**Pseudione tuberculata** Richardson, 1904 (Isopoda: Bopyridae): un parásito de juveniles de centolla *Lithodes santolla* (Molina, 1782) (Anomura: Lithodidae) en el estrecho de Magallanes, Chile

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**Resumen.**- El isópodo parásito *Pseudione tuberculata* Richardson, 1904 infesta la cavidad branquial de especies de la familia Lithodidae en el extremo sur de Sudamérica. Ha sido descrito previamente como parásito de *Neolithodes* en el Archipiélago de los Chonos, Chile, así como *Paralomis granulosa* (Jacquinot, 1847) y *Lithodes santolla* (Molina, 1782) en aguas someras del canal Beagle, Argentina. Es la primera vez que el parásito es documentado en Chile en el estrecho de Magallanes, ubicado alrededor de 640 km al norte del canal Beagle, parasitando juveniles de *L. santolla* (23.0 a 51.6 mm LC en hembras y entre 24.0 a 48.7 mm en machos). La frecuencia del parásito en centollas fue de 27.97% en hembras y 21.43% en machos. La frecuencia de infestación fue mayor a la descrita en otros crustáceos chilenos parasitados por *Pseudione*. Cada centolla portaba una pareja de *P. tuberculata* dentro de la cavidad branquial en el lado izquierdo del carapaz. Las altas tasas de parasitismo de *P. tuberculata* en centollas juveniles en el área podría ocurrir en aguas someras habitadas por *Macrocystis pyrifera* kelp debido a su efecto en las condiciones hidrodinámicas locales, reduciendo el flujo y amortiguando el oleaje, proporcionando hábitats para diversos organismos marinos. Se concluye que *P. tuberculata* como parásito de *L. santolla*, infestando juveniles de esta especie, responde de manera similar al compararse con los valores de infestación de estudios previos desarrollados en el canal Beagle, Argentina, donde ha sido reportada infestando *P. granulosa* y *L. santolla*.

Palabras clave: Bentos subantártico, litódidos, parasitismo, bopíridos, región magallánica

**Abstract.**- The parasitic bopyrid isopod *Pseudione tuberculata* Richardson, 1904 infests the branchial chamber of species of the family Lithodidae found along the southern tip of South America. It was previously known only as a parasite of *Neolithodes* off the Chonos Archipelago, Chile, as well as *Paralomis granulosa* (Jacquinot, 1847) and *Lithodes santolla* (Molina, 1782) from shallow waters of the Beagle Channel, Argentina. This is the first time the parasite is documented in Chile at the Magellan Strait, located about 640 km north of the Beagle Channel, infesting mainly on juveniles of *L. santolla* (23.0 to 51.6 mm CL in females and from 24.0 to 48.7 mm in males). Prevalence of the parasite in crabs was 27.9% in females and 21.4% in males. Prevalence was higher than those reported in other Chilean crustaceans parasitized by other *Pseudione* species. Each king crab carried a single pair of *P. tuberculata* within the branchial chamber on the left side of the carapace.

High rates of parasitism of *P. tuberculata* on juvenile king crabs in this area could occur in shallow water inhabited by *Macrocystis pyrifera* kelp due to the plant’s effect on the local hydrodynamic conditions, reducing flow and damping waves, providing habitats for several organisms. It is concluded that *P. tuberculata* infesting *L. santolla* at the Magellan strait responds in a similar way when compared with prevalence values from previous studies developed at the Beagle Channel, Argentina, where it has been reported infesting *P. granulosa* and *L. santolla*.

Key words: Subantarctic benthos, lithodids, parasitism, bopyrids, Magellan region

**Introduction**

Bopyrid isopods are ectoparasites that can cause sterilization or reduce gametogenesis, and modify the external characters in the definitive host. Bopyrids have three larval stages, the first stage, the epicardium lives attached to a calanoid copepod, where it develops into the microniscus larval stage. Upon reaching the following cryptoniscus stage, the individual leaves the intermediate
host and attaches to the definitive host, usually a decapod crustacean (Beck 1980). The first cryptoniscus larva infesting the definitive host develops into a female, while the next to arrive develops into a dwarf male, which remains attached to the female (Anderson 1990).

Infestation by bopyrid parasites has been frequently observed in species of several decapod infraorders, including thalassinideans, brachyurans, anomurans (Dall et al. 1990, Thatje 2003). The genus Pseudione has the most described species. According to Miranda-Vargas & Roccagagliata (2004), five species in this genus have been described from the southern part of South America (Chile-Argentina) including: Pseudione brattstroemi Stuardo et al., 1986, parasitic on the ghost shrimp Neotrypaea uncinata (H. Milne-Edwards, 1837); Pseudione humboldtensis Pardo et al. 1998, parasitic on the squat lobsters Cervimunida johni Porter, 1903 and Pleuroncodes monodon (H. Milne-Edwards, 1837); and Pseudione chiloensis Román-Contreras & Werthmann, 1997, parasitic on the hippolytid shrimp Nauticaris magellanica (A. Milne-Edwards, 1891) (Stuardo et al. 1986, Román-Contreras & Werthmann, 1997, Pardo et al. 1998). Recently, Miranda-Vargas & Roccagagliata (2004) re-described P. tuberculata, originally described by Richardson (1904), as a parasite on the king crab Neolithodes diomedeae from the Chonos Archipelago in southern Chile. Several studies analyzed the parasitic relationships of this species in Argentina. Vinuesa (1989) reported an unidentified bopyrid infesting Paralomis granulosa (Jacquinot, 1847) and Lithodes santolla (Molina, 1782) in the Beagle Channel. Lovrich (1991) analyzed additional material of P. granulosa-bearing bopyrids. More recently, Roccagagliata & Lovrich (1999) carried out an intense sampling program in the study of the association between P. granulosa and P. tuberculata, and later, Miranda-Vargas & Roccagagliata (2004) presented a re-description and reported a new host for the parasitic bopyrid isopod Pseudione tuberculata on 17 females and 16 males of the king crab Lithodes santolla. Nevertheless, no information on the infestation percentage and prevalence by sex of host were mentioned in the above-cited studies.

During a study to describe the recruitment cycle of Southern king crab Lithodes santolla in the kelp beds of Macrocystis pyrifera located in two shallow, sandy-rocky embayments at less than 10 m in depth in the Magellan Strait, Chile, we discovered juvenile king crabs with the left side of their carapace inflated in the region of the branchial chamber. One large female parasite identified as Pseudione tuberculata Richardson, 1904 was observed inside the crab’s branchial cavity.

In spite of the economic importance of L. santolla and an extensive history of research on the exploited portion of this population, few studies have been published on its early benthic stages (Lovrich 1997, Tapella & Lovrich 2006, Cárdenas et al. 2007). The present study reports for the first time, the presence of the parasitic isopod P. tuberculata in the king crab Lithodes santolla in Chilean waters, as well as data on the parasitic relationship between P. tuberculata and L. santolla juveniles in the Magellan Strait, Chile.

Material and methods

Study area

San Juan Bay (53°38’S, 70°56’W), is shallow, with a sandy bottom typically less than 10 m in depth over most of its area, located on the eastern coast of Brunswick Peninsula, Magellan Strait (Fig. 1). There is a small section of subtidal rocky bottom at its northeastern end. The San Juan River delivers freshwater into this bay, with an average flow of 18.02 m³ s⁻¹, causing a decrease in salinity. The flow of freshwater into the bay is reduced during the summer (6.3 to 9.4 m³ s⁻¹) and attains maximum values of 29.0 to 32.7 m³ s⁻¹ of during the spring (September - October). The second site was Steamer Bay (53°36’S; 70°55’W), located 1 km north to San Juan Bay. It is a small coastal indentation, measuring only about 400 m in length and 150 m wide, with an average depth of 5 m. The zone closest to the coastline is surrounded by a band of rocks and boulders, changing with depth to shelly sands. A kelp bed consisting of Macrocystis pyrifera occupies the bottom in a band parallel to the coast from depths of 3 to 5 m (Cárdenas et al. 2007).

Collection of L. santolla juvenile

Samples of L. santolla juvenile were collected by SCUBA diving from a boat between 1-8 m depth at Punta Santa Ana, San Juan Bay (53°38’S, 70°56’W), and Steamer Bay (53°36’S; 70°55’W), Magellan Strait, Chile (Fig. 1) in October-November, 2005 and September 2006, during a total diving time of about 4 h over an area of about 200 to 300 m² in Macrocystis pyrifera beds. Crabs were found associated with M. pyrifera holdfasts under the sporophylls and fronds in contact with the bottom; in some cases, the crabs were found under stones of about 30 to 60 cm in diameter. Profiles of temperature, salinity and density were recorded with a Sea Bird Electronics 19-3 CTD device at each sampling station.

All specimens of L. santolla sampled were measured and examined by stretching the lateral swelling of the carapace from the body in order to determinate whether the parasite was present following the procedure.
proposed by Roccatagliata & Lovrich (1999). The carapace length (CL) of each crab was measured from the posterior edge of the basis of the rostrum to the centre of the posterior edge of the carapace, as commonly used in this species (Roccatagliata & Lovrich 1999, Lovrich et al. 2004, Cárdenas et al. 2007). Growth models provided by Campodónico et al. (1974) and Lovrich (1997) were used to assess the size/age relationship of the specimens. The infested juvenile were dissected to extract bopyrids by removal of the left side of the branchial chamber. P. tuberculata tends to occur on the left side of the branchial chamber of their host as described by Roccatagliata & Lovrich (1999) and Miranda-Vargas & Roccatagliata (2004). The wet weights of all the juvenile king crabs collected were determined with a precision of ± 0.1 g. The body length of each Pseudione was measured using an ocular micrometer in a stereo microscope. The length of the females was measured from the anterior margin of the cephalon to the anterior margin of pleotelson. Males were measured from the anterior margin of cephalon to the posterior margin of pleotelson.

**Taxonomic identification**

Taxonomic identification was made following the literature on Pseudione spp., including Benedict (1894), Stuardo et al. (1986), Pardo et al. (1998), Román-Contreras & Werthmann (1997) and Miranda-Vargas & Roccatagliata (2004). A confirmation of the identity of Pseudione tuberculata was made by Dr. Daniel Roccatagliata of the Universidad de Buenos Aires, Argentina.

The diagnostic characters used in the identification included: body oval in shape, almost or all symmetrical, coxal plates not visible in dorsal view, the pleonal lateral plates and pleopods are moderately developed and the uropods are uniramous; uropods covered by pleopods; epimera of pleomeres slightly less produced; first oostegite, postero-lateral projection extending almost straight back; tubercules on marsupium; pleopods in all specimens barely extending beyond sides of pleon, and leaving mid-ventral surface of pleon exposed (marsupial female).

Voucher specimens of P. tuberculata (3 males/3 females) were deposited at the Museo Argentino de Ciencias Naturales in Buenos Aires, Argentina (MACN-36.692).

**Data analysis**

An analysis of variance (ANOVA) was used to determine significant differences in prevalence of infestation between males and females of Lithodes santolla, using Statistica 7.0 computer software. When significant differences were found, a posteriori Newman-Keuls test.
was applied to the data (Zar 1999). All our conclusions were based on a 95% ($P$<0.05) confidence level.

**Results**

**Levels of infestation**

A total of 216 *L. santolla* juvenile were collected at the Magellan Strait site. Sizes of the crabs ranged from 20.0-69.0 mm CL for females and from 18.5-75.0 mm CL for males. Overall, 54 (25.0%) of the *L. santolla* juveniles analyzed were infested by *Pseudione tuberculata*. Of the 118 females examined, 33 were infested by *P. tuberculata* (27.9%), while of 98 males, 21 (21.4%) were infested. No significant differences were found between sexes in relation to possible effects of *P. tuberculata* on the crab size ($P$ = 0.991) and weight ($P$ = 0.107). In all cases infestation consisted of one pair of bopyrids (adult female with a dwarf adult male) (Fig. 2). No multiple infestations were observed. *P. tuberculata* was always found on the left side of the carapace of the host (Fig. 3), with the exception of one case, in which a juvenile king crab was infested on the right side. In one case a juvenile was infested by *P. tuberculata* and also by the rhizocephalan *Briarosaccus callosus*, a rhizocephalan commonly reported infesting lithodids crabs (Lovrich et al. 2004). This is the first time *P. tuberculata* is reported infesting *L. santolla* in Chile.

**Figure 2**

Dorsal view of adult female of the bopyrid isopod *Pseudione tuberculata* collected in the Magellan Strait, Chile, parasitic on the king crab *Lithodes santolla*. The small square depicts the ventral posterior end of an adult female and the dwarf adult male (white arrow). Scale (both figures) = 0.5 mm

**Figure 3**

Posterior end of the *Lithodes santolla* juvenile with the left side inflated by the presence of the bopyrid parasite *Pseudione tuberculata* (black arrow). Carapace length of this specimen = 26 mm
Sizes of infested female crabs ranged from 23.0 to 51.6 mm CL, while male infested crabs ranged from 24.0 to 48.7 mm CL. The length-weight relationship between the infested and uninfested male and female crabs is shown in Fig. 4. No infested crabs of either sex were larger than 51.6 mm CL. No significant differences in the length-weight relationship were observed between males ($P=0.684$; $P=0.165$) and females ($P=0.755$; $P=0.352$). Weight of infested females ranged from 4.8 to 55.9 g, while the males weighed from 6.2 to 39.7 g. No significant differences were found between length and weight of parasitized and unparasitized juveniles ($P= 0.0991$; $P= 0.107$).

The average length of the parasite was 13.9 ± 2.2 mm ($N = 32$). The average total weight of each parasite pair was 0.61 ± 0.45 g ($N = 32$) in the crab females and was 0.49 ± 0.34 g ($N = 20$) in males. The average weight of parasitized crab females was 19.2 ± 14.9 g ($N = 33$), while in males it was 15.1 g ± 9.7 g ($N = 20$). The average weight of unparasitized crab females was 24.31 g ± 29.27 g ($N = 85$), while in males was 24.8 g ± 30.5 ($N = 77$).

**Discussion**

The presence of *P. tuberculata* in the branchial chamber of juvenile *L. santolla* analyzed in this paper was reported earlier by Richardson (1904) on *Neolithodes diomedeae* in the Chonos Archipelago, Chile. Later, Stuardo *et al.* (1986), Román-Contreras & Werthmann (1997) and Pardo *et al.* (1998) reported the presence of another member of the isopod genus in other benthic crustaceans of the Chilean coast. Recently, Miranda-Vargas & Roccatagliata (2004) re-described *P. tuberculata* and cited the presence of this parasite in the lithodids *Paralomis granulosa* and *L. santolla* in the Beagle Channel, Argentina.

The present study is the first report of *P. tuberculata* infecting *L. santolla* in Chile, with a new location at the Magellan Strait, about 640 km north of the Beagle Channel.
where it was first reported on *L. santolla*.

Miranda-Vargas & Roccatagliata (2004) did not provide data on the prevalence on *L. santolla*; to our knowledge, the prevalence presently reported is the first for this host-parasite pair. Roccatagliata & Lovrich (1999) reported that the prevalence of infestations by *P. tuberculata* on *P. granulosa*, decreased with crab size, from 45.6% at 10 to 20 mm CL to 0% at 90 to 100 mm CL. High infestation levels were found in *L. santolla* juveniles at the study site in the present work (27.9% in females and 21.4% in males). Parasite prevalence was high considering the low number of juveniles analysed. Prevalence values of this study are high when compared with infestation levels reported by González & Acuña (2004) for the galatheid crustaceans *Cervimunida johni* and *Pleuroncodes monodon* off the northern coast of Chile, which varied between 6.8% and 13.6% for the former species and between 0.6 to 18.2% for the latter, based on 1460 and 1677 specimens analysed, respectively.

As mentioned by Roccatagliata & Lovrich (1999), most branchial bopyrids occur nearly equally in the right and left side of the branchial chamber. There are, however, species that occur only or exclusively in one side. These all belong to the primitive Pseudioninae, and most are parasites of hermit crabs. However, reasons explaining this situation are still unknown. Preference of *P. tuberculata* to occur on the left branchial chamber of their hosts, has been reported for *P. granulosa* (99.6%) as well as for *L. santolla* (100%) sampled at the Beagle Channel (Miranda-Vargas & Roccatagliata 2004). In our study, *P. tuberculata* occupied left branchial chambers in 98.1% of the *L. santolla* specimens analysed, confirming this preference suggested by previous works.

There is much information showing that bopyrids can reduce or even completely stop growth of the host (Petriella & Boschi 1997). Bopyrid isopods can affect the reproduction of their definitive hosts by partially or totally inhibiting gonad development, modifying secondary sexual characters in males, inhibiting growth, and producing nutritional deficiency in their hosts (Reinhard 1956, Beck 1980, Van Wyk 1982, McDermott 1991, Muñoz & George-Nascimento 1999, Astete-Espinoza & Cáceres 2000). In other cases it has been suggested that hosts grow faster because of parasite-induced hunger, eating more food than unparasitized individuals (Choi et al. 2004). Information available about the effect of presence and prevalence of parasites in crustacean decapods in South America is still lacking in the literature. Roccatagliata & Lovrich (1999) suggested that the reproductive potential of the population of *Paralomis granulosa* is not seriously affected by the sterilizing effect of *P. tuberculata*. Nevertheless effects of *P. tuberculata* have not been tested empirically.

Crabs without parasites reached larger body length and weight (Fig. 4) than those parasitized. There are three possible explanations for these results, 1) parasitized crabs grow less than the non-parasitized hosts because of the nutritional demands that the parasite has (Astete-Espinoza & Cáceres 2000), 2) parasitized crabs died earlier than those non-parasitized, or 3) crabs over 50 mm length were never parasitized by bopyrid isopods. According to Muñoz & George-Nascimento (1999) these isopods used to reach young hosts only, so large and non-parasitized hosts were never parasitized by isopods. This suggests that *P. tuberculata* may have an important role in population control of juvenile king crabs.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Carapace length (mm)</th>
<th>Weight of crab (g)</th>
<th>Length of <em>P. tuberculata</em> (mm)</th>
<th>Weight of <em>P. tuberculata</em> (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female average ± SD</td>
<td>34.5± 8.4</td>
<td>19.2± 14.9</td>
<td>15.5± 3.2</td>
<td>0.61± 0.45</td>
</tr>
<tr>
<td>Range</td>
<td>23.0-51.6</td>
<td>4.8-55.9</td>
<td>10.0-21.8</td>
<td>0.12-1.96</td>
</tr>
<tr>
<td>Male Average ± SD</td>
<td>32.9± 6.6</td>
<td>15.1± 9.7</td>
<td>15.5± 2.7</td>
<td>0.49± 0.34</td>
</tr>
<tr>
<td>Range</td>
<td>24.0-48.7</td>
<td>6.2-39.7</td>
<td>11.8-19.4</td>
<td>0.07-1.12</td>
</tr>
</tbody>
</table>
All parasites were mature females, each typically carrying a small male specimen attached to the abdomen. The length of the female isopods and that of their host were positively correlated, suggesting that the parasites infest *L. santolla* early in the life of the host, and persist in and grow along with the host throughout life.

Several authors have suggested different explanations concerning the relationship of prevalence of infestation and host size. Rousset *et al.* (1996) suggested that a decrease in the parasitic load or its dispersion with host age can be considered as evidence of host mortality induced by the parasite. According to González & Acuña (2004), the strong decrease of bopyrid prevalence in larger sizes of the host could be a consequence of host mortality induced by the parasite or by growth inhibition of the host. However, they also suggested that the parasite could be lost after several ecdyses. Roccatagliata & Lovrich (1999) reported that the prevalence of the parasite *P. tuberculata* in the Beagle Channel decreased with increasing size in *Paralomis granulosa*, suggesting a high mortality rate for small parasitized crabs. Nevertheless, they suggested that the absence of *P. tuberculata* in larger sizes (<60 mm CL) could be explained by the shorter life-span of the parasite, assuming a longevity of about eight years in the range of size between 20 to 60 mm CL. This is probably the same situation in juveniles of *L. santolla*, supported by the high infestation values up to a determinate size (~50 mm CL), as observed in this study, although more research is required to clarify this situation in the future.

During this study, the water column was nearly homogeneous from surface to bottom. The variation in salinity was from 29 to 30.64 psu, temperature varied from 6.5 to 6.6°C, and density from 23.5 to 24.0 s units in both sampled sites and in both years. These values were typical in this area of the Magellan Strait (Panella *et al.* 1991, Antezana 1999, Valdenegro & Silva 2003). According to Silva *et al.* (1995, 1998) and Sievers *et al.* (2002), Magellan Strait waters with a salinity of less than 32 psu is a typical estuarine condition. Slight seasonal variations in the salinity of seawater in the embayment studied could promote larval retention and recruitment to the benthos for *Lithodes santolla* as well as other local benthic invertebrates (Strathmann 1982, Levin 1983). Kelp beds provide important habitats for a variety of marine organisms as well as, contribute to wave damping, which affects local hydrodynamic conditions, providing protection from water motion (Ekman *et al.* 1989, Balch & Scheibling 2000). These effects could increase the retention of larval stages of parasitic isopods as it has been postulated for other larval stages of invertebrates as well as for detritus and organic matter (Ekman *et al.* 1989; Duggins *et al.* 1990, Pakhomov *et al.* 2002). One or more of these characteristics of kelp beds may help to explain the high levels of infestation of *P. tuberculata* on *L. santolla* recruits that settle in kelp beds. Also, because

### Table 2

**Comparison of the prevalence of the bopyrid isopod *Pseudione tuberculata* in two species of lithodids (*Paralomis granulosa* and *Lithodes santolla*) from two locations at the southern tip of South America**

<table>
<thead>
<tr>
<th>Lithodid species</th>
<th><em>Paralomis granulosa</em> (Beagle Channel, Argentina)</th>
<th><em>Lithodes santolla</em> (Magellan Strait, Chile)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Host size (mm CL)</td>
<td>Prevalence</td>
<td>Prevalence</td>
</tr>
<tr>
<td>&lt; 10</td>
<td>0</td>
<td>not caught</td>
</tr>
<tr>
<td>10 to 20</td>
<td>45.6</td>
<td>65</td>
</tr>
<tr>
<td>20 to 30</td>
<td>35.0</td>
<td>22</td>
</tr>
<tr>
<td>40 to 50</td>
<td>8.7</td>
<td>≤ 2</td>
</tr>
<tr>
<td>90 to 100</td>
<td>&lt; 1</td>
<td>not caught</td>
</tr>
<tr>
<td>General</td>
<td>not indicated</td>
<td>28 (♀) to 21.5 (♂)</td>
</tr>
<tr>
<td>Side of carapace infested</td>
<td>Left</td>
<td>Left</td>
</tr>
<tr>
<td>Size range of host (mm)</td>
<td>10 to 100</td>
<td>23 to 52</td>
</tr>
<tr>
<td>Reference</td>
<td>Roccatagliata &amp; Lovrich (1999)</td>
<td>This study</td>
</tr>
</tbody>
</table>
sites studied were shallow with homogeneously oceanographic features in the water column, larval retention, *Pseudione* survival, and infestation rates may be higher in the present study because of the homogenous water column as opposed to sites in stratified areas (Sulkin *et al.* 1980, Roegner 2000). Recently, Cárdenas *et al.* (2007) described the aggregate behavior, known as podding, of juvenile *L. santolla* at the same area studied here. Aggregations of organisms could explain high parasite prevalence due to the local abundance of hosts available. This podding may explain why there was a higher level of parasitism in this study in comparison with other species (without presence of this aggregation behaviour) infested by *Pseudione* in other parts of Chile. Nevertheless, this situation should be clarified in future studies.

The presence of *P. tuberculata* infesting *L. santolla* and *P. granulosa* contradicts the assumed degree of host specificity by bopyrids and the apparently restricted distributions of bopyrid parasites relative to those of their host, as suggested by Kazmi & Boyko (2005) based on their preliminary data. An important conclusion of the present study is that the parasite responds in a similar way in both *Lithodes santolla* and *Paralomis granulosa*, independently of the location in the southern end of South America. Thus, high prevalence of *P. tuberculata* is found in crabs of 10-20 mm CL in both crustaceans and remains near to 40-50 mm (Table 2). Differences in the percentage of infestation could be because of the differences in sampling methods. Argentinean researchers used information based on fishery activities (Roccatagliata & Lovrich 1999). However, in our study, we targeted mainly the smallest individuals found in shallow water. In the future, more studies will be needed to clarify the relationship of prevalence of infestation and host size.

Finally, we propose that the study area is a good experimental site for research on ecological recruitment and the effects of parasitism in *Lithodes santolla*. For over two years we have been able to predict the months (winter) when the king crab recruits begin to colonize shallow waters, which coincides with periods of higher flux of freshwater discharged by the San Juan River. Future studies are required to clarify any relationship between increase in freshwater discharge and the presence of *L. santolla* recruits and infestations of *P. tuberculata*.

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