

Epibionts on *Arenaeus cribrarius* (Brachyura: Portunidae) from Brazil

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ABSTRACT. Mean prevalence and intensity of infestations by epibionts were evaluated in *Arenaeus cribrarius* (Lamarck, 1818), based on monthly samplings (May/1991 to April/1993), in Ubatuba, Brazil. Bryozoans were quantified in terms of colony numbers and barnacles by the number of specimens. Prevalence of infestation was determined in 1,914 individuals of *A. cribrarius* and assessed with respect to sex, maturity stage and season. No significant interaction was detected between epibionts and biological host factors. Males showed a higher infestation rate by *Chelonibia patula* (Ranzani, 1818) when compared to mature non-ovigerous females, yet *Octolasmis lowei* Darwin, 1851 infestation was associated to adult crabs. The ovigerous females of *A. cribrarius* showed a higher prevalence of infestation than males and non-ovigerous females, with lower infestations being recorded during winter. A synchrony between the life cycle of the epibionts and their hosts was evident and promotes the continuity of the former in the area.

KEY WORDS. Bryozoan; *Chelonibia patula*; epibiosis; *Octolasmis lowei*.

In unconsolidated benthic environments, the carapaces of decapod crustaceans are among the few solid surfaces that are available for colonization by the benthic invertebrates. These solid surfaces are utilized by specialized or facultative epibionts (ROSS 1983, ABELLÓ *et al.* 1990, GILI *et al.* 1993), and, to avoid the settlement of such epibionts, crustaceans employ anti-infestation behaviours, which include carapace cleaning with specific appendages and burying in the sediment (BAUER 1989, BECKER & WAHL 1996). In epibiosis studies, the terminology used varies according to the degree of association between the host and the infesting organism. WAHL (1989) defined epibiosis as the process of colonization of live surfaces by sessile organisms, whereas other authors have mentioned distinct terminologies according to the infestation position, distinguishing in ecto- and endosymbionts (ABELLÓ *et al.* 1990), or simply referring to these organisms as epizoots (KEY *et al.* 1996). Due to the considerable variation in the terminology that refers to the host/infesting organism relationship, in this study, the term 'epibiosis' as defined by WAHL (1989) was adopted hereafter. The term describes only the organic interaction, without quantifying the degree of association (positive or negative).

In crustaceans, the degree of infestation by epibionts may be influenced by various factors (WAHL & LAFARGUE 1990), such as the pool of potential colonizers, the reproductive period of the infesting organism, and the amount of time the surface is exposed to the infestation. In addition, age, moult stage, sex, physiological condition, and the efficiency of anti-infestation defences from the host are relevant variables (BARNES & BAGENAL 1951, MALDONATO & URIZ 1992, DAVIS & WHITE 1994). In general, epibiosis is unfavourable to the host organism and explains the necessity for the development of mechanisms to avoid in-

festations (WAHL 1989, ABELLÓ *et al.* 1990). This has led the relationships between hosts and epibionts to be rarely species-specific (WAHL & MARK 1999). An ecdysis of the host, however, is potentially detrimental to the epibionts as they will be discarded along with the exuvia (ABELLÓ *et al.* 1990, ITANI *et al.* 2002).

The present study evaluated the mean prevalence and intensity of infestations on the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) from the Ubatuba region, state of São Paulo, Brazil by several groups of epibionts, focusing more specifically on infestations (1) on the exoskeleton by the bryozoans and the barnacle *Chelonibia patula* (Ranzani, 1818) (Cheloniidae) and (2) in the branchial chambers by the stalked barnacle *Octolasmis lowei* Darwin, 1851 (Poecilasmataidae).

MATERIAL AND METHODS

Collection of *A. cribrarius* were carried out monthly from May/1991 to April/1993, at Fortaleza Bay and Ubatuba Bay, in the city of Ubatuba, on the northern coast of the state of São Paulo (23°25'00"-23°35'00"S and 45°00'00"-45°12'00"W). Specimens were captured with an otter-trawl towed by a commercial shrimp fishing boat, and two tows (1.5 hour) were performed, for a total of three hours of effort/capture/month. Individuals collected were frozen for analysis in the laboratory.

Samples were defrosted and the specimens were sexed, measured with a calliper (CW = carapace width without lateral spines) and classified by the maturity stage following PINHEIRO & FRANSOZO (1998). The remaining epibionts occurring on the exoskeleton (bryozoans and the barnacle *C. patula*) were recorded and quantified. The bryozoans were quantified by the number of colonies present. To record the presence of the bar-

nacle *O. lowei*, the cephalothorax of each specimen was removed and the branchial filaments in each side of the branchial chamber (left and right) were carefully inspected.

The prevalence of infestation, i.e. the proportion between infested hosts and the total number of crabs (KEY *et al.* 1997), was analyzed by log-linear models of contingency tables. The interaction amongst the following variables was examined: 1) season (spring, summer, fall, winter); 2) sex (males and non-ovigerous females); 3) maturity (juveniles and adults); and 4) frequency of infestation (present or absent). The G-test was applied to examine the obtained data. When significant interactions were observed, the analysis was decomposed into 2x2 frequency tables and re-evaluated using G-test or Tukey test for multiple proportions (ZAR 1999, SOKAL & ROHLF 2003). Similarly, this procedure was applied to examine the variability of the prevalence of infestation (frequency: present or absent) during the reproductive period of the females, and the following variables were investigated: 1) season (spring, summer, fall, winter); 2) reproductive condition (ovigerous and non-ovigerous adult females).

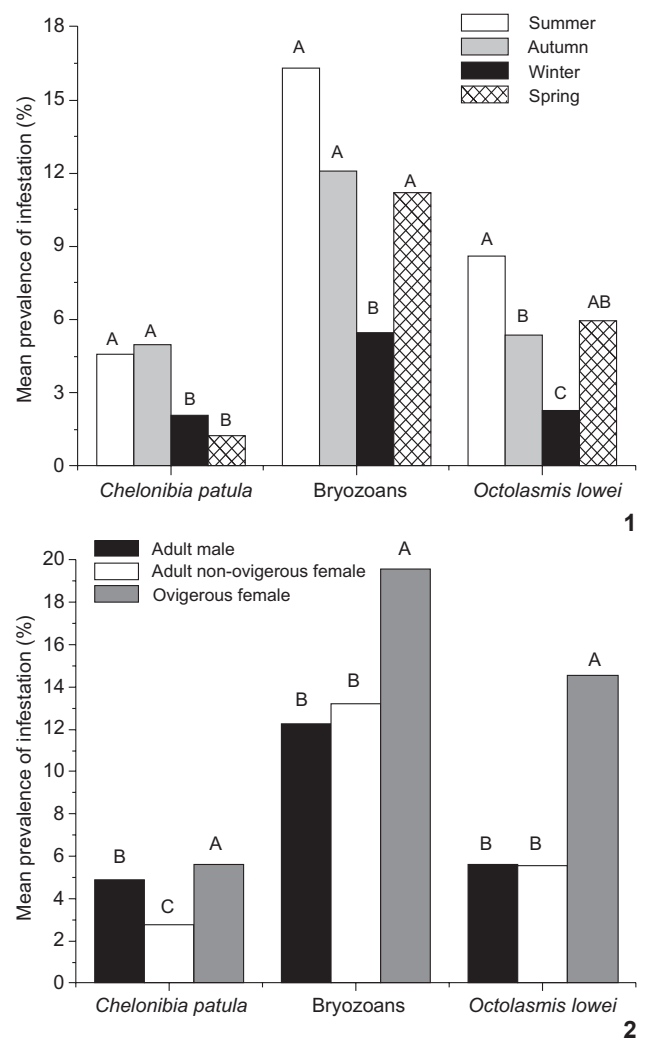
To investigate the intensity of infestation, which describes the number of epibionts present in each host (KEY *et al.* 1997), a two-way ANOVA was performed for the variables: sex (male and female) and season (spring, summer, fall, winter). Homocedasticity was tested with the Barlett test and when homogeneity of variance assumption was not met, the Mann-Whitney test (for variable 'sex') and the Median test (for variable 'season') were applied. The correlation between intensity of infestation of epibionts and host size was evaluated using the Spearman Rank Correlation test. All analyses were performed at 5% significance level.

RESULTS

A total of 1,914 specimens of *A. cribrarius* was sampled during the study period, of which 1,398 were mature and 516 immature individuals, respectively. Infestation was found only on mature crabs, with bryozoans corresponding to main epibiont group (12.7% of infested mature animals), followed by *C. patula* and *O. lowei* (on 5.6% and 3.8% of mature crabs, respectively) (Tab. I). The prevalence of infestation varied significantly with the variables tested (sex, maturity and season); however, no significant interactions were found (Tabs II and III). No significant seasonal variation was observed in the infestation of the crabs by the bryozoans (Tab. II) (Bartlett, $\chi^2 = 21.34$, $p = 0.003$; Median Test, $\chi^2 = 1.59$, $p = 0.661$), *C. patula* (ANOVA d.f. = 2, MS = 20.08, F = 1.32, $p = 0.277$) and *O. lowei* (Bartlett, $\chi^2 = 57.50$, $p < 0.0001$; Median Test, $\chi^2 = 4.71$, $p = 0.203$). Whilst a variation in the intensity of these taxa was not observed throughout the seasons, a significantly lower prevalence was noted during the winter (Fig. 1). In addition, the prevalence of infestation by *C. patula* was significantly lower during spring, and elevated rates of epibiosis were observed during the summer and the fall (Fig. 1).

The intensity of infestation on males and non-ovigerous

females did not vary significantly for bryozoans (U = 3567.00, $p = 0.27$), *C. patula* (d.f. = 1, MS = 9.065, F = 0.598, $p = 0.4437$) nor *O. lowei* (U = 743.00, $p = 0.86$). Nonetheless, males showed significantly higher prevalence of infestation by *C. patula*, when compared to non-ovigerous females (Fig. 2). A different pattern was observed for the bryozoans and *O. lowei* (Tab. II). However, the ovigerous condition of the females was proven as important for the establishment of all the analyzed groups of epibionts in the present study, which could be verified by their prevalence when compared with non-ovigerous condition and males, respectively (Tab. III, Fig. 2). Adults showed significantly higher



Figures 1-2. *Arenaeus cribrarius*. Mean prevalence of infestation (%) by *C. patula*, Bryozoans and *O. lowei* in relation to: (1) season; and (2) group of interest (adult male, non-ovigerous adult female, ovigerous female). Equal letters on the same group of vertical bars in each figure denote non-significant differences ($p > 0.001$).

Table I. *Arenaeus cribrarius*. Total number of mature crabs infested by epibionts in each season from the specimens collected in Ubatuba (São Paulo), from May/1991 to April/1993. (Total) Total number of crabs collected in each category, (Crabs) total of crabs infested, (Epibionts) total number of individuals or colonies of epibionts.

| Season | Sex | Total | Bryozoans | | <i>C. patula</i> | | <i>O. lowei</i> | |
|--------|---------|-------|-----------|-----------|------------------|-----------|-----------------|-----------|
| | | | Crabs | Epibionts | Crabs | Epibionts | Crabs | Epibionts |
| Summer | Males | 141 | 28 | 203 | 14 | 33 | 6 | 9 |
| | Females | 100 | 33 | 218 | 13 | 66 | 8 | 10 |
| Fall | Males | 204 | 21 | 135 | 9 | 16 | 15 | 61 |
| | Females | 327 | 31 | 298 | 15 | 43 | 9 | 27 |
| Winter | Males | 175 | 11 | 32 | 2 | 3 | 8 | 26 |
| | Females | 160 | 13 | 121 | 6 | 35 | 3 | 5 |
| Spring | Males | 157 | 23 | 133 | 13 | 49 | 4 | 15 |
| | Females | 134 | 18 | 108 | 6 | 25 | 0 | 0 |

Table II. *Arenaeus cribrarius*. Significance of the Source of Variation (S.V.) of the log-linear models for the prevalence of infestation (I; present or absent) from the specimens collected in Ubatuba, São Paulo, from May/1991 to April/1993. (E) Season: spring, summer, fall, winter; (S) sex: males and non-ovigerous females; (M) maturity: juveniles and adults.

| S.V. | d.f. | Bryozoans | | <i>C. patula</i> | | <i>O. lowei</i> | |
|---------|------|--------------|---------|------------------|---------|-----------------|---------|
| | | G | p | G | p | G | P |
| E*I | 3 | 25.49 | <0.0001 | 10.36 | 0.016 | 14.56 | 0.002 |
| S*I | 1 | 0.36 | 0.551 | 41.14 | <0.0001 | 0.62 | 0.432 |
| M*I | 1 | 58.44 | <0.0001 | 6.46 | 0.0110 | 17.26 | <0.0001 |
| E*S*I | 3 | 3.79 | 0.285 | 4.58 | 0.205 | 6.12 | 0.106 |
| E*M*I | 3 | 2.49 | 0.476 | 2.71 | 0.439 | 2.39 | 0.496 |
| S*M*I | 1 | 0.86 | 0.355 | 0.10 | 0.752 | 0.69 | 0.408 |
| E*S*M*I | 3 | 0.07 | 0.996 | 0.29 | 0.963 | 0.22 | 0.975 |

Values in bold letters correspond to significance.

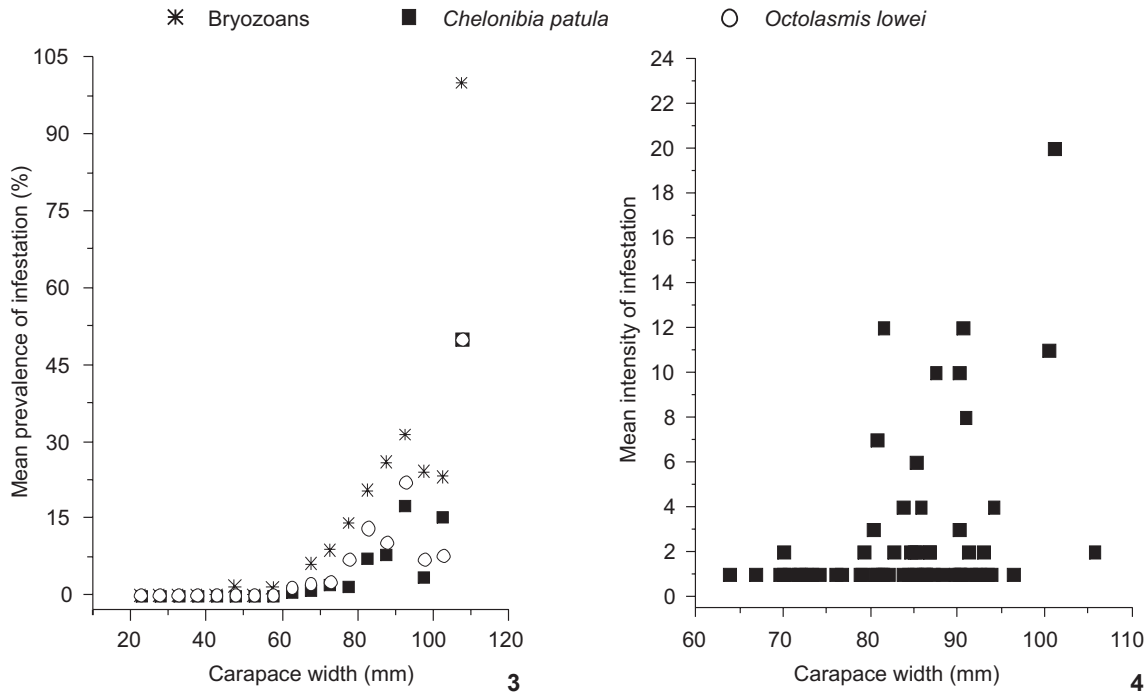
Table III. *Arenaeus cribrarius*. Significance of the Source of Variation (S.V.) of the log-linear models for the prevalence of infestation (I; present or absent) from the adult females collected in Ubatuba (São Paulo), from May/1991 to April/1993. (E) Season: spring, summer, fall, winter; (RC) reproductive condition: non-ovigerous females and ovigerous females.

| S.V. | d.f. | Bryozoans | | <i>C. patula</i> | | <i>O. lowei</i> | |
|--------|------|-----------|-------|------------------|---------|-----------------|---------|
| | | G | p | G | p | G | p |
| RC*I | 1 | 5.09 | 0.024 | 56.0 | <0.0001 | 15.84 | <0.0001 |
| E*RC*I | 3 | 7.18 | 0.066 | 6.58 | 0.086 | 2.16 | 0.541 |

prevalence of infestation than juveniles for all epibionts studied (Tab. II). Only for *C. patula* a significant correlation between the intensity of epibiont infestation and the host size was detected (Spearman $r = 0.33$, d.f. = 51, $t = 2.50$, $p = 0.016$, Figs 3 and 4). The remaining epibionts showed no correlation between the intensity of infestation and the size of the crabs (Spearman $r = 0.058$, d.f. = 176, $t = 0.7661$, $p = 0.445$, for bryozoans; and Spearman $r = 0.15$, d.f. = 76, $t = 1.3271$, $p = 0.188$, for *O. lowei*, Figs 3 and 4).

DISCUSSION

The presence of epibiont organisms on portunid crabs have been recorded by several authors, e.g. NEGREIROS-FRANZOZO *et al.* (1995) for *Callinectes danae* Smith, 1869 and *C. ornatus* Ordway, 1863, SANTOS (2002) for *Portunus spinimanus* Latreille, 1819, and MANTELATTO *et al.* (2003) for various portunid species sampled in the coast of the state of São Paulo, Brazil. In the species studied



Figures 3-4. *Arenaeus cribrarius*. Spearman correlation analysis of prevalence (%) and intensity of infestation by the epibionts in relation to the host size: (3) prevalence of infestation (%); (4) intensity of infestation.

by those authors, the presence of the same epibionts registered in the present study could be verified. We detect the presence of *Chelonibia patula* in *C. danae* and *C. ornatus*; and *Octolasmis lowei* in *A. cribrarius*, *C. danae*, *C. ornatus* and *P. spinimanus*, indicating that these animals are generalists, due to wide diversity of hosts with which they are associated.

The interaction between bryozoans and the exoskeleton of portunids has been investigated previously, and studies have shown epibionts to cause variable effects. These varied from a negative impact to the host due to the increase in body weight, to benefits from the mimetic effects (INGLE 1983, KEY *et al.* 1999, OVERSTREET 1983, RASMUSSEN 1973, WAHL 1989), which is particularly important for the decorator crabs (PARAPAR *et al.* 1997, WICKSTEN 1980). Nonetheless, the infestations caused by bryozoans – *Alcyonidium albescens* Winston & Key, 1999, *Membranipora arborescens* (Canu & Bassler, 1928) and *Triticella elongata* (Osburn, 1912) – have a minimal negative impact towards the host, as verified in *C. sapidus* by KEY *et al.* (1999), where no special symbiosis was observed between the organisms. The pattern of the bryozoan colonies merges with the reticulated pattern of the carapace from *A. cribrarius*, and the bryozoans may benefit against predators by this association. Moreover, bryozoans benefit from the hosts through the additional substrates for settlement, feeding and reproduction. Despite the elevated infestation rate observed in the present study, the impact on the crab is low due to the negligible weight of the bryozoans.

Bryozoans are common infestants of sessile substrates and are also found as epibionts of mobile organisms, in both nektonic and benthonic hosts (KEY *et al.* 1996). Although there is a high diversity of described species (approximately 5,500 species according to ROCHA & D'HONDT 1999), a low diversity of bryozoans was observed as epibiont of mobile organisms as crabs, probably due to the frequent ecdysis process of the host. Among the epibiont bryozoans, species of *Triticella* (Gymnolaemata: Ctenostomata: Triticellidae), as *Triticella flava* Dalyell, 1848, *Triticella capsularis* Gordon & Wear, 1999 and *Triticella elongata* (Osburn, 1912) were observed on crustacean decapods, mainly on portunid crabs (e.g. EGGLESTON 1971, ABELLÓ & CORBERA 1996, KEY *et al.* 1999, GORDON & WEAR 1999 FERNANDEZ-LEBORANS 2003). In addition, other Ctenostomata, the species *Alcyonidium mamillatum* Alder, 1857, and species of Cheilostomata, as *Acanthodesia tenuis* (Desor, 1848), *Membranipora arborescens* (Canu & Bassler, 1928) and *Membranipora membranacea* (Linnaeus, 1767), were observed associated with brachyuran crabs (ABELLÓ & CORBERA 1996, KEY *et al.* 1999, MCGAW 2006, WINTER & MASUNARI 2006). Further studies about the identity of the bryozoans on *A. cribrarius* can bring important contributions to the knowledge about the interactions between both groups.

Amongst the various groups of invertebrate epibionts, barnacles are one of the most common, either by internal or external infestation (CHRISTIE & DALLEY 1987). The barnacles associated with brachyurans are represented by the Coronulidae

and Balanidae families, and particularly, by the *Chelonibia* Leach, 1817 (Chelonibiidae) and *Amphibalanus* Darwin, 1854 (Balanidae) genera, respectively (PHILIPS & CANNON 1978, HAEFNER 1985, VAN ENGEL 1987, NEGREIROS-FRANZOZO *et al.* 1995). Barnacles of *Chelonibia* occur on the carapaces and appendages of pelagic crabs, on sea turtles and on other floating objects (KEY *et al.* 1997, PASTERNAK *et al.* 2002). According to OVERSTREET (1983), the barnacle *C. patula* may infest the portunid crabs of *Callinectes* (STUBBINGS 1967, NEGREIROS-FRANZOZO *et al.* 1995, KEY *et al.* 1997) and *Portunus* (SHIELDS 1992), and has also been recorded in a number of majids of *Libinia* Leach, 1815 (Pisinae) (PEARSE 1952). The distribution of *C. patula* on the host carapace is better correlated to larval settlement (PASTERNAK *et al.* 2002) than to the abrasion processes of the exoskeleton during burying (KEY *et al.* 1997). For PASTERNAK *et al.* (2002), cypris of *C. patula* chose the orientation and the location of settlement, and settled preferentially on the most elevated and central region of the carapace where water flow is more intense. Also, the role of chemical cues on larvae settlement has been described (MOLENOCK & GOMEZ 1972) influencing the dynamics of barnacle recruitment (ZARDUS & HADFIELD 2004) but never directly tested in the settlement of commensal barnacles.

The prevalence of infestation by the barnacle *C. patula* has also been recorded in males and females of other portunid crabs. In *C. sapidus*, infestation rate by this barnacle was higher in females than males, occurring in 70% of the females (KEY *et al.* 1997), corroborating earlier studies showing infestation by *C. patula* in females that had previously spawned two or three times (TAGATZ 1968, CRISP 1983). Hence, many authors have concluded that the higher infestation rate observed in females of *C. sapidus* could be explained by females entering anecydysis soon after puberty while males continue to grow (TRUITT 1939, VAN ENGEL 1958, TAGATZ 1968, PERRY 1975, OVERSTREET 1983, CRISP 1983). In the present study, males of *A. cribrarius* showed higher a infestation rate by *C. patula* compared to non-ovigerous females. This pattern could be the result of the significant correlation between host size and infestation intensity. As males reach larger sizes than females (PINHEIRO & HATTORI 2006), the former becomes more susceptible to settlement of cypris of *C. patula*.

Several species of brachyurans host stalked barnacles of *Octolasmis* (Gray, 1825) in their branchial chamber. A few authors have registered the occurrence of this barnacle in crabs (Dorippidae, Calappidae, Leucosiidae, Majidae, Portunidae and Xanthidae) and lobsters (Scyllaridae and Palinuridae) (JEFFRIES & VORIS 1983, JEFFRIES *et al.* 1984, 1991). In Brazil, YOUNG (1990), SANTOS (2002), SANTOS & BUENO (2002) and MANTELAI TO *et al.* (2003) reported the infestation of the brachyurans by *O. lowei*. The association of the species from *Octolasmis* is due to the facilitated nutrient acquisition and the protection provided by the branchial chambers of the crabs, where the development of the epibiont is completed. These epibionts tend to select preferentially hosts in intermoult (SANTOS 2002) and settlement tends to increase after sexual maturity is reached. Moreover, according

to JEFFRIES *et al.* (1992), in the crab *Scylla serrata* (Forsk., 1775), individuals having less than 12 instars are not infested by octolasmids because of the short intermoult period, which would prevent the growth and reproduction of the epibiont. The results from the present investigation concur with the above studies because adults of *A. cribrarius* showed higher prevalence of infestation by *O. lowei*, and the intermoult period in the adults would be sufficient for settlement, growth and reproduction of the epibiont to occur before the moulting of the host.

The duration of the intermoult period, the habitat distribution, and the burying behaviour of the host are determinant factors in the distribution of the species of *Octolasmis* (ROSS 1983, JEFFRIES *et al.* 1992), and explain the clear differences in the prevalence amongst the host species (SANTOS & BUENO 2002). Furthermore, the epibionts can explore only a portion of the host population, affecting specific age, sex and even the environment (VORIS *et al.* 1994). The presence of *Octolasmis* species in the branchial chamber can affect the host in many ways: 1) reducing the water circulation and the gas exchange of the gills due to the fixation of the barnacle; 2) consuming the oxygen in the ventilatory water of the crab; and 3) obstructing of the ventilatory current in the host, which would elevate the energy spent in ventilation. However, according to GANNON & WHEATLY (1992), *Octolasmis muelleri* Coker, 1902 (Poecilasmidae) depends on the ventilatory current from *C. sapidus* to survive, and those authors have not observed any significant perturbation caused by the presence of the epibiont. This barnacle may be detrimental to the host only during intense infestation, which is contrary to evidence from most of the brachyurans studied, where the interaction between the species of *Octolasmis* and the host is common.

Seasonal analysis is one of the methods to evaluate the interaction between the epibionts and the hosts, where it is possible to determine the compatibility of their life cycles. In the present study, there was a significant seasonal difference in the prevalence of infestation for *C. patula*, bryozoans and *O. lowei*, with lower infestation occurring during the winter. These results suggest that the epibionts have a synchronous life cycle with their hosts. As ovigerous females (along with males and non-ovigerous females) are less abundant during the coldest months (PINHEIRO & FRANZOZO 2002), therefore occur a subsequent reduction of the hosts available for epibiont settlement. Moreover, considering that the epibionts are available equally throughout the year, we should expect an increase in epibiont settlement per host. As the hosts showed lower proportion of infestation during the winter months suggesting that epibiont are also in lower availability during this season.

The quantitative analysis of the epibionts investigated has shown a higher prevalence of infestation in ovigerous females when compared to the remaining reproductive groups studied. Similar results were obtained in other portunid species (SHIELDS 1992, KEY *et al.* 1999, SANTOS & BUENO 2002), where the different infestation rates observed were regarded as the

result of the differential behaviour of the ovigerous females. Studying the infestation of bryozoans in *C. sapidus*, KEY *et al.* (1999), suggested that the higher infestation on ovigerous females, following the puberty moult, could be explained by the lower frequency of moults in females in relation to males. Thus, the infestation on ovigerous females in the present study may be caused by other factors, such as: 1) greater age and longer susceptibility to the settlement of bryozoan larvae; 2) the higher attractiveness to larval settlement; and 3) a longer period spent in high salinity waters. For the host species investigated in the present study, PINHEIRO & FRANSOZO (2002) have demonstrated that ovigerous females of *A. cribrarius* prefer deeper waters, higher salinities and sediment composed by coarser sand, which is utilized to shape their egg mass. During this period, females excavate a small depression in the sediment and use it as an incubation chamber, while their carapace stays partially uncovered and susceptible to colonization by epibionts (PINHEIRO & FRANSOZO 1999). In general, this species remains buried in the sediment, exposing only the rostral region and the upper surface of the chelipeds, where most of the epibiosis have been recorded. In addition, when females are carrying the egg mass, their natatory activity is slowed and cryptic behaviours are observed, which might enhance the settlement of the epibionts.

In crustaceans, ecdysis is the most limiting and relevant biological process affecting the epibiont/host interaction because the occurrence of ecdysis is directly related to the intermoult period. Therefore, the succession pattern of epibionts in crabs can be analysed, not only according to size, but also by the moult stage of the host. Accordingly, this pattern could provide evidence for the existence of a terminal moult in the host, which is unknown in many species of crustaceans (ABELLÓ *et al.* 1990, SHIELDS 1992, NEGREIROS-FRANSOZO *et al.* 1995). One possible explanation to this pattern is that epibiosis is correlated with the maturity size of the host because the epibionts are not relatively fast to establish and develop in juvenile crabs, since these age-classes undergo ecdysis more frequently before puberty. On the other hand, the epibionts can develop continuously in adult crabs, where the intermoult period is longer (ABELLÓ *et al.* 1990). The prevalence of infestation was positively correlated to the host size in all groups examined, possibly, due to the larger area available for larval settlement. Conversely, larger crabs did not present infestation rates close to 100%, which would be evidence for the existence of a terminal moult, as suggested by ABELLÓ *et al.* (1990). Thus, in agreement with other portunids, *A. cribrarius* do not undergo a terminal moult after reaching sexual maturity.

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LITERATURE CITED

- ABELLÓ, P. & J. CORBERA. 1996. Epibiont bryozoans (Bryozoa, Ctenostomatida) of the crab *Goneplax rhomboides* (Brachyura, Goneplacidae) off the Ebro delta (western Mediterranean). *Miscelania Zoologica* 19: 43-52.
- ABELLÓ, P.; R. VILLANEUVA & J.M. GILI. 1990. Epibiosis in deep-sea crab populations as indicator of biological and behavioural characteristics of the host. *Journal of the Marine Biological Association of the United Kingdom* 70: 687-695.
- BARNES, H. & T.B. BAGENAL. 1951. Observation on *Nephrops norvegicus* (L.) and on an epizoic population of *Balanus crenatus* Brug. *Journal of the Marine Biological Association of the United Kingdom* 30: 369-380.
- BAUER, R.T. 1989. Decapod crustacean grooming: functional morphology, adaptive value and phylogenetic significance, p. 49-74. *In*: B.E. FELGENHAUER & L. WATLING & A.B. THISTLE (Eds). **Functional morphology of feeding and grooming in Crustacea**. Rotterdam, Crustacean Issues, vol. 6, 320p.
- BECKER, K. & M. WAHL. 1996. Behaviour patterns as natural antifouling mechanisms of tropical marine crabs. *Journal of Experimental Marine Biology and Ecology* 203: 245-258.
- CHRISTIE, A.O. & R. DALLEY. 1987. Barnacle fouling and its prevention, p. 419-433. *In*: A.J. SOUTHWARD (Ed). **Barnacle Biology**. Rotterdam, Crustacean Issues, vol. 5, 496.
- CRISP, D.J. 1983. *Chelonibia patula* (Ranzani), a pointer to the evolution of the complementary male. *Marine Biology Letters* 4 (5): 281-294.
- DAVIS, A.R. & G.A. WHITE. 1994. Epibiosis in a guild of sessile subtidal invertebrates in southeastern Australia: a quantitative survey. *Journal of Experimental Marine Biology and Ecology* 177: 1-14.
- EGGLESTON, D. 1971. Synchronization between moulting in *Calocaris macandrea* (Decapoda) and reproduction in its epibiont *Triticella (sic) koreni*. *Journal of the Marine Biological Association of the United Kingdom* 51: 409-410.
- FERNANDEZ-LEBORANS, G. 2003. Protist-bryozoan-crustacean hyperepibiosis on *Goneplax rhomboides* (Linnaeus, 1758) (Decapoda, Brachyura) from the NW Mediterranean coast. *Crustaceana* 76 (4): 479-497.
- GANON, A.T. & M.G. WHEATLY. 1992. Physiological effects of an ectocommensal gill barnacle, *Octolasmis muelleri* on gas exchange in the blue crab *Callinectes sapidus*. *Journal of Crustacean Biology* 12 (1): 11-18.
- GILI, J.M.; P. ABELLÓ & R. VILLANEUVA. 1993. Epibionts and intermoult duration in the crab *Bathynectes piperitus*. *Marine Ecology Progress Series* 98: 107-113.
- GORDON, D.P. & R.G. WEAR. 1999. A new ctenostome bryozoans ectosymbiotic with terminal-moult paddle crabs (Portunidae) in New Zealand. *New Zealand Journal of Zoology* 26: 373-380.

- HAEFNER JR, P.A. 1985. Morphometry, reproduction, diet, and epizoites of *Ovalipes stephensoni* Williams, 1976 (Decapoda, Brachyura). **Journal of Crustacean Biology** 5 (4): 658-672.
- INGLE, R.W. 1983. Shallow-water crabs. **Synopses of the British Fauna New Series** 25: 1-206.
- ITANI, G.; M. KATO & Y. SHIRAYAMA. 2002. Behaviour of the shrimp ectosymbionts, *Peregrinamor ohshimai* (Mollusca: Bivalvia) and *Phyllodurus* sp. (Crustacea: Isopoda) through host ecdyses. **Journal of the Marine Biological Association of the United Kingdom** 82: 69-78.
- JEFFRIES, W.B. & H.K. VORIS. 1983. The distribution, size, and reproduction of the pedunculate barnacle, *Octolasmis mülleri* (Coker, 1902), on the blue crab, *Callinectes sapidus* (Rathbun, 1896). **Fieldiana Zoology** 16: 1-10.
- JEFFRIES, W.B.; H.K. VORIS & C.M. YANG. 1984. Diversity and distribution of the pedunculate barnacle *Octolasmis* Gray, 1825, epizoic on the scyllarid lobster, *Thenus orientalis*. **Crustaceana** 46 (3): 300-308.
- JEFFRIES, W.B.; H.K. VORIS & C.M. YANG. 1991. Species recognition among the pedunculate barnacles (Cirripedia: Thoracica) on the mangrove crabs, *Scylla serrata*. **Raffles Bulletin of Zoology** 40 (1): 83-92.
- JEFFRIES, W.B.; H.K. VORIS & S. POOVACHIRANON. 1992. Age of the mangrove crab *Scylla serrata* at colonization by stalked barnacles of the genus *Octolasmis*. **Biological Bulletin** 182: 188-194.
- KEY JR, M.M.; J.E. WINSTON; J.W. VOLPE; W.B. JEFFRIES & H.K. VORIS. 1999. Bryozoan fouling of the blue crab *Callinectes sapidus* at Beaufort North Carolina. **Bulletin of Marine Science** 64 (3): 513-533.
- KEY JR, M.M.; J.W. VOLPE; W.B. JEFFRIES & H.K. VORIS. 1997. Barnacles fouling of the blue crab *Callinectes sapidus* at Beaufort, North Carolina. **Journal of Crustacean Biology** 17 (3): 424-439.
- KEY JR, M.M.; W.B. JEFFRIES; H.K. VORIS & C.M. YANG. 1996. Epizoic bryozoans, horseshoe crabs, and other mobile benthic substrates. **Bulletin of Marine Science** 58 (2): 368-384.
- MALDONATO, M. & M.J. URIZ. 1992. Relationship between sponges and crabs: patterns of epibiosis on *Inachus aguiarii* (Decapoda: Majidae). **Marine Biology** 113: 281-286.
- MANTELATTO, F.L.; J.J. O'BRIEN & R. BIAGI. 2003. Parasites and symbionts of crabs from Ubatuba Bay, São Paulo State, Brazil. **Comparative Parasitology** 70 (2): 211-214.
- MCGAW, I.J. 2006. Epibionts of sumpatric species of *Cancer* crabs in Barkley Sound, British Columbia. **Journal of Crustacean Biology** 26 (1): 85-93.
- MOLENOCK, J. & E.D. GOMEZ. 1972. Larval stages and settlement of the barnacle *Balanus (Conopea) galeatus* (L.) (Cirripedia Thoracica). **Crustaceana** 23: 100-108.
- NEGREIROS-FRANZOZO, M.L.; T.M. COSTA & A. FRANZOZO. 1995. Epibiosis and molting in two species of *Callinectes* (Decapoda: Portunidae) from Brazil. **Revista Biologia Tropical** 43 (1-3): 257-264.
- OVERSTREET, R.M. 1983. Metazoan Symbionts of Crustaceans, p. 155-250. In: A.J. PROVENZANO JR (Ed). **The Biology of Crustacea: Pathobiology**. New York, Academic Press, vol. 6, 290p.
- PARAPAR, J.; L. FERNANDEZ; E. GONZALEZ-GURRIARAN & R. MUIÑO. 1997. Epibiosis and masking material in the spider crab *Maja squinado* (Decapoda: Majidae) in the Ria de Arousa (Galicia, NW Spain). **Cahiers de Biologie Marine** 38 (4): 221-234.
- PASTERNAK, Z.; A. ABELSON & Y. ACHITUV. 2002. Orientation of *Chelonibia patula* (Crustacea: Cirripedia) on the carapace of its crab host is determined by the feeding mechanism of the adult barnacles. **Journal of the Marine Biological Association of the United Kingdom** 82: 583-588.
- PEARSE, A.S. 1952. Parasitic Crustacea from the Texas coast. **Publication Institute of Marine Science, University of Texas** 2 (2): 5-42.
- PERRY, H.M. 1975. The blue crab fishery in Mississippi. **Gulf Research Reports** 5: 39-57.
- PHILIPS, W.J. & L.R.G. CANNON. 1978. Ecological observations on the commercial sand crab, *Portunus pelagicus* (L.), and its parasite, *Sacculina granifera* Boschma, 1973 (Cirripedia: Rhizocephala). **Journal of Fish Diseases** 1: 137-149.
- PINHEIRO, M.A.A. & A. FRANZOZO. 1998. Sexual maturity of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Decapoda, Brachyura, Portunidae), in the Ubatuba littoral, São Paulo state, Brazil. **Crustaceana** 71 (4): 434-452.
- PINHEIRO, M.A.A. & A. FRANZOZO. 1999. Reproductive behavior of the swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Crustacea, Brachyura, Portunidae) in captivity. **Bulletin of Marine Science** 64 (2): 243-253.
- PINHEIRO, M.A.A. & A. FRANZOZO. 2002. Reproductive of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Brachyura, Portunidae), on the north coast of São Paulo State, Brazil. **Journal of Crustacean Biology** 22 (2): 416-428.
- PINHEIRO, M.A.A. & G.Y. HATTORI. 2006. Growth of the speckled swimming crab, *Arenaeus cribrarius* (Lamarck, 1818) (Crustacea, Brachyura, Portunidae), in Ubatuba (SP), Brazil. **Journal of Natural History** 40 (21-22): 1331-1341.
- RASMUSSEN, E. 1973. Systematic and ecology of the is fjord marine fauna (Denmark). **Ophelia** 11: 1-495.
- ROCHA, R.M. & J.-L. D'HONDT. 1999. Filo Ectoprocta ou Bryozoa, p. 241-249. In: A.E. MIGOTTO & C.G. TIAGO (Eds). **Biodiversidade do Estado de São Paulo, Brasil: síntese do conhecimento ao final do século XX**. São Paulo, FAPESP, vol. 3, 310p.
- ROSS, D.M. 1983. Symbiotic relations, p. 163-212. In: F.J. VERNBERG & W.B. VERNBERG (Eds). **The biology of Crustacea: behavior and ecology**. New York, Academic Press, vol. 7, 383p.
- SANTOS, C. & S.L.S. BUENO. 2002. Infestation by *Octolasmis lowei* (Cirripedia: Poecilasmidae) in *Callinectes danae* (Decapoda: Portunidae) from São Sebastião, Brazil. **Journal of Crustacean Biology** 22 (2): 241-248.

- SANTOS, S. 2002. Symbiosis between *Portunus spinimanus* Latreille, 1819 (Decapoda, Portunidae) and *Octolasmis lowei* (Darwin, 1852) (Thoracica, Poecilasmatidae) from Ubatuba, São Paulo, Brazil, p. 205-209. *In*: E. ESCOBAR-BRIONES & F. ALVAREZ (Eds). **Modern Approaches to the study of Crustacea**. New York, Kluwer Academic Publishers, 376p.
- SHIELDS, J.D. 1992. Parasites and symbionts of the crab *Portunus pelagicus* from Moreton Bay, Eastern Australia. **Journal of Crustacean Biology** 12 (1): 94-100.
- SOKAL, R.R. & F.J. ROHLF. 2003. **Biometry: the principles and practice of statistics in biological research**. New York, W.H. Freeman, 3rd ed., 887p.
- STUBBINGS, H.G. 1967. Cirriped fauna of tropical West Africa. Bulletin of the British Museum Natural History. **Zoology** 15: 1-39.
- TAGATZ, M.E. 1968. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. **Fishery Bulletin-NOAA** 67: 17-33.
- TRUITT, R.V. 1939. **Our water resources and their conservation**. Solomons, Chesapeake Biological Laboratory, Contribution 27, 103p.
- VAN ENGEL, W.A. 1958. The blue crab and its fishery in Chesapeake Bay. Part 1. Reproduction, early development, growth, and migration. **Commercial Fisheries Review** 20: 6-17.
- VAN ENGEL, W.A. 1987. Factors affecting the distribution and abundance of the blue crab in Chesapeake Bay, p. 178-209. *In*: S.K. MAJUMDAR; L.W. HALL JR & H.M. AUSTIN (Eds). **Contaminant problems and management of living Chesapeake Bay resources, Pennsylvania**. Philadelphia, Academy of Sciences, 573p.
- VORIS, H.K.; W.B. JEFFRIES & S. POOVACHIRANON. 1994. Patterns of distribution of two barnacle species on the mangrove crab, *Scylla serrata*. **Biological Bulletin** 187: 346-354.
- WAHL, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. **Marine Ecology Progress Series** 58: 175-189.
- WAHL, M. & F. LAFARGUE. 1990. Marine Epibiosis II. Reduced fouling on *Polysyncraton lacazei* (Didemnidae, Tunicata) and proposal of an antifouling potential index. **Oecologia** 82: 275-282.
- WAHL, M. & O. MARK. 1999. The predominantly facultative nature of epibiosis: experimental and observational evidence. **Marine Ecology Progress Series** 187: 59-66.
- WICKSTEN, M.K. 1980. Decorator crabs. **Scientific American** 242: 146-154.
- WINTER, V.C. & S. MASUNARI. 2006. Macroepizoísmo em *Libinia ferreirae* (Crustacea, Brachyura, Majidae). **Iheringia, Série Zoologia**, 96 (2): 135-140.
- YOUNG, P.S. 1990. Lepadomorph cirripeds from the Brazilian coast. I – Families Lepadidae, Poecilasmatidae and Heteralepadidae. **Bulletin of Marine Science** 47: 641-655.
- ZAR, J.H. 1999. **Biostatistical Analysis**. New Jersey, Prentice Hall, 4th ed., 121p.
- ZARDUS, J.D. & HAEDFIELD, M.G. 2004. Larval development and complemental males in *Chelonibia testudinaria*, a barnacle commensal with sea turtles. **Journal of Crustacean Biology** 24 (3): 409-421.

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