propose that the entire western margin of the Magellan region is a suitable area for studies of the population and spatial dynamics of the host-parasite interaction of *L. santolla* and *P. tuberculata*. New research should clarify whether the areas in the channels provide more favorable environmental conditions for parasite infestation than exposed areas like those along the Argentinean coast or the Falkland/Malvinas Islands.

There are few animal health regulations for Chilean fishing resources compared to the regulations for important aquacultural species (SERNAPESCA, 2013). For instance, there are regulations employing criteria of World Organization Animal Health regarding pests and high risk diseases that could be introduced by highly valued alien species, as well as programs for monitoring high risk diseases among introduced fish, mollusks and crustaceans (*e.g.*, Moreno *et al.*, 2006). Chilean authorities are required to investigate and develop a list of diseases caused by native parasites that could, under certain conditions, give rise to epidemics that have adverse social, economic and environmental consequences. There are no publications in the scientific literature summarizing the current status of parasite pathologies of Chilean benthic resources or describing the most relevant epidemiological features.

Lovrich & Tapella (2014) summarized the current state of knowledge about parasite diseases of lithodid crab populations from the Beagle Channel, Magellan region and San Jorge Gulf. These authors stressed that it is necessary to maintain continuous observation of infestation levels in the protected areas of Magellan and Tierra del Fuego channels, which is justified by the fact that prevalence is as high as 65% in the Strait of Magellan (Cañete *et al.*, 2008; Lovrich & Tapella, 2014). Such values are notable given the absence of *Pseudione* in the Falkland/Malvinas Islands and the low values (<10%) observed in the San Jorge Gulf (Vinuesa & Balci, 2010).

The authors suggest the authorities make the study of diseases of high latitude fishing resources like southern king crab a priority and strengthen communication between scientific community and fisheries management authorities (Richardson & Weaver, 2014). Permanent epidemiological monitoring programs should be introduced as part of new studies to identify southern king crab stocks to better understand parasitization relationships and infestation levels in both the recruitment and early development stages. According to Torres-Mura *et al.* (2008), habitat modification, overexploitation, pollution and disease are among the most important causes of biodiversity loss in Chile. All these topics should be explicitly and urgently considered in the context of crustacean fishery management in Chile.

Finally, we consider this type of study to be vital given the economic importance of *L. santolla*. In addition, despite the long history of research of this fishing resource (Campodonico *et al.*, 1974; Lovrich, 1997; Stevens, 2014), there have been few works studying the early benthic development phases of this species in southern South America (Lovrich, 1997; Tapella & Lovrich, 2006; Cárdenas *et al.*, 2007; Cañete *et al.*, 2008). Indirect assessments highlight the need to increase our knowledge about factors determining natural mortality and recruitment to improve fishery sustainability (Powell & Nickerson, 1965; Shirley & Shirley, 1989; Stevens & Kittaka, 1998; Shanks & Roegner, 2007; Yáñez *et al.*, 2008; Xue *et al.*, 2008; Smith & Eckert, 2011; Stevens, 2014), as well as to better understand possible ecological bottle necks experienced by populations of large crustacean (Duggins *et al.*, 1990; Cañete *et al.*, 2008; Hall & Thatje, 2009).

Considering the 11 lithodid species reported at different depths in the biogeographic province of Magallanes (Gorny, 1999; Spalding *et al.*, 2007; Lovrich & Tapella, 2014), we envision extraordinary opportunities to carry out comparative studies of the parasite fauna affecting this crustacean family in the study area.

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