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Research Article

Temporal dynamic of the relationship between the parasitic isopod *Aporobopyrus curtatus* (Crustacea: Isopoda: Bopyridae) and the anomuran crab *Petrolisthes armatus* (Crustacea: Decapoda: Porcellanidae) in southern Brazil

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ABSTRACT. The prevalence of the parasite *Aporobopyrus curtatus* in *Petrolisthes armatus* from southern Brazil was determined, and the effect the parasite had on host reproduction was evaluated. Of all 775 crabs sampled in Araçá region from March 2005 to July 2006, 3.2% presented bopyrid parasites. All the parasitized individuals had one branchial chamber occupied by two mature parasites, with no preference for the right or left chamber. Male and female hosts were infested in equal proportions. Parasitized juveniles, large individuals and ovigerous females were not found in our study. The absence of parasitized ovigerous females seems to be insufficient evidence to support the hypothesis of parasitic castration and would require a histological study to confirm their reproductive death. The percentage of infestation observed in our study (3.1%) is lower than the one found in other studies and it could indicate the existence of factor(s) regulating the density of *A. curtatus* in the Araçá region. At least in this population, the low but constant presence of the bopyrid *A. curtatus* population did not appear to have a negative effect on the porcellanid population, and parasitized individuals did not play a significant role in the natural history of *P. armatus*.

Keywords: parasitism, castration, porcelain crab, southern Brazil, Atlantic Ocean.

Dinámica temporal en la relación entre el isópodo parásito *Aporobopyrus curtatus* (Crustacea: Isopoda: Bopyridae) y el cangrejo anomuro *Petrolisthes armatus* (Crustacea: Decapoda: Porcellanidae) en el sur de Brasil

RESUMEN. Se determinó la prevalencia del parásito *Aporobopyrus curtatus* en *Petrolisthes armatus* en el sur de Brasil y se evaluó el efecto de su presencia en la reproducción de su huésped. De marzo de 2005 a julio de 2007 se muestreó en la Región de Araçá un total de 775 cangrejos, de los cuales el 3,2% presentó bopíridos parásitos. Todos los individuos parasitados presentaron una cámara branquial ocupada por dos parásitos maduros, sin preferencia por la cámara derecha o izquierda. Machos y hembras hospedadores fueron infectados en la misma proporción. La ausencia de parásitos en hembras ovígeras no es evidencia suficiente para apoyar la hipótesis de castración parasítica, y se necesita un estudio histológico para confirmar la muerte reproductiva. El porcentaje de infección observado (3,1%) es inferior al encontrado en otros estudios y puede ser indicativo de la existencia de factor(es) que regulan la densidad de *A. curtatus* en la región de Araçá. En conclusión, estos resultados sugieren que, al menos en esta población, la baja y constante incidencia del bopírido *A. curtatus* parece no afectar la población del porcelánido, y los individuos parasitados no tienen un papel significativo en la historia natural de *P. armatus*.

Palabras clave: parasitismo, castración, cangrejo de porcelana, sur de Brasil, océano Atlántico.

INTRODUCTION

Parasites are exploitative organisms that typically take nutrients and energy from their hosts, and perhaps benefit from transport, protection and a thermally regulated environment provided by the host's body (Barnard, 1990). Bopyrid isopods are obligate parasites, most commonly found on the gills and/or abdomen of decapod hosts, which may be castrated (Van Wyk, 1982; O'Brien & Van Wyk, 1985). The Bopyridae (*sensu stricto*, not included Entoniscidae and Dajidae) is the most speciose and best studied family of epicaridean parasites of decapod hosts, with 595 described species distributed worldwide and a large number of species underreported (Markham, 2003; Boyko & Williams, 2009).

These isopods require two host species to complete their life cycle and the definitive host is a decapod crustacean (Cheng, 1968). The female parasite produces broods of eggs that leave the marsupium as epicaridium larvae, a free-swimming stage with sucking mouthparts. This larva searches for a free-living planktonic copepod, to which it attaches and undergoes successive molts, to reach the microniscium larval stage and cryptoniscus larval stage (the former is attached to the copepod, the latter moves off to seek out a definitive host) (O'Brien & Cheng, 1968; Beck, 1979; Van Wyk, 1985). Cryptoniscus larvae are sexually undifferentiated and adapted to a planktonic phase, during which the isopod searches for the definitive host. Sexual differentiation of the newly settled isopod (bopyridium) is dependent on the presence or absence of another parasite attached to the host. If the host is unparasitized, cryptoniscus larva that will become a female bopyridium. If the host already harbors a parasite, the cryptoniscus larva becomes a male and attaches itself to the female's body (Reinhard, 1949; Lima, 1978; O'Brien & Van Wyk, 1985). Typically, the definitive host will shelter only one bopyrid female per gill chamber, followed by one or more dwarf males (O'Brien & Van Wyk, 1985). Pardo *et al.* (1998) described an exception to this pattern for the galatheid *Pleuroncodes monodon*, a case in which many females were found parasitizing one individual.

The effects of parasitism on the growth and reproduction of the hosts are explored in the literature (Van Wyk, 1982; O'Brien & Van Wyk, 1985; Somers & Kirkwood, 1991), although the mechanisms through which parasites influence the molt cycles and reproduction of their hosts are still unknown (Van Wyk, 1982). The first investigators of this subject believed that the molt cycle of decapods was limited to a short period of the host's life when a parasite was

present (Bonnier, 1900). This hypothesis was revised and after studies showed that, even parasitized, some host individuals are still able to molt and reproduce, although less frequently and efficiently (Van Wyk, 1982; O'Brien & Van Wyk, 1985).

According to Letitia *et al.* (2000), there exists no general pattern among arthropods, but the specific biology of hosts and parasites may produce biases one way or the other in some host-parasite species combinations. Members of the genus *Aporobopyrus* Nobili, 1906 are branchial-chamber parasites of anomuran crabs of the family Porcellanidae, e.g. *Pachycheles rudis* (Stimpson, 1859; Van Wyk, 1982), *Petrolisthes armatus* (Gibbes, 1850; Oliveira & Masunari, 1998), *Petrolisthes politus* (Gray, 1830; Scelzo, 1985) and *Porcellana sayana* (Leach, 1820; A. Meireles, *pers. com.*), shrimps of the families Hippolytidae (Calado *et al.*, 2005; Román-Contreras & Romero-Rodríguez, 2005; Terossi & Mantelatto, 2010) and Palaemonidae (Beck, 1979; Cash & Bauer, 1993), and brachyuran crabs (Jordá & Roccatagliata, 2002).

The species of the Brazilian coast are poorly investigated and only *Aporobopyrus curtatus* Richardson, 1904 is known to infest the porcellanid crabs *Petrolisthes armatus* (Oliveira & Masunari, 1998, 2006), *P. galathinus* (Bosc, 1802), *P. marginatus* Stimpson, 1859, *Pachycheles ackleianus* A. Milne-Edwards, 1880, *P. greeleyi* (Rathbun, 1900) and *Porcellana sayana* (see Markham, 1975 and Lima, 1978 for review).

We evaluated the presence and possible interference effect of *A. curtatus* on a population of *P. armatus* in southeastern Brazil. Patterns observed were compared with previously studied members of the family Porcellanidae, in order to detect any variability in the effects of these parasites on the life cycle of their hosts.

MATERIAL AND METHODS

Specimens sampling protocol

The Araçá region (23°48'78.1''S, 45°24'46.9''W) is a human impacted remnant mangrove area located near the São Sebastião Channel on the northern coast of São Paulo. The effects of human and industrial impacts are easily seen in this area (see Vergamini & Mantelatto, 2008 for review).

Porcellanid crabs were collected by two people by hand at two-month intervals in the Araçá region from March 2005 to July 2006, in a rocky intertidal area near the waterline. Specimens were collected under rocks at low tide for 1 h and 30 min. This

methodology was previously tested and allowed different representative sizes of small and adult crabs to be caught in this population (Miranda & Mantelatto, 2009). Water temperature ranged from 24° (July 2005) to 32°C (March 2006), with a mean of $25.9 \pm 2.9^\circ\text{C}$. Mean salinity was 34.7 ± 1.7 psu, ranging between 30 (July 2005) and 36 psu (May 2005).

The animals were frozen and transported to the laboratory. They were thawed prior to analysis. Individuals were counted; identified to sex by the presence, position and number of pleopods; and their carapace width (CW) was measured to the nearest 0.1 mm with a caliper rule, or under a stereomicroscope.

Hosts (porcellanid crabs) and parasites (isopods) were preserved in 80% ethyl alcohol and deposited in the Crustacean Collection of the Department of Biology, Faculty of Philosophy, Sciences and Letters of Ribeirão Preto (CCDB/FFCLRP/USP) under catalogue numbers 1832 to 1844 and 2099, respectively.

In order to better assess temporal variations, the months were grouped into dry season 1 (March, May and July 2005), rainy season (September, November and January 2005), and dry season 2 (March, May and July 2006). The reproductive period was estimated from the occurrence of ovigerous females in each month. The recruitment period for *P. armatus* was determined based on the occurrence of individuals in the first size class (CW < 2.0 mm) and its fluctuation each month (Pardo *et al.*, 2007). Individuals sized 2.0 < CW < 4.0 mm were classified as juveniles according to analysis of relative growth Miranda & Mantelatto, (2010).

Statistical analyses

A Kolmogorov-Smirnov test was performed to verify the normality of population data according to the size of individuals. Monthly frequencies of sexes, size classes, and the occurrence of individuals in relation to seasons were tested using Chi-square tests (χ^2). Kruskal-Wallis One-Way ANOVA was used to evaluate size variations in relation to month and season. The prevalence was calculated as the number of parasitized individuals in relation to all the potentially infected individuals within a population, expressed as percentage. All statistical tests were conducted according to Zar (1996), adopting the significance level $\alpha < 0.05$.

RESULTS

Host population

Of the 775 porcellanid crabs collected from March 2005 to July 2006, 24 (3.1%) were parasitized by

Aporobopyrus curtatus. Of these, 13 were males and 11 were non-ovigerous females (54.2 and 45.8% of the total infested, respectively) (Fig. 1). Distribution in size classes was unimodal and normal for infested crabs (KS = 0.091; $P > 0.20$), which differed from the bimodal and non-normal distribution pattern recorded for non-infested crabs (Fig. 2). The sex ratio of infested crabs was not significantly different from 1:1 (1.18:1; $\chi^2 = 0.22$; $P > 0.05$; $n = 775$), similar to that of non-infested crabs (0.90:1).

The prevalence varied by month, from 0.0% (July 2005 and March 2006) to 9.6% (January 2006). There was no preferential infestation in relation to the sex of the hosts ($\chi^2 = 0.22$; $P > 0.05$). All individuals collected had only one branchial chamber occupied by a pair of mature parasites, with no apparent preference for the right or left chamber ($\chi^2 = 2.83$; $P > 0.05$).

There were no infested juveniles; the smallest parasitized individuals were found in the fourth size class (4.7 to 6.1 mm CW), with none between 11.7 to 14.5 mm (Fig. 2). The proportions of parasitized individuals in relation to non-parasitized population, by size class, reached a maximum of 6.2% (7.5 to 8.9 mm CW).

The hosts and parasites (both sexes of adult isopods) showed synchronous growth. There was a significant positive relationship between the carapace width of the host, and the maximal body width of the respective parasite ($r = 0.73$; $P < 0.05$) (Fig. 3). There was no significant difference between the size of parasitized and non-parasitized individuals ($P = 0.166$; $P > 0.05$) (Fig. 4).

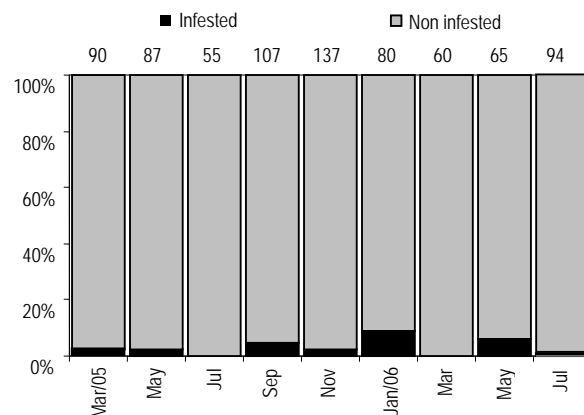


Figure 1. Prevalence of *Aporobopyrus curtatus* parasitizing *Petrolisthes armatus* individuals during the sampling period (numbers above bars correspond to total number of individuals collected).

Figura 1. Ocorrência de *Aporobopyrus curtatus* parasitando indivíduos de *Petrolisthes armatus* durante el periodo de muestreo (el número bajo las barras corresponde al total de individuos colectados).

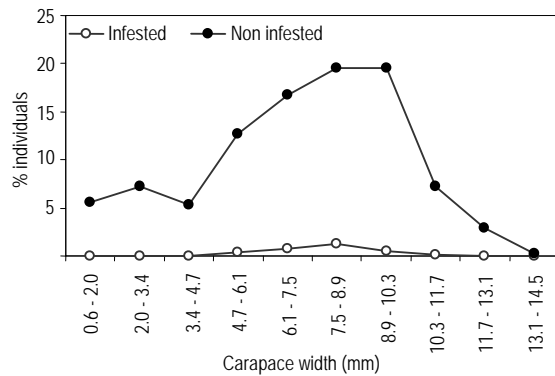


Figure 2. *Petrolisthes armatus*. Distribution of parasitized and non-parasitized individuals by *Aporobopyrus curtatus* according to size classes.

Figura 2. *Petrolisthes armatus*. Distribución de individuos parasitados y no parasitados por *Aporobopyrus curtatus* según la clase de tamaño.

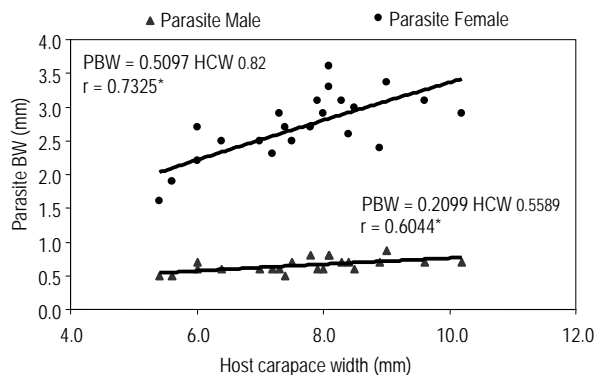


Figure 3. Correlation between the carapace width of *Petrolisthes armatus* and maximal body width of males and females of the parasite *Aporobopyrus curtatus* (PBW = parasite body width; HCW = host carapace width).

Figura 3. Correlación entre el ancho del cefalotórax de *Petrolisthes armatus* y el ancho máximo del cuerpo de machos y hembras del parásito *Aporobopyrus curtatus* (PBW = ancho del cuerpo del parásito; HCW = ancho del cefalotórax del huésped).

Parasite population

Associated with the 23 hosts, there were found 44 parasites (one host and its bopyrids were damaged, and this individual was excluded from the statistical analyses). All of them occurred in couples of one mature female and only one mature male: 22 males (48.9%), 11 non-ovigerous females (24.4%) and 11 ovigerous females (24.4%). One of the 23 hosts had a branchial chamber with an expansion, but it was empty (2.2%).

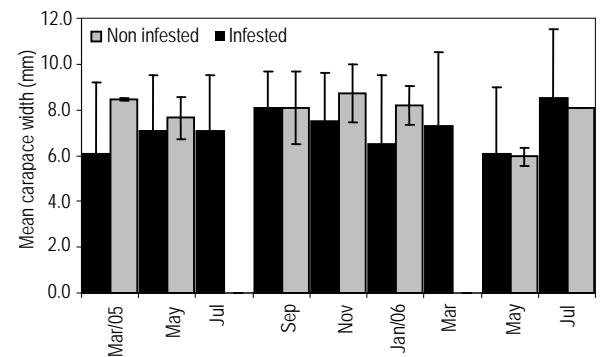


Figure 4. *Petrolisthes armatus*. Mean sizes (with standard deviation) reached by infested and non-infested crabs in the months of sampling (numbers above bars correspond to total number of individuals collected).

Figura 4. *Petrolisthes armatus*. Tamaño promedio (con desviación estándar) alcanzado por cangrejos infestados y no infestados en los meses de muestreo (el número bajo las barras corresponde al total de individuos colectados).

Males reached sizes between 0.5 to 0.9 mm of body width (0.66 ± 1.10 mm) while females reached sizes between 1.6 to 3.6 mm (2.72 ± 0.16 mm) distributed normally (KS = 0.091; $P > 0.20$).

Aporobopyrus curtatus showed discontinuous reproductive activity during the sampling period, with percentages of ovigerous females ranging from 0.0 (March, May, and July 2005; March and July 2006) to 100.0 % (November 2005, the peak of reproductive activity). In relation to seasonality, *A. curtatus* was found in significantly higher numbers in the rainy season (χ^2 Dry1 – Rainy = 14.24; χ^2 Rainy–Dry2 = 7.41; $P < 0.05$).

DISCUSSION

We observed different patterns of parasitized individuals in this population, especially in relation to juveniles and ovigerous females. High positive correlation between size of hosts and parasites was found and some authors considered it as an indication of early infestation on hosts' life (Cash & Bauer, 1993; Roccatagliata & Lovrich, 1999) which could remain during their entire life. Studying other population of the same species, Oliveira & Masunari (1998) considered this relation between parasite and host sizes an evidence of weak or nil effect of on the host population. This assertion about the absence of alterations on host population induced by the presence of parasite seems to be effective for us as it can be proved by some host population characteristics that

are compatible to a well established population (even sex ratio, continuous reproductive activity, settlement and rapid embryonic development) (see Miranda & Mantelatto, 2009 for review).

The percentage of infestation observed in our study (3.1%) is lower than the 9.5% found by Oliveira & Masunari (1998), even considering the difference on abundance of hosts at Araçá and Farol Island. Additionally, at Farol Island, *A. curtatus* population presents a high density of individuals than at Araçá, which is evidenced on the presence of hosts with a number of parasites found that ranged from one to six (see Oliveira & Masunari, 1998 for review). These differences found on the density of *A. curtatus* populations can be an indicative that parasite population at Araçá has been regulated by some factor or group of factors.

Bradley (1972) recognized some ways by which the upper limits of parasite populations can be limited: by regulation at the level of host population, involving host death due to heavy parasite burden or the host immune response and by regulation at the level of individual host, involving a partial immune response or intraspecific competition between parasites. Also, low percentages of infestation can be related parasite losses during the host molting process (Van Wyk, 1982; Cash & Bauer, 1993). Both studies observed that a low percentage of parasite pairs did not survive host ecdysis, being expelled during the process.

Indirect evidence that branchial bopyrid parasites may suffer mortality while on the host comes from observations that the swollen branchiostegite of infected hosts keeps its shape through a period of molts even if the parasite has been lost or removed (Van Wyk, 1982). Hosts with a swollen and empty branchial chamber were registered by us and by Oliveira & Masunari (1998) for *P. armatus* in Brazil and other parasitized anomurans, e.g. *Paralomis granulosa* (Jacquinot, 1847) (Roccatagliata & Lovrich, 1999), and *Pachycheles rudis* (Van Wyk, 1982). Unfortunately, our data don't allow us to determine the exact cause or causes responsible for the difference on parasite incidence between Farol Island and Araçá populations.

Neither our study nor Oliveira & Masunari (1998) found any juveniles, ovigerous females, or individuals in the largest size classes of crabs to be parasitized. The absence of parasites in juvenile crabs occurs during the phase when growth rates in porcellanids are high, and could be related to the several molts during this phase, which could impede the settlement of the parasite on hosts. On the other hand, Oliveira & Masunari (1998) have recorded juveniles of *P.*

armatus infested by it parasites in early developmental stages. Indeed, is well established that a high percentage of parasites can be retained after host molt (Van Wyk, 1982; Cash & Bauer, 1993; Calado *et al.*, 2005). To explain the absence of parasitism in the largest individuals Van Wyk (1982) have hypothesized some possibilities: 1) higher mortality rates in the parasitized group, 2) loss of parasites by the host, probably caused by differences in duration of the life cycles of the organisms involved, and/or 3) it could be that growth is reduced due to parasitism and this restricts maximum size. Considering that the infested crab population achieved the same sizes as the uninfested one (see Fig. 4), the third hypothesis can be rejected. As our study of the interaction between *A. curtatus* and *P. armatus* do not provided evidence to confirm either of the other two hypotheses, the probably explanation is related to the low abundance of juveniles and large individuals (see Fig. 2). Similar results were reported by Oliveira & Masunari (1998), studying a population in a relatively pristine area in the state of Paraná, southern Brazil.

The effects of the presence of a bopyrid parasite on its host decapod can range from permanent anecdyis, which means that the host has its somatic growth interrupted, to total castration, which signifies inhibition of reproductive activity (Van Wyk, 1982). There may be additional, less-profound alterations such as the typical expansion on the carapace over the branchial chamber, in which the parasite shelters, without causing other damage to its host's growth and reproduction (Beck, 1979; Van Wyk, 1982).

Beck (1979) suggested that suppression of ovarian development and changes in secondary sex characters of males and females parasitized by bopyrids may be a result of secretion of a hormonal gonad inhibitor by the parasite or by the hosts, induced by the presence of the invader, and that this situation continues while the parasites are adhered to host, although reversion is possible after elimination of the cause. In respect to these alterations in secondary sex characters, we have not observed any differences in the morphology of parasitized and non-parasitized individuals of *P. armatus*. However, we have to consider the existence of evidences that secondary sex characteristics may remain unmodified from bopyrid action (C. Boyko, *pers. com.*).

The absence of parasitized ovigerous females observed in the present study can be a strong evidence of parasitic castration but we do not suggest that this absence is sufficient evidence to support the hypothesis of parasite castration proposed by Oliveira & Masunari (1998). The lack of a histological examination of the gonads is imperative to evaluate

whether the presence of a parasite causes changes that prevent a parasitized female from performing its reproductive functions normally. Thus, we do not feel comfortable to make a firm conclusion as to whether the presence of a bopyrid on *P. armatus* causes castration in Araçá population.

In the Araçá area, no preferential infestation for one branchial chamber or bilateral infestation were observed. On the other hand, Roccatagliata & Lovrich (1999) found a strong tendency of *Pseudione tuberculata* Richardson, 1904 to infest the left branchial chamber of *P. granulosa*. According to these authors, the majority of bopyrids that infest the branchial chamber occur in the same proportion in both chambers, and a clear preference for one chamber may increase the possibility of a second infestation.

There is a natural tendency for male crabs to be more frequently infested by parasites than females (Letitia *et al.*, 2000). This situation is probably due to the association between immunosuppression associated with androgenic hormones responsible for the emergence of secondary sexual characters, and typical male behavior (Alexander & Stimson, 1988). In contrast, female hormones may provide immunity to some kinds of infection, which may make males more susceptible (Grossman, 1985). Also, the extreme parental care performed by most females during the ovigerous period may help explain differences in infestation between sexes. These divergent hormone patterns, associated with different degrees of exposure of males and females to parasites because of behavioral and/or morphological differences, might result in an apparent tendency of parasites to favor males.

In addition to these factors, males probably have less energy available to invest in immune responses than do females, considering that males are constantly involved in intra-sexual competitions and in mating (Letitia *et al.*, 2000). Likewise, in population with males reaching higher sizes than females, a greater percentage of males were parasitized which could be advantageous to parasites, since parasite brood sizes are correlated with host size (Beck, 1979). On the other hand, Lester (2005) and Beck (1979), recorded shrimps and crab females more frequently parasitized, with males being less affected.

No evidence of preferential infestation by one sex was observed by us: males and females of *P. armatus* were infested in equal proportions; a similar situation was reported by Oliveira & Masunari (1998). Likely causes to this situation are the equal proportion of males and females on host population and the fact that males and females of *P. armatus* at Araçá are equal in size (see population data in Miranda & Mantelatto,

2009). These reports, added to data available in other studies, will corroborate the conclusion of Letitia *et al.* (2000) that arthropods appears to have any general sex bias in parasite infections, as also found in other groups such as mammals and birds. Also, possible mechanisms involved on a sexual selection by immature parasites are difficult to conceive, considering the absence of external sexual differentiation on very young hosts (Beck, 1979).

The percentage of parasitized individuals varied in the sampling period. This profile can occur due to differential migration of parasitized and non-parasitized individuals, or interactions between the period of larval isopod attachment, the production of young hosts and their mortality (Beck, 1979; Jordá & Roccatagliata, 2002). The number of parasitized individuals higher in the Rainy season is probably related to recruitment of younger possible hosts seen in Dry season 1 (see Miranda & Mantelatto, 2009 for review).

In conclusion, the results are indicative that, at least in this population, the low but constant presence of the *A. curtatus* population did not appear to affect the porcellanid population, and parasitized individuals did not play a significant role in the natural history of *P. armatus*. Otherwise, *A. curtatus* population seems to be regulated by some factor or group of factors undefined at this moment. To better understand the causes and the role, if any, played by this bopyrid parasite in the natural history of porcelain crabs, histological studies of gonads and observations on mechanisms of infestation in males and females in a controlled laboratory setting will be necessary.

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