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Infestation of the squat lobster *Munida gregaria* (Anomura: Galatheidae) by *Pseudione galacanthae* (Isopoda: Bopyridae) in San Jorge Gulf, Argentina

MARTÍN VARISCO[1,2] AND JULIO VINUESA[1,3]

[1]Instituto de Desarrollo Costero—Universidad Nacional de la Patagonia San Juan Bosco (IDC–UNPSJB) y Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), [2]Facultad de Ciencias Naturales. UNPSJB, [3]Facultad de Humanidades y Ciencias Sociales, UNPSJB, Campus Universitario, Ruta 1 km 4 (9000) Comodoro Rivadavia, Chubut, Argentina

We estimated the prevalence of the bopyrid Pseudione galacanthae *parasitizing the population of the squat lobster* Munida gregaria *in San Jorge Gulf and analysed some aspects concerning the effect of the parasite on host reproductive potential. The relationship between the development stages of the parasite and the host size was also analysed. The squat lobsters were caught as by-catch in the coastal area of the gulf from vessels operating in the fisheries of hake* Merluccius hubbsi*, southern king crab* Lithodes santolla *and Argentine red shrimp* Pleoticus muelleri*. The samples were collected between October 1997 and June 2009. In the laboratory, squat lobsters were sexed and the length of their carapace was measured. In males, the length of the right cheliped was recorded and gonadal development was examined. In females, the size and number of carried eggs were determined and the length of the pleopods III, IV and V were measured. All squat lobsters parasitized exhibit a gross bulge in the right side of carapace. Prevalence ranged between 0 and 1.43% ($N = 21{,}519$). No significant differences in prevalence were found for sexes, depths and seasons. The prevalence was higher for the size interval 7–10 mm CL (0.79%) than for the rest of the intervals. Parasitism had no effect on the secondary sex characters. Parasitized males displayed gonad development. There was no difference in prevalence between ovigerous and non-ovigerous squat-lobster females. Parasitized females had smaller eggs than non-parasitized ones, but their fecundity was similar. The linear relationship between the parasite and host sizes and the presence of larvae and immature stages of* P. galacanthae *in small-sized squat lobsters suggest that the host is infected early in its development. The low prevalence could be related to oceanographic conditions which favour larval dispersal of the parasite and host. The infestation by* P. galacanthae has little impact *on the* M. gregaria *population, mostly due to the low prevalences of infestation and the minor impact in reproductive function.*

Keywords: parasitism, prevalence, bopyrid, Galatheidae, Southern Atlantic Ocean

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INTRODUCTION

The family Bopyridae is composed of numerous subfamilies whose members are branchial or abdominal parasites of Crustacea (Markham, 1986). The life cycle of the bopyrids typically includes the epicaridium larva, which is ectoparasite of calanoid copepods and undergoes two larval stages known as microniscus and cryptoniscus. The latter larval stage leaves the copepod in search of a decapod crustacean. The first larva reaching the branchial chamber develops as a female and the next one arriving develops as a male, which remains attached to uropods of the female (Beck, 1980).

The interaction between bopyrids and galatheids is widely known, with the latter being the most ancient crustacean hosts as evidenced by the fossil record (Markham, 1986). There are about 60 species of galatheids acting as hosts for bopyrids. *Pseudione* and ten other genera of the subfamily Pseudioninae are ectoparasites of the members of genus *Munida* (Román-Contreras & Boyko, 2007). Prevalences of infestation with bopyrids have been reported for many squat lobsters such as *M. rugosa* (Fabricius, 1775) (Bourdon, 1968), *M. tenuimana* Sars, 1872 (Mori *et al.*, 1999), *M. intermedia* A. Milne-Edwards and Bouvier, 1899 (Gramito & Froglia, 1998), *M. longipes* A. Milne-Edwards, 1880, *M. iris iris* A. Milne-Edwards, 1830 and *M. microphtalma* Milne-Edwards, 1880 (Lewis-Wenner & Windsor, 1979).

The infestation of *Munida gregaria* (Fabricius, 1973) by *Pseudione galacanthae* (Hansen, 1897) has been reported by Rayner (1935). Later, it has been mentioned in various localities along the Argentine coast such as the Beagle Channel, Puerto Deseado (Miranda-Vargas & Roccatagliata, 2004) and Puerto San Julián (Varisco, unpublished). Rayner (1935) reported a single prevalence value for a large region in the Argentine Sea not including San Jorge Gulf. Prevalence may be affected by local conditions and seasonal variations linked to the life cycle and biology of both parasite and host (Muñoz & George-Nascimento, 1999; Cañete *et al.*, 2008). In particular, there are no data on the prevalence of *P. galacanthae* in the squat lobster population in San Jorge Gulf.

Corresponding author:
M. Varisco
Email: martinvarisco@hotmail.com

Bopyrid infestation may play an important role in the regulation of some decapod populations. González & Acuña (2004) points out that the bopyrid *P. humboldtensis* Pardo, Guisado, and Acuña, 1998 has a remarkable impact on commercially exploited populations of *Pleuroncodes monodon (*Milne-Edwards, 1837) and *Cervimunida johni* Porter, 1903 from northern Chile. The deleterious effects of parasite infestation on a population are reflected in high prevalence and mortality rates and in a reduction in the reproductive potential of the host (Reinhard, 1956; Beck, 1980; Astete-Espinoza & Cáceres, 2000). Females are usually more affected than males because they have a higher reproductive investment; parasitism usually causes ovarian dysfunction and, in some decapod species, a decrease in the size of pleopods (Bourdon, 1968; Mori *et al.*, 1999). In males, parasites most often induce modifications in secondary sex characters (Reinhard, 1956).

In this study, the impact of the parasite *P. galacanthae* on the *M. gregaria* population in San Jorge Gulf is investigated. For this purpose, the prevalence of the parasite was analysed in relation to sex, host size, season and water depth. The effect of infestation on the reproductive potential of the squat lobster and the relationship between host size and size and degree of development of the parasite were also analysed.

MATERIALS AND METHODS

Study area and field sampling

The study area encompassed the inner central shelf of San Jorge Gulf, which is the widest sea entrance along the Patagonian Atlantic coast. The gulf extends from Cape Dos Bahías in the north to Cape Tres Puntas in the south (Figure 1) with a maximum depth of approximately 100 m (Vinuesa, 2005). The convergence of sub-Antarctic waters of the Malvinas Current and warm temperate waters from the north-east result in a large ecotone of considerable biogeographical importance, lining the Patagonian coasts from 42° to 47°S approximately. Along the coastal patagonic waters was observed a minimum of salinities ($S < 33.6$) that represents the Patagonian current (Brandhorst & Castello, 1971), resulting from low salinity waters flow from the Magallanes Strait and Tierra del Fuego, with lateral mixing and warming of the pure sub-Antarctic waters. No coastal 'fronts' were described for inner waters of San Jorge Gulf (Guerrero & Piola, 1997), but no detailed studies were conducted here. Stratifications were observed in several parts of the Argentine continental platform during summer, but are unlikely to happen in the coastal area, due to the existence of macrotides and high frequency of strong winds. The coastal area off the localities of Comodoro Rivadavia and Caleta Córdova shows soft bottoms with a gentle slope. It becomes steeper at 45–55 m depth, reaching depths less than 80 m at a distance of 10 km to the coast.

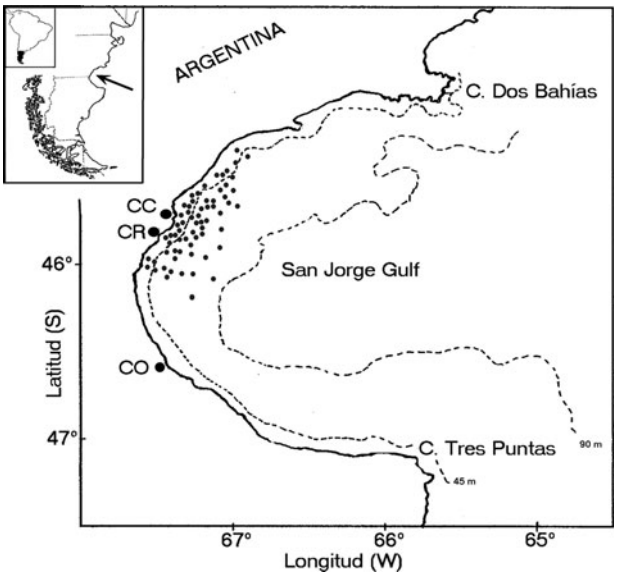

Fig. 1. San Jorge Gulf, Argentina, south-western Atlantic Ocean. CR, Comodoro Rivadavia; CC, Caleta Córdova; CO, Caleta Olivia.

The squat lobsters were sporadically sampled between 1997 and 2009. They were obtained from vessels involved in the fisheries of hake, *Merluccius hubbsi* Marini, 1933, the southern king crab *Lithodes santolla* (Molina, 1782) and the Argentine red shrimp *Pleoticus muelleri* (Bate, 1888), operating from the harbours of Comodoro Rivadavia, Caleta Olivia and Caleta Córdova. The geographical position and depth of capture were recorded each time. Pelagic juvenile specimens were collected using a 300-μm mesh plankton net with 0.7 m of diameter of mouth from a vessel, from tidal pools and alive recently stranded on the beach in 2009. The samples were fixed in 4% formaldehyde until further analysis.

Laboratory analysis

In the laboratory, adult specimens were sexed and their caparace length (CL) measured to the nearest 0.01 mm with a digital caliper. Carapace length was the distance between the posterior orbital margin and the posterior median margin. Juveniles were measured with a graduated eyepiece under a stereoscopic microscope, but only those larger than 10 mm CL were sexed. The branchial chambers of each squat lobster were examined under a stereoscopic microscope to search for bopyrids. To evaluate the effect of parasitism on male reproductive potential, the right cheliped length was measured and the gonadal development was evaluated under a stereoscopic microscope. The presence of eggs in infested females was recorded, and these were measured to the nearest 0.1 mm using a graduated eyepiece in a stereoscopic microscope.The pleopods III–V of parasitized females were measured to evaluate the effect on secondary sex characteristic. Fecundity was also determined, following the procedures described in an earlier work (Vinuesa, 2007). These procedures were repeated with a similar number of uninfested males and females.

The parasites recovered were measured. The total length (TL) was measured from the anterior margin of cephalon to the posterior margin of uropods for females, and from the anterior margin of cephalon to the posterior margin of pleotelson for males. In addition, the maturity status of females was assessed according to the criteria of Roccatagliata & Torres Jordá (2002) with minor modifications.

Statistical analysis

The non-parametric Chi-square test with Yates correction (Sokal & Rohlf, 1995) was applied for the comparison of

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prevalence between individuals caught below and above 45 m depth. At this depth there is a change in the slope of the sea bottom off Comodoro Rivadavia and Caleta Córdova. Specimens recently stranded on the beach were not included in this analysis. Differences in prevalence among seasons were tested with an exact test. The exact test is a generalization of the Fisher procedure and calculates an exact probability value for the relationship between two variables in larger tables (Agresti, 1992). Carapace length values were grouped into eight size-classes. An exact test was used to determine independence between prevalence and host size, followed by Bonferroni-corrected pairwise comparisons. For each size-class, the Fisher's exact test was used to test independence between sexes.

The Chi-square test with Yates correction was employed to determine whether infestation caused the castration of females. A comparison was made between the prevalence of ovigerous and non-ovigerous squat lobsters larger than 13 mm CL, which is the size at which all females are mature (Vinuesa, 2007). To evaluate the effect of parasitism on egg size, eggs of parasitized and non-parasitized lobsters were compared using one-way analysis of variance. Normality and homogeneity of variances were tested by the Kolmogorov–Smirnov and Cochran tests, respectively. Covariance analysis was used to test for differences in the development of chelipeds in males and pleopods in females. The assumption of homogeneity of slopes was previously tested.

To determine the relationship between host size and parasite size, regression analyes were performed in males and females separately. The determination coeficient was estimated too.

RESULTS

Characterization of the host population

A total of 21,519 squat lobsters from San Jorge Gulf were captured between 1997 and 2009. The CL ranged between 3.6 and 32.4 mm in non-infested and between 8.3 and 26.3 mm in infested squat lobsters. The male:female proportion was 1.37:1 for specimens >10 mm CL, but there were seasonal and local variations. Juvenile squat lobsters (<10 mm CL) were collected during summer and early autumn. Specimens of the morphotype *gregaria* were found in waters of San Jorge Gulf in 2008 (N = 13) and 2009 (N = 1220). In previous years only squat lobster of the *subrugosa* morphotype were collected. Despite the small number of *gregaria* specimens captured, both morphs were found parasitized.

Bopyrid infestation

The parasitized squat lobsters (N = 69) exhibited a gross bulge on the side where the parasite was found. The parasite was present in all specimens with distorted carapace. In all cases the parasite occupied the right branchial chamber (Figure 2). The female bopyrid was found with its head pointing toward the host's abdomen and its dorsal surface in contact with the gills, which were slightly flattened in fixed specimens. Branchial filaments had no visible lesions and no evidence of multiple infestations was observed in any of the squat lobsters infested.

Fig. 2. Specimen of *Munida gregaria* (carapace length = 18.5 mm) showing the carapace bulge caused by the bopyrid *Pseudione galacanthae* in San Jorge Gulf, Argentina.

Prevalence

The prevalence of *P. galacanthae* in *M. gregaria* was very low throughout the study, with a mean value of 0.34% (90% confidence interval limit: 0.27–0.41). The highest prevalence obtained in a sample was 1.43% (Table 1). No significant differences in prevalence were found between specimens collected below and above 45 m depth (χ Yates correction = 1.00; $P = 0.31$) (Table 2) and among seasons ($\chi = 4.04$; df = 3; $P = 0.25$) (Table 3). The prevalence differed significantly among size-classes ($P = 0.010$). The *a posteriori* test revealed that this difference was due to higher prevalences in the size-class 7.0–9.9 mm CL (χ Yates corrected = 10.69, $P = 0.001$). There were no significant differences in prevalence between sexes in each size-class (Table 4).

Bopyrid effect on host reproductive potential

In males, the presence of the parasite had no effect on the propodite of the first pair of pereiopods (ANCOVA df = 1; f = 2.82; $P = 0.098$). In addition, developed testes and distended deferent ducts were observed in parasitized males during the reproductive season.

Seven parasitized ovigerous females were collected, with complete broods and recently spawned eggs. There was no significant difference in prevalence between non-ovigerous and ovigerous females (>13 mm CL) (χ Yates corrected = 1.80, $P = 0.17$) (Table 5). No differences were found in the size of pleopods III–V between infested and uninfested females (Table 6). The egg size of parasitized females was significantly lower (ANOVA, df = 1; f = 5.85; $P = 0.03$) than that of non-parasitized females. Infested and non-infested ovigerous females had similar fecundity values, but statistical comparisons were not made due to the small number of the former.

Relationship between bopyrid and host size

Bopyrid females were always present in squat lobsters showing distorted carapaces. Only one dwarf male was found on the female abdomen. Although males were missing in some of the parasitized hosts, the arrangement of the female's

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Table 1. Prevalence of *Pseudione galacanthae* in *Munida gregaria*, in the central area of San Jorge Gulf, Argentina.

Date	N	Parasite	Prevalence
Oct-97	588	2	0.34
Dec-97	596	5	0.84
May-98	382	1	0.26
Aug-98	464	1	0.22
Dec-98	420	2	0.48
Jan-99	441	2	0.45
Feb-99	467	0	0.00
Apr-99	342	1	0.29
May-99	595	0	0.00
Jun-99	688	3	0.44
Jul-99	1067	3	0.28
Aug-99	340	1	0.29
Sep-99	310	3	0.97
Oct-99	70	1	1.43
Nov-99	545	1	0.18
Dec-99	535	2	0.37
May-00	2394	4	0.17
Jul-00	226	3	1.33
May-01	439	1	0.23
Aug-01	504	1	0.20
Oct-01	342	1	0.29
Jan-02	956	7	0.73
Jan-06	75	0	0.00
May-06	126	0	0.00
Jul-06	102	1	0.98
Aug-06	120	1	0.83
Nov-06	80	0	0.00
Jun-08	1301	3	0.23
Aug-08	597	0	0.00
Sep-08	83	0	0.00
Jan-09	714	2	0.28
Feb-09	1813	7	0.39
Mar-09	846	2	0.24
Abr-09	530	1	0.19
May-09	1494	8	0.54
Jun-09	598	1	0.17
Aug-09	329	2	0.61

pleopods provided evidence of their earlier presence. The size of bopyrid females was directly related to host size ($P = 0.000$, $N = 53$). The male size was also directly related to host size ($P = 0.000$; $N = 33$) (Figure 3). In addition, a postmoult squat lobster had a parasite with soft carapace.

Squat lobsters in the size-class 7–10 mm CL harboured immature females with cryptoniscii larvae. One of these lobsters had five larvae attached to the pleon of the parasitic female. The larvae and early stages of the parasite were found during summer, simultaneously with a higher abundance of the host juvenile stages. No larvae were detected in specimens <7 mm CL. Immature females of *P. galacanthae* were found in squat lobsters >7 and <10 mm CL during summer and early autumn. The specimens in the remaining size-classes were infested with mature females (Figure 4). Ovigerous bopyrid females were observed in hosts between 10 and 26.3 mm CL all year round.

Table 2. Prevalence of the bopyrid *Pseudione galacanthae* in *Munida gregaria* specimens collected below and above 45 m depth; 95% confidence interval limit with continuity correction in parentheses. Specimens stranded on the beach were not included in the analysis.

	<45 m	>45 m
Parasitized	22	38
Non-parasitized	6206	14552
Prevalence (%)	0.35	0.26
	(0.22–0.53)	(0.18–0.35)

DISCUSSION

Bopyrid infestation

The preference for one branchial chamber is common in the subfamily Pseudioninae (Markham, 1986). There may be a link between the exclusive presence of the parasite in the right branchial chamber and the absence of multiple infestations. A similar behaviour has been observed for bopyrids parasitizing other sub-Antarctic anomurans, such as *Lithodes santolla* (Vinuesa, 1989; Cañete *et al.*, 2008) and *Paralomis granulosa* (Jacquinot, 1847) (Vinuesa, 1989; Roccatagliata & Lovrich, 1999). Rayner (1935) in the south-west Atlantic Ocean reported a preference of 92% for the right branchial chamber and double infestation in 3.3% in *Munida gregaria*.

In contrast to other host–parasite interactions described in the literature, *Pseudione galacanthae* was always found in lobsters from San Jorge Gulf with carapace swelling. This suggests that infested individuals cannot remove the parasite through successive moults. Some authors indicate that bopyrids missing in decapods with signs of a former infestation (carapace with bulge) had been removed by the hosts (Sommers & Kirkwood, 1991; Cash & Bauer, 1993; Roccatagliata & Lovrich, 1999).

Prevalence

The species of genus *Munida* usually have low prevalence values of bopyrid infestation. The prevalence of *Anuropodione carolinesis* Markham, 1973 in the squat lobster *Munida iris iris* from the north-western Atlantic Ocean was found to range between 2 and 5% (Lewis-Wenner & Windsor, 1979). Prevalences of 0.06 and 0.6% were reported for *Munida tenuimana* and *Munida intermedia* respectively (Gramito & Froglia, 1998; Mori *et al.*, 1999). The highest prevalences recorded for *Munida longipes* and *Munida microphtalma* were about 5% (Lewis-Wenner & Windsor, 1979) and a prevalence of about 1–2% was reported for *Munida rugosa* (Bourdon, 1968). The infestation of *M. gregaria* by *P. galacanthae* in the Argentine continental shelf showed a prevalence of 7.4% in the *subrugosa* morphotype and 3.7% in the *gregaria* morphotype (Rayner, 1935). The low prevalences found in the present study are in agreement with the results obtained for other species of the genus, but lower than that observed by Rayner (1935). This difference may be related to the local conditions in the central area of San Jorge Gulf.

Environmental conditions play a major role in the prevalence of bopyrid infestation among decapod populations. High prevalences of *P. tuberculata* in the southern king crab *Lithodes santolla* from the Magellan Strait were attributed to a reduction in the water flow due to the presence of *Macrocystis pyrifera*, (L) Agardh 1820, forests (Cañete *et al.*, 2008). Muñoz & George-Nascimento (1999) found that the prevalence of *Ionella agassizi* Bonnier, 1900 parasitizing the

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Table 3. Prevalence of the bopyrid *Pseudione galacanthae* in *Munida gregaria* by season; 95% confidence interval limit with continuity correction in parentheses.

	Winter	Spring	Summer	Autumn
Parasitized	20	8	27	18
Non-parasitized	6316	2010	5990	7130
Prevalence (%)	0.31 (0.19–0.47)	0.39 (0.17–0.74)	0.44 (0.30–0.64)	0.25 (0.15–0.38)

ghost shrimp *Neotrypaea uncinata* (H. Milne-Edwards, 1837) was higher in estuaries than on open coasts. *Pseudione humboldtensis* Pardo, Guisado & Acuña, 1998 has been reported parasitizing the galatheids *Cervimunida johni* and *Pleuroncodes monodon* with variable values at different localities along the Chilean coast (Pardo *et al.*, 1998; González & Acuña, 2004). It has been suggested that the high prevalence of the parasitic barnacle *Briarosaccus callosus* Boschma, 1930 in the golden king crab *Lithodes aequispina* (Benedict, 1894) is related to high larval retention, as commonly observed in fjords (Sloan, 1985). These findings suggest that prevalences are higher in areas with low water circulation, even if the life cycle of the parasite includes an intermediate host, as is the case with bopyrids. In the central area of the San Jorge Gulf, *M. gregaria* occurs mainly on coastal soft bottoms (Vinuesa, 2005). The low prevalence values obtained for specimens from the coastal area (<45 m) and deeper waters (>45 m) may be explained by the lack of benthic algae and bottom irregularities which could reduce currents flow and promote larval retention.

Differences in the prevalences between sexes are related to the higher energetic cost of reproduction for female (Astete-Espinoza & Cáceres, 2000). No difference in bopyrid prevalence was found between males and females of *M. iris iris* (Lewis-Wenner & Windsor, 1979), *M. intermedia* (Gramito & Froglia, 1998) and *Cervimunida johni* (González & Acuña, 2004). Likewise, in San Jorge Gulf squat lobsters of both sexes did not differ in prevalence, independently of their size. This would be related to a minor negative effect of parasitism on females. The relationship among prevalence, season and host size is discussed below.

Effect on host reproductive potential

A negative effect of bopyrid parasitism on reproduction (e.g. reduced gonads and poor development of secondary sexual characteristics) has been reported in several species (Beck, 1980; Schuldt & Rodrigues-Capítulo, 1985; Muñoz & George-Nascimento, 1999; Roccatagliata & Torres Jordá, 2002). Reinhard (1956) states that parasites may affect adversely the secondary sex characters of males. Many authors have reported feminization in parasitized males (Reinhard, 1956; Beck, 1980; Muñoz & George-Nascimento, 1999) and no effect on testis development (Beck, 1980; Schuldt & Rodrigues-Capítulo, 1985; Muñoz & George-Nascimento, 1999). In San Jorge Gulf, the bopyrid affected neither the testis development nor secondary sex characters of infested males, indicating no negative impact on their reproductive function. However, variations in sperm production and behaviour of infested males should not be ruled out.

According to Reinhard (1956), gonadal development is more affected than the secondary sex characters in females parasitized by epicaridean isopods. However, a decrease in the length of the last three pleopods has been observed in parasitized specimens of *M. tenuimana* (Zariquiey Alvarez, 1958; Bourdon, 1968). The parasitized females of *M. gregaria* from San Jorge Gulf showed normal secondary sex characters. Moreover, the similar prevalence of *P. galacanthae* in ovigerous and non-ovigerous females suggests the absence of parasite-induced castration. The lack of significant effect on egg size suggests a low parental investment related to the energetic cost of parasitism. Fecundity did not seem to be affected by the bopyrid, but this issue is worthy of more detailed investigation. These results together suggest that the reproductive potential of *M. gregaria* in San Jorge Gulf would not be reduced by the parasitic infestation.

Relationship between bopyrid and host size

In other Anomura, prevalence decreases as size increases, with the highest values being recorded at early development stages

Table 4. Prevalence of the bopyrid *Munida gregaria* in *Pseudione galacanthae* by host size-class (carapace length in mm). For each size-class, the *P* value in the last column indicates the probability of rejecting the null hypothesis of independence between infestation and sex.

Carapace length (mm)	Female		Male					Fisher's
	N	Prevalence	N	Prevalence	Parasitized	Total	Prevalence	exact (*P*)
<7	.....	.....	.....	.....	0	402	0.00	.....
7–9.99	.....	.....	.....	.....	13	1645	0.79	.....
10–12.99	1586	0.12	1736	0.17	5	3322	0.15	0.3
13–15.99	1160	0.25	1247	0.16	5	2407	0.21	0.3
16–18.99	3348	0.32	1897	0.42	19	5245	0.36	0.159
19–21.99	2008	0.29	2928	0.34	16	4936	0.35	0.19
22–24.99	101	1.98	2442	0.40	12	2543	0.43	0.07
≥25	4	0	1015	0.30	3	1019	0.29	0.98

N, number of specimens; *P*, probability.

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Table 5. Prevalence of the bopyrid *Pseudione galacanthae* in ovigerous and non-ovigerous females of *Munida gregaria* >13 mm carapace length; 95% confidence interval limit with continuity correction in parentheses.

	Non-ovigerous	Ovigerous
Parasitized	15	7
Non-parasitized	5385	1214
Prevalence (%)	0.27 (0.15–0.44)	0.57 (0.24–1.11)

(Rocattaglatia & Lovrich, 1999; González & Acuña, 2004). A reduction in the prevalence of *P. humboldtensis* in the squat lobsters *Cervimunida johni* and *Pleuroncodes monodon* from Chile has been attributed to the removal of the parasite (González & Acuña, 2004). However, this is not likely the case in the parasite–host interaction studied here.

The prevalence was significantly higher in the size-class 7–9.99 mm CL than in the remaining ones. Infestation may occur in this size-class as suggested by the presence of immature females and cryptoniscii larvae. A substantial decrease in the prevalence coincided with the onset of sexual maturity in the bopyrid females. The ovarian maturation of the parasitic female may exert additional pressure on the host caused by increased energetic demand; this would lead to an increase in mortality, and ultimately, to a decrease in the prevalence of larger size intervals. The stabilization of the prevalence at larger sizes may reflect low parasite-induced host mortality (Roccatagliata & Lovrich, 1999). The early stages of the parasite observed during summer and at the beginning of autumn occurred simultaneously with an increase in the number of *M. gregaria* juveniles. This developmental synchrony between host and bopyrid has been mentioned for other anomurans such as *Munida iris iris* (Lewis-Wenner & Windsor, 1979), *Paralomis granulosa* (Roccatagliata & Lovrich, 1999) and *Petrolisthes armatus* Gibbes, 1850 (Oliveira & Masunari, 2006). Roccatagliata & Lovrich (1999) suggested that the presence of mature females of the bopyrids at early host stages reveals an early infestation. Also, a linear relationship between host body size and parasite size would be evidence of an early infestation, parallel growth and moulting synchronicity of host and parasite. Furthermore, this relationship between parasite and host size and larger infested squat lobster suggests a life-long relationship.

The wide size-range of ovigerous females of *P. galacanthae* may indicate that it undergoes multiple spawnings during its lifetime. Some bopyrid species are known to spawn four or five times over their lifespan (Pike, 1960). Bopyrids occurring at low latitudes are expected to exhibit prolonged reproductive periods (Román-Contreras & Romero-Rodríguez, 2005; Oliveira & Masunari, 2006). An interruption in the

Table 6. Covariance analysis to test the efect of parasitism on secondary sex characters in females of *Munida gregaria*.

Sex	Character	df	F	*P*
Female	Pleopod III	1	1.47	0.229
	Pleopod IV	1	3.41	0.069
	Pleopod V	1	2.71	0.104

df, degree of freedom; F, F ratio; *P*, probability values associated with F values.

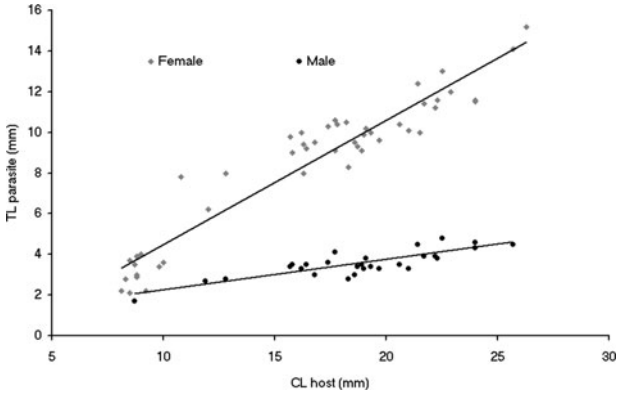

Fig. 3. Relationship between carapace length (CL, mm) of the *Munida gregaria* and total length (TL, mm) of the parasite *Pseudione galacanthae*. Equation for the regression of bopyrid females and probability value: TL = 1.58 + 0.608 CL ($P = 0.000$) ($R^2 = 0.90$). Equation for the regression of bopyrid males and probability value: TL = 0.79 + 0.148 CL ($P = 0.000$) ($R^2 = 0.69$).

reproductive activity in winter time has been documented in *Petrolisthes armatus* at mid-latitudes (Oliveira & Masunari, 2006) and in *Uca uruguayensis* Nobili, 1901 (Torres Jordá & Roccatagliata, 2002). In this work, ovigerous females of *Pseudione galacanthae* occurred throughout the year. Their wide temporal distribution was inconsistent with the short infestation period in juvenile squat lobsters. A continuous reproduction with an infestation period of six months has been reported by McDermott (1991) for the bopyrid *Leidya bimini* Pearse, 1951. In order to explain this behaviour, Torres Jordá & Roccatagliata (2002) suggested that epicaridium larvae would remain for a longer time in the intermediate copepod host until environmental conditions become favourable. Other factors related with epicaridium–copepod interaction and physical dynamics of water column may influence the infestation period.

Effect on squat lobster population

Finally, the prevalence of *P. galacanthae* in the natural *M. gregaria* population from San Jorge Gulf was found to be related to host size but not to depth, season or host sex. The temporal distribution of juvenile lobsters would be the major regulating factor of infestation. The parasite seems to have a minor impact on the *M. gregaria* population because

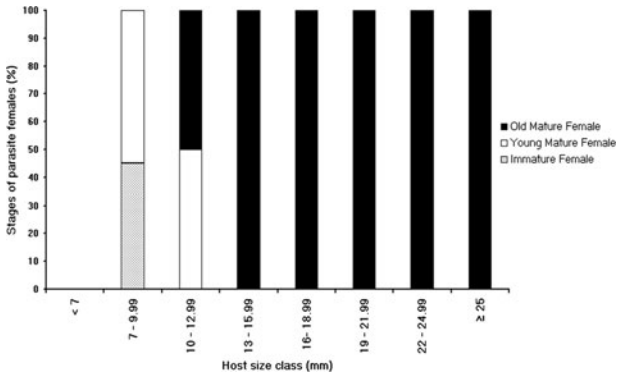

Fig. 4. Relationship between developmental stages of *Pseudione galacanthae* females and *Munida gregaria* carapace length.

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of the low and similar prevalences in males and females, absence of castration and little influence on the reproductive potential. This is also supported by the absence of multiple infestations. Therefore, *P. galacanthae* plays a minor role in regulating the *M. gregaria* population in San Jorge Gulf.

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Correspondence should be addressed to:
M. Varisco
Instituto de Desarrollo Costero—Universidad Nacional
de la Patagonia San Juan Bosco (IDC–UNPSJB)
y Consejo Nacional de Investigaciones
Científicas y Técnicas (CONICET)
Campus Universitario, Ruta 1 km 4 (9000)
Comodoro Rivadavia, Chubut, Argentina
email: martinvarisco@hotmail.com

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