

Parasitization of the white spotwrist hermit crab, *Pagurus criniticornis* (Dana, 1852) (Decapoda, Anomura), by the rhizocephalan barnacle *Peltogasterella socialis* (Müller, 1863) (Cirripedia, Rhizocephala) from southeastern Brazil

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Abstract—Hermit crabs of the species *Pagurus criniticornis* (Dana, 1852) parasitized by the poorly known colonial rhizocephalan *Peltogasterella socialis* (Müller, 1863), were collected in the infralittoral rocky/sandy area of Anchieta Island (São Paulo), Brazil. We report the presence and pattern of occurrence of this rhizocephalan in the *P. criniticornis* population. The hermit crabs were obtained monthly during 1999 by two people using SCUBA methods. A total of 992 hermit crabs were captured and examined for rhizocephalans. The studied population showed non-normal size distribution and only 2.11% of the sample specimens carried externae of *P. socialis*. The parasite occurrence was seasonal and varied with host size. Some signs of feminization were observed on *P. criniticornis* pleopods (elongation of the endopod and reduction of the exopod of pleopods for males and reduction in the size of endopods for females). This is the first report on this parasite/host relationship for this South American host species. This is the first record of *P. socialis* (Müller, 1863) subsequent to the species' description, and possible occurrence of the parasite on hermit crabs in the Bahamas is also reported.

Keywords: barnacle; paguridae; parasite; rhizocephalan.

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INTRODUCTION

The Rhizocephala is an order of the Cirripedia, comprising about 260 species distributed in nine families: Chthamalophilidae, Clistosaccidae, Duplorbidae, Lernaeodiscidae, Mycetomorphidae, Peltogastridae, Polysaccidae, Sacculinidae, and Thompsoniidae (Høeg and Lützen, 1995; Lützen and Takahashi, 1996; Høeg et al., 2005). All species parasitize marine and a few freshwater Crustacea. Rhizocephalan cirripedes are important parasitic castrators of anomuran and brachyuran crabs in marine ecosystems (Hines et al., 1997), interfering with host reproduction and sometimes regulating population dynamics. The rhizocephalan fauna of the Brazilian coast is poorly known, and to date only nine species have been reported: *Peltogaster purpureus* (Müller, 1862), *Peltogaster socialis* Müller, 1863 (now *Peltogasterella socialis*), *Lernaeodiscus porcellanae* Müller, 1862, *Triangulus bilobatus* (Boschma, 1925) (= *Lernaeodiscus* sp. of Young, 1993; see Boyko and Harvey, 2000), *Loxothylacus panopaei* (Gissler, 1884), *Ptychascus glaber* Boschma, 1933, *Sacculina hirsuta* Boschma, 1925, an unidentified barnacle parasite (see Young, 1998 for review) and *Peltogasterella sulcata* (Lilljeborg, 1859). However, the citation of *Peltogasterella sulcata* from Brazil is based on the work of Reischman (1959) who placed *Peltogaster socialis* Müller, 1863 in synonymy with the eastern Atlantic and Mediterranean *Peltogasterella sulcata* (Lilljeborg, 1859), so in reality only eight species of rhizocephalans are known from Brazil. *Peltogaster socialis* as described by Müller (1863, fig. 1) is a colonial form occurring on unidentified hermit crabs and has only been recorded once from Florianópolis Island, Santa Catarina State, Brazil. It was placed by Boschma (1959) in *Gemmosacculus* which is now



Figure 1. *Peltogasterella socialis* (Müller, 1863). Reproduced fig. 59 in Müller (1869), no scale given in original.

considered a synonym of *Peltogasterella*; therefore the correct name for this species is *Peltogasterella socialis* (Müller, 1863). The homonym *Peltogasterella socialis* (Krüger, 1912) is now considered a synonym of *Peltogaster gracilis* (Boschma, 1931), the latter being used as the correct name for the species due to homonymy of the senior synonym. *Peltogasterella socialis* (Müller, 1863) was placed in synonymy with *Peltogasterella sulcata* by Reischman (1959) solely on the basis of its gregarious nature and a figure of the [*Peltogasterella*] rhizocephalan root system published in Möller (1921: fig. 13, not Möller, 1915, as cited by Reischman). In the absence of any additional Brazilian material, this synonymy has been followed by all subsequent workers (e.g., Høeg and Lützen, 1985; Øksnebjerg, 2000).

The utilization of crustaceans as hosts by parasites and their relationships constitutes an important but often neglected aspect of the natural history of ecosystems (Mantelatto et al., 2003), in particular for the Brazilian crustacean fauna. As far as we know, there is no information available on the relationship between hermit crabs and rhizocephalans assessed through long-term studies in Brazil. The aim of this study was to examine the prevalence and the pattern of infestation of the colonial rhizocephalan *Peltogasterella socialis* on the hermit crab *Pagurus criniticornis* (Dana, 1852) population inhabiting the infralittoral rocky/sandy area of Anchieta Island in southern Brazil. To evaluate a possible effect of the parasite on the morphology of the host, the relationships between infestation versus size and sex of the host were assessed.

MATERIAL AND METHODS

Study area

Located in Ubatuba region, São Paulo State, Anchieta Island ($23^{\circ}33'S$ and $45^{\circ}05'W$) is the second largest island on the north coast of São Paulo State. This island has been affected by anthropogenic activities such as tourist and fisheries industries and in 1977 it was declared an ecological reserve of São Paulo State. During the last eight years, a Brazilian group has been working on this Island, recently declared a national park, as part of a long-term study to identify the decapod fauna with special attention to hermit and brachyuran crabs (Mantelatto and Garcia, 2002; Mantelatto et al., 2004).

Host biology

Pagurus criniticornis, popularly named the white spotwrist hermit crab, is distributed in the western Atlantic Ocean, including the coast of the USA, Gulf of Mexico, Antilles, Brazil (from Pernambuco to Rio Grande do Sul), Argentina and Uruguay, at depths ranging from intertidal areas to 50 m. This small sized hermit crab is one the most common and abundant species in the calm and shallow waters of the São Paulo coast (Melo, 1999; Mantelatto and Garcia, 2002).

Sampling and analyses

Samples were obtained monthly in the infralittoral rocky/sandy area of Anchieta Island from January to December 1999. The hermit crabs were captured by two people using SCUBA methods during 30 min over an area of about 800 m². After collecting, the animals were frozen and transported to the laboratory where they were fixed in 70% EtOH for later analysis. Each specimen was carefully removed from the occupied shell in an anticlockwise fashion, counted, measured for cephalothoracic shield length (CSL, from the tip of rostrum to the v-shape groove at the calcified posterior edge), and weighed (WW = wet weight), including the egg clutches. The percentage of externally parasitized individuals in the population was recorded according to the size and sex of the hermit crabs. The size frequency distribution and the number and weight of individuals parasitized and non-parasitized, in relation to sex were obtained. Internal evidences of parasites were not checked. The voucher crabs were deposited in the Crustacean Collection of the Biology Department of FFCLRP (CCDB), University of São Paulo (Catalogue number: 1732, 1733 and from 1741 to 1745).

The frequency distribution was tested for normality with the Kolmogorov-Smirnov Normality test (KS). The chi-square test (χ^2) was used to compare the number of males and females parasitized and non-parasitized. The mean size of the individuals of both sexes was compared by the Mann-Whitney Ran Sun test (Zar, 1996).

The lengths of the endopod (ENL = the straight-line distance between base and tip of endopod) and the exopod (EXL = the straight-line distance between base and tip of exopod) of the pleopods were measured in 10 non-parasitized males, 10 non-parasitized females, 13 juveniles (5 females and 8 males) and parasitized males and females. A preliminary classification of maturity for the crab was based on shape, coloration and size of the gonads (after dissection under stereomicroscope) and on size of the smallest ovigerous female captured. The animals that lacked developed, or developing, gonads were considered juveniles (Biagi and Mantelatto, 2006). The t-test (Zar, 1996) was used to compare the median sizes of ENL and EXL between parasitized and non-parasitized individuals of both sexes in order to compare morphological modifications.

A linear regression analysis was carried out between CSL, ENL and EXL. CSL was used as the independent variable because it has been used to indicate size in many studies of hermit crabs (Mantelatto and Martinelli, 2001; Biagi and Mantelatto, 2006). The pattern of allometry was established for each parameter using the slope ($b = 1$, isometry; $b < 1$, negative allometry; $b > 1$, positive allometry). The Student t-test was used to detect departures from isometry ($H_0 : b = 1$; $H_1 : b \neq 1$).

RESULTS

A total of 992 hermit crabs [432 males (43.55%), 263 non-ovigerous females (38.31%) and 297 ovigerous females (18.14%)] was collected and analyzed. The

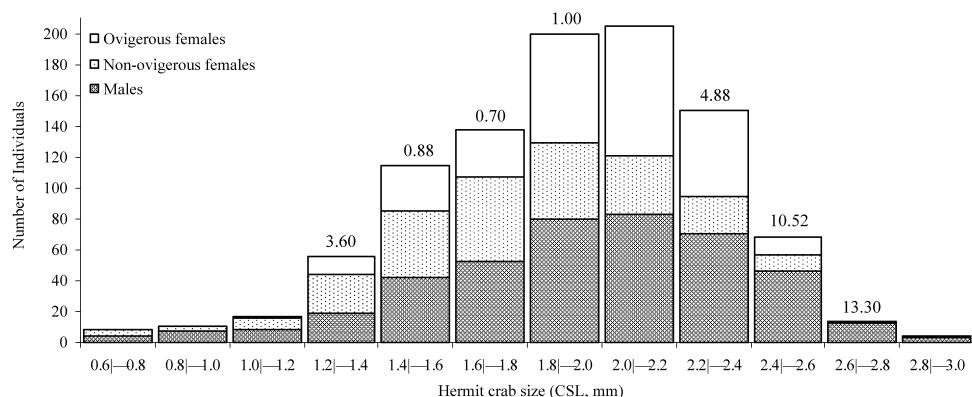


Figure 2. *Pagurus criniticornis* (Dana, 1852). Size frequency distribution of individuals collected during 1999 in Anchieta Island, Brazil. The values above the column correspond to the percentage of parasitized individuals per size class.

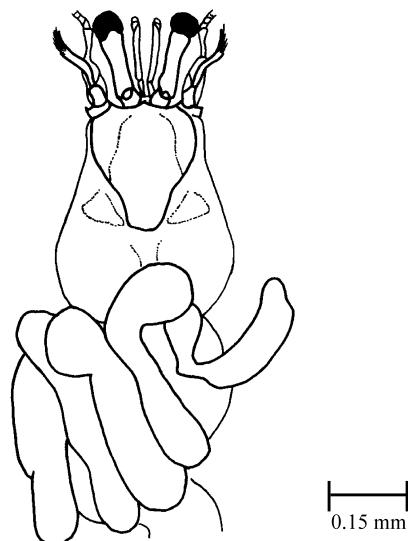


Figure 3. *Pagurus criniticornis* (Dana, 1852), male collected from Anchieta Island, Brazil (January 1999) parasitized by *Peltogasterella socialis* (Müller, 1863) in external stage.

size frequency histograms presented non-normal distribution ($KS = 0.076$; $P < 0.0001$) for the total number of individuals and for each sex separately (fig. 2).

On parasitized hermit crabs the external stage of the rhizocephalans are located on the anterior part of the abdomen (fig. 3). Twenty three specimens (2.11%) of the total sample were found parasitized by *Peltogasterella socialis* in the externa stage of development; of these, 72.7% were males and 27.3% were non-ovigerous females. No ovigerous females were found parasitized.

The maximum number of externae per crab was 6 and the minimum was 1 (mean = 2.6, SD = 1.2, host n = 23; fig. 4).

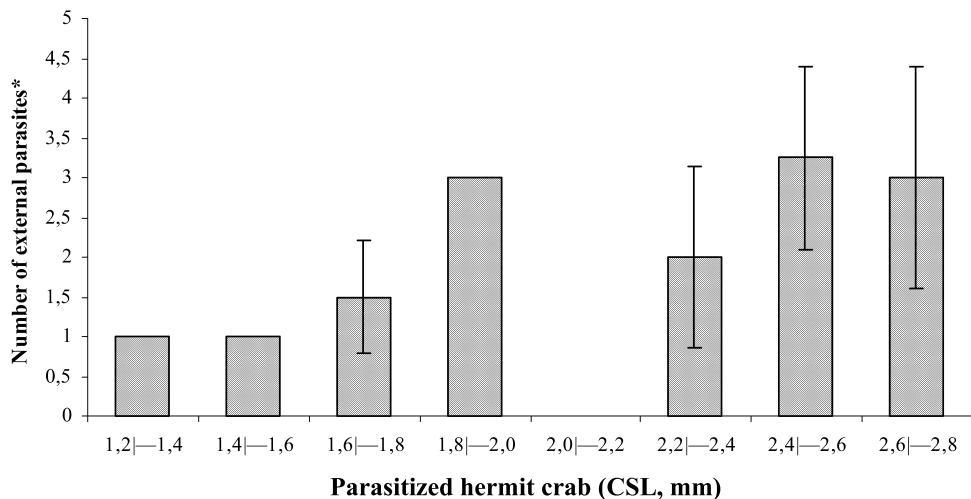


Figure 4. Size frequency distribution of external parasite in *Pagurus criniticornis* (Dana, 1852) collected during 1999 in Anchieta Island, Brazil (*= mean values \pm SD).

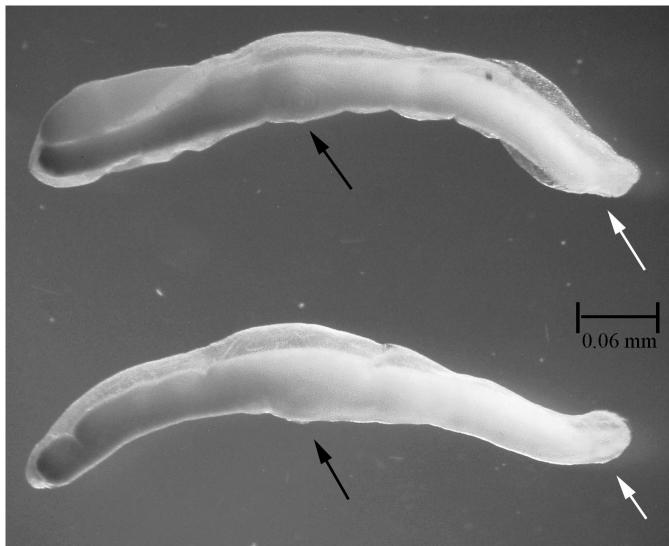


Figure 5. *Peltogasterella socialis* (Müller, 1863). Two specimens from a male *Pagurus criniticornis* collected from Anchieta Island, Brazil, April 1999. White arrows indicate mantle openings; black arrows indicate position of stalk.

Individual externae were attached to the host by a very short and thin stalk. Late externae were cylindrical to sausage-shaped, usually slightly curved and elongated (fig. 5). Young externae were light pink and almost transparent, older specimens were light to dark yellow.

The highest occurrence (45.4%) of the parasitized specimens was observed during spring and among those hosts measuring 1.2 to 2.6 mm CSL, with greatest

prevalence in the 2.2 — 2.8 mm CSL size classes (fig. 2). The mean weight of parasitized individuals (0.052 ± 0.027 g) differed significantly ($P < 0.05$) from the mean weight obtained for non-parasitized crabs (0.067 ± 0.027 g) in the same size classes.

The mean value of EXL for non-parasitized males (1.02 ± 0.34 mm) was significantly higher ($P < 0.05$) than those for parasitized males (0.97 ± 0.17 mm) and for parasitized and non-parasitized females (0.78 ± 0.18 and 0.77 ± 0.14 mm, respectively). The mean value of ENL for non-parasitized males (0.33 ± 0.13 mm) was significantly smaller than those for parasitized males (0.53 ± 0.16 mm), parasitized females (0.53 ± 0.09 mm) and non-parasitized females (0.71 ± 0.12 mm). With respect to females, the mean value of ENL for non-parasitized individuals (0.71 ± 0.12 mm) was significantly larger than that for parasitized individuals (0.47 ± 0.16 mm).

The regression equations of hermit crab dimensions for the relative growth analysis are presented in table 1. Parasitized males showed changes in the pattern of growth for both endopods (positive allometry) and exopods (isometry). Adult non-parasitized males showed isometry for endopods and positive allometry for exopods, whereas parasitized females showed changes in the pattern of growth only for endopods (isometry) and positive allometry for endopods for non-parasitized females.

DISCUSSION

Although parasitism by an unspecified rhizocephalan on *P. criniticornis* from different areas has previously been mentioned (Hebling, 1978; Rieger, 1997; Markham, 2003), no detailed information is available to determine the parasite's identity, the relationship between the parasite and host or even the prevalence of infestation. In general, the low prevalence of infestation recorded here is similar to those detected for rhizocephalans on brachyuran crabs in the same area (Mantelatto et al., 2003), and other hermit crabs worldwide (see Rybakov and Shukalyuk, 2004).

That our rhizocephalan material belongs to the genus *Peltogasterella* is unquestionable: there is no shield present around the stalk (no growth rings), and the morphology of the body is very elongated (fig. 5). In overall morphology, the specimens appear closer to *P. sulcata* than *P. gracilis*, as the stalk arises near the middle of the body, rather than terminally or subterminally.

Two of the three species in the genus *Peltogasterella* [*P. sulcata* (Lilljeborg, 1859) and *P. gracilis* (Boschma, 1931)] have distributions restricted to cold waters: circumboreal and Mediterranean for *P. sulcata* and along the Pacific north-west and Californian coasts of the United States, Alaska, Japan, Siberia, and coast of Chile for *P. gracilis* (see Reischman, 1959; Høeg and Lützen, 1985; Coloma and Moyano, 2002). The only species of *Peltogasterella* recorded from Brazil is *P. socialis* (Müller, 1863) that was recorded as a colonial parasite from unidentified hermit crabs. Because Müller (1863) did not give a sufficient description of the

Table 1.

Pagurus criniticornis. Regression equations for the relations: CSL = Cephalothoracic Shield Length, EXL = Exopod Length and ENL = Endopod Length [r_s = correlation coefficient, A = allometry; (=) isometry, (+) positive allometry, (-) negative allometry; JV = juveniles; ANP = non-parasitized animals; AP = parasitized animals, and N = number of individuals].

Groups	Variables	Category	N	Y = ax ^b	ln Y = ln a + b ln X		r _s	A	b ≠ unity
					ln EXL = -1.05 + 1.29 ln CSL	0.69			
JV	CSL × EXL	total	13	EXL = 0.35CSL ^{1.29}	ln EXL = -1.05 + 1.29 ln CSL	0.69	=	0.69 ^{ns}	
	CSL × ENL	female	5	ENL = 0.19CSL ^{2.41}	ln ENL = -1.57 + 2.41 ln CSL	0.99	+	11.63*	
		male	8	ENL = 0.11CSL ^{1.39}	ln ENL = -2.16 + 1.39 ln CSL	0.62	=	0.55 ^{ns}	
	CSL × EXL	female	10	EXL = 0.37CSL ^{0.95}	ln EXL = -0.98 + 0.95 ln CSL	0.96	=	-0.65 ^{ns}	
ANP	CSL × EXL	male	10	EXL = 0.11CSL ^{2.83}	ln EXL = -2.22 + 2.83 ln CSL	0.81	+	2.48*	
	CSL × ENL	female	10	ENL = 0.20CSL ^{1.72}	ln ENL = -1.63 + 1.72 ln CSL	0.99	+	10.62*	
		male	10	ENL = 0.04CSL ^{2.53}	ln ENL = -3.21 + 2.53 ln CSL	0.68	=	1.58 ^{ns}	
	CSL × EXL	female	8	EXL = 0.21CSL ^{1.75}	ln EXL = -1.58 + 1.75 ln CSL	0.84	=	1.33 ^{ns}	
AP	CSL × ENL	male	15	ENL = 0.52CSL ^{0.77}	ln ENL = -0.64 + 0.77 ln CSL	0.88	=	-0.92 ^{ns}	
	CSL × EXL	female	8	EXL = 0.23CSL ^{1.12}	ln ENL = -1.47 + 1.12 ln CSL	0.81	=	0.29 ^{ns}	
		male	15	ENL = 0.11CSL ^{1.07}	ln ENL = -2.24 + 1.97 ln CSL	0.84	+	2.45*	

ns = not significant; * P < 0.05.

species, and none of his material is extant (Boyko and Harvey, 2000), we can never be fully certain that our material is conspecific with Müller's taxon, but given the locality of collection and type of host (hermit crab), as well as the lack of any other described *Peltogasterella* species from Brazil, we feel justified in identifying our material as *P. socialis*. The yellow color of mature externae of *P. socialis* was noted by Müller (1869), and this color, also present in our material, is similar in both *P. socialis* from *Peltogasterella sulcata* (erroneously reported as dark red in the mature state by Høeg and Lützen, 1985, but in fact yellow fide Høeg, pers. commun.). Morphologically, the two specimens examined in detail both have a flattened end bearing the mantle cavity which is situated ventrally, unlike the end of *P. sulcata* which is rounded and bears the mantle opening on the tip (see Reischman, 1959). A full description of *P. socialis* (utilizing a combination of histology and SEM on the larvae in the manner of Rybakov et al., 2002) and examining the retinacula in detail (see Rybakov and Høeg, 2002) is beyond the scope of this work but, along with a neotype designation, will be undertaken in the future once difficulties in exchanging material between Brazil and New York have been resolved. It should be noted that specimens of a very similar yellow rhizocephalan have been found in the Bahamas on two *Pagurus stimpsoni* (A. Milne-Edwards and Bouvier, 1893) and three *P. brevidactylus* (Stimpson, 1859) (Boyko, unpubl.) and may prove to belong to the same species as the Brazilian *Peltogasterella* and significantly extend the range of the species northward into the Caribbean.

Not all rhizocephalans are parasitic castrators of their hosts (Høeg, 1995), but those that are employ three basic process: 1) retardation of development of the host's gonads or destruction of the sex cells which may result in complete atrophy of the gonad; 2) changes in patterns of allometric growth and, 3) changes in the molt cycle of host (Reinhard, 1956; Nielsen, 1970; Høeg, 1982; O'Brien and Wyk, 1985; Glenner and Høeg, 2002).

The size-specific prevalence curve indicates some tendency for increase of prevalence with increasing host size. O'Brien and Wyk (1985) verified that there is little variation in this size-specific pattern within the Peltogastridae. It was observed that a decrease in the prevalence among intermediate sized individuals corresponds to the phase when growth rate of hermit crabs is high. Prevalence of *Peltogasterella socialis* in *P. criniticornis* was recorded from direct observation of externae protruding from the abdomens of their hosts. Since this external stage is result of a prior infection event followed by a prolonged endoparasitic phase (Glenner and Høeg, 2002), the population surveys based on external examination of hermit crabs underestimate the real prevalence of parasitism. Analogously, González and Acuña (2004) conducted population studies on a bopyrid (Isopoda: Bopyridae) infesting galatheid squat lobsters (Decapoda: Galatheidae) in northern Chile. These authors observed that infested hosts were much smaller than uninfected hosts and showed a negative effect of the parasites on host growth and/or that hosts could lose their parasites as they grew larger.

It is probable that the life cycle of *Peltogasterella socialis* is synchronized with that of *P. criniticornis* in the study area, considering that this population has shown seasonal reproductive cycles concentrated during the summer (Faria, 2004; Mantelatto et al., in press) and the highest occurrence of mature parasites occurred during the spring, a period during which hermit crabs attain the puberty molt. Hochberg et al. (1992) postulated that temporal relationships between the relative abundance of parasitized individuals and proportions of ovigerous females in a population are indicative of a life-cycle relationship between parasite and host. According to O'Brien and Wyk (1985), there exists an optimal, but limited, period of parasite reproduction which would result in infective female cyprids being present when hosts are most vulnerable. Glenner and Werner (1998), in a study with *Sacculina carolini*, concluded that intermolt crabs are less attractive for settlement by cyprids than are recently-moulted crabs, in this way the infestation period probably coincides with the juvenile recruitment period of *P. criniticornis* in the studied area, which may occur in the Fall (Faria, 2004; Mantelatto et al., in press), when individuals have short intermolt intervals.

The sex ratio of hermit crabs parasitized by *Peltogasterella socialis* in the external stage of development did not follow the pattern of sex ratio of the unparasitized population; with males being parasitized more often even when females were more abundant (Faria, 2004; Mantelatto et al., in press). Since there are no prior reports that suggest the presence of any selective behavior of rhizocephalan larvae at the time of infection, two explanations may be possible: 1) females are less vulnerable or 2) the effect of parasitization is stronger in females than males, causing premature death of females. Vulnerability of hosts to parasitism by rhizocephalans is greatest after molting (O'Brien, 1999; Glenner and Werner, 1998), so it is possible that differential rates of molting in male vs. female hermit crabs would explain the observed skew in the sex ratio of infested hosts, but such a study is beyond the scope of this project.

The reduced weight presented by parasitized individuals is related to damage of the hepatopancreas. Reinhard (1956) and Nielsen (1970) reported a decrease in the fat content of the hepatopancreas in the hosts for peltogastrids. Nevertheless, this energetic cost may be equivalent to the energy allocated for reproduction, i.e., parasitic castrators utilize the reproductive energy resources of their hosts, and not necessarily the energy the hosts need to survive (O'Brien, 1999).

In our study, a negative effect of parasites on host growth (morphology) was found. Parasitic castration is very often associated with modifications of secondary sex characters, and appears to be caused by an inhibition of the androgenic gland in males and the ovary in females by the ramifying internae of the rhizocephalan (see Attril, 1989 for a discussion on hormonal mechanisms behind these modifications). According to Nielsen (1970), in some species of hermit crabs these modifications comprise changes in the pattern of growth of the pleopods in both males and females, as was observed in the present study for *P. criniticornis*. Feminization of the male hosts was reflected in an elongation of the endopod and reduction of the

exopod of pleopods. For females, the modifications were more evident in relation to the endopod which showed a reduction in growth. Considering that deformities in pleopods of hermit crabs are not caused by occupation of alternative shelters (tubular shells, sepolid tubes, bivalve shells, among others) to gastropod shells (Garcia et al., 2003; Meireles et al., 2003), we assume that signs of feminization are caused by parasitic action. Attrill (1989) found a series of modifications in pleopod structures (size, form and setae pattern) for males and females of *Munida sarsi* Huus (Crustacea, Galatheidae) parasitized by the rizocephalan *Triangulus munidae* Smith.

The ecological implications of parasitic castration are profound. Castrated hosts do not contribute to the gene pool of the next host generation but remain in the habitat competing for food and space with unparasitized hosts (O'Brien, 1999). According to Iossi et al. (2005) 41.4% of the ovigerous females ($n = 297$) of *P. criniticornis* in the study area showed aborted eggs. This implies a catastrophic consequence of parasitization by *P. socialis* in the population of *P. criniticornis* studied.

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