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ORIGINAL ARTICLE

Infestation by the epibiont *Octolasmis lowei* in a portunid crab assemblage from a subtropical coast

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ABSTRACT

We investigated the infestation by *Octolasmis lowei* Darwin, 1851 in branchial chambers of the portunid *Achelous spinimanus* (Latreille, 1819), *Arenaeus cribrarius* (Lamarck, 1818), *Callinectes danae* Smith, 1869, and *Callinectes ornatus* Ordway, 1863. We evaluated how infestation is related to host maturity, molt stage, carapace width and sex. The infestation probability increases with host carapace width, and infested crabs were more likely to be adults in intermolt stage. Infestation prevalence did not differ between sexes, except for *C. ornatus*, in which females had higher infestation than males. Infestation intensity was higher for males than females in *A. cribrarius* and *A. spinimanus*, while *C. ornatus* showed an opposite pattern. Association of *O. lowei* with portunid seems to be tightly related to the biological traits of its host. Some of these traits, such as host size, maturity and molt stage, are likely to affect infestation in a similar way for all host species, while the effect of other traits, such as sex identity, seems to vary among hosts. We suggest a deeper understanding of the factors driving host use by generalist epibionts such as *O. lowei* depends on investigating their occurrence on a variety of potential hosts, as well as performing manipulative studies to evaluate the factors driving host preferences by this epibiont.

KEY WORDS

Decapods, epibiosis, infestation patterns, stalked barnacle.

INTRODUCTION

In marine habitats dominated by soft bottoms, some benthic organisms have an important role in providing hard substrate for the settlement and growth of other species such as algae, barnacles and bryozoans (Jeffries *et al.*, 1992; Wahl and Hay, 1995; Becker and Wahl, 1996; Key *et al.*, 1999). In this epibiont-host interaction, hosts can enhance access to food sources and optimize epibiont dispersal (review in Wahl, 1989). However, some hosts can be negatively affected (e.g. increase in weight and surface friction), which may cause reduced mobility (Dixon *et al.*, 1981) depending on the number and species of epibionts. Among host organisms, marine benthic decapods have been extensively reported in sheltering epibionts (Abelló and Macpherson, 1992; Jeffries *et al.*, 1992; Becker and Wahl, 1996; Key *et al.*, 1999; Santos and Bueno, 2002; Cordeiro and Costa, 2010). Epibiont infestation in decapods is often related to the biological traits of these hosts, such as behavior, size, sex, maturity and molt stage (Abelló and Macpherson, 1992; Jeffries *et al.*, 1992; Becker and Wahl, 1996; Key *et al.*, 1999; Cordeiro and Costa, 2010).

The infraclass Cirripedia is a typical group of epibionts which occur in decapods (Abelló and Macpherson, 1992; Jeffries *et al.*, 1992; Key *et al.*, 1997; Costa *et al.*, 2010). These sessile invertebrates are found attached to the carapace (Key *et al.*, 1997; Costa *et al.*, 2010) and branchial chambers of their hosts (Abelló and Macpherson, 1992; Jeffries *et al.*, 1992; Santos and Bueno, 2002). Among cirripedians, the stalked barnacle of the genus *Octolasmis* Gray, 1825 is an exclusive epibiont, often found adhered to the gills of decapods such as lobsters (Jeffries *et al.*, 1984; 1991) and crabs (Dinamani, 1964; Jeffries *et al.*, 1982; Voris *et al.*, 1994; Cordeiro and Costa, 2010). Usually, the host is not negatively affected by the epibiont, unless when there is a large number of the latter, which may cause negative effects in host gas exchanges (Wahl, 1989). In addition, *Octolasmis* species have a planktonic larval stage, followed by settlement and metamorphosis to adult form in the branchial chambers of their hosts, completing its life cycle during host intermolt stage (Walker, 1974; Gili *et al.*, 1993; Jeffries and Voris, 1996).

Although infestation by the genus *Octolasmis* in decapods is well documented (Jeffries and Voris, 1983; Young, 1990; Shields, 1992; Walker, 2001; Santos and Bueno, 2002; Yan *et al.*, 2004; Cordeiro and Costa, 2010; Costa *et al.*, 2010; Farrapeira, 2010; Machado *et al.*, 2013), few studies have attempted to simultaneously investigate the association of these epibionts in a variety of sympatric host species (Humes, 1941; Jeffries *et al.*, 1982; Kumaravel *et al.*, 2009; Machado *et al.*, 2013). Such approach is important for understanding host usage range in epibionts, as well as to evaluate the effect of biological traits (e.g. maturity, size and sex) on infestation, which could improve our knowledge of the factors influencing epibiont-host interaction. In Brazil, the occurrence of *Octolasmis lowei* Darwin, 1851 has been reported in the branchial chambers of crabs from the families Aethridae, Epialtidae, Leucosiidae and Portunidae (Young, 1990; Santos and Bueno, 2002; Cordeiro and Costa, 2010; Costa *et al.*, 2010; Machado *et al.*, 2013). However, these findings are reported in different areas and for few host species per study. Herein, we evaluated the infestation of the stalked barnacle *O. lowei* in branchial chambers of four portunid species, investigating how infestation by this epibiont is related to host maturity, size, sex and molt stage.

MATERIAL AND METHODS

Portunid crabs were collected monthly in the Ubatuba bay, on the northern coast of the state of São Paulo, Brazil (23°30' to 23°23'S; 45°05' to 44°47'W) from November 2001 to April 2002 (except December 2001). Sampling was carried out using an otter trawl towed by a commercial fishing boat, along transects parallel to the coastline, covering depths from 5 to 25 m. We trawled 6 to 10 transects monthly, totalizing 43 transects. Samples were bagged and maintained frozen until analysis. Crabs were identified in accordance to Melo (1996). For each individual, maximum carapace width (CW in mm) was measured, excluding lateral spines. Crabs were sexed based on abdomen shape (Williams, 1974) and the number of pleopods (Melo, 1996). Molt stage (intermolt or molt activity) was determined according to carapace consistency (Skinner, 1985). After removing the dorsal carapace, we inspected the branchial chambers in *O. lowei* using a stereo-microscope and determined maturity stage (adult or juvenile) based on gonad state (Costa and Negreiros-Fransozo, 1998).

For all host species, data analyses were restricted to adult crabs, since juveniles are unlikely to be infested (Machado *et al*., 2013). Only one juvenile (a female of *Callinectes ornatus* Ordway, 1863) was found to be infested, but it was excluded from the analysis. For each host species, we compared carapace width and proportion of individuals in intermolt stage between males and females applying Student's t test (assuming equal or unequal variances) and a Chi-squared test, respectively. Homogeneity of variance was verified by a Cochran test. Infestation (considering crab condition: infested or non-infested) was analyzed using logistic regression, with CW and sex as explanatory variables. Also, for each host, the effect of CW on infestation was tested in both sexes with a logistic regression and, from the resulting models, we estimated odd ratios of infestation (the ratio of the probability of being infested to the probability of not being infested) according to CW. Prevalence (%) and intensity of infestation (number of epibionts per infested host) were compared between males and females using a Chi-squared test and a generalized linear model (GLM), respectively. All GLM applied to the intensity of infestation comparisons among sexes were tested using Negative Binomial distribution. Statistical difference was considered when $p < 0.05$.

RESULTS

A total of 1840 adult portunid crabs were sampled, represented by the following species: *Achelous spinimanus* (Latreille, 1819) (N = 246), *Arenaeus cribrarius* (Lamarck, 1818) (N = 112), *Callinectes danae* Smith, 1869 (N = 164), and *Callinectes ornatus* (N = 1318). Highest infestation prevalence by *O. lowei* was observed in *C. danae* (22.56%) followed by *A. cribrarius* (13.39%), *C. ornatus* (10.85%) and *A. spinimanus* (8.13%). Among infested host species, *A. spinimanus* showed higher infestation intensity values (11.1 ± 16.4 epibionts/ind.) than those observed in *C. ornatus* (7.4 ± 8.4), *C. danae* (3.3 ± 3.2) and *A. cribrarius* (3.1 ± 3.4). Males had larger CW than females in all host species (*A. cribrarius*: t = 3.204, df = 83.41, $P = 0.002$; *C. danae*: t = 3.745, df = 26.06, $P = 0.001$; *C. ornatus*: t = 15.523, df = 1092.8, $P < 0.0001$), except in *A. spinimanus* (t = 1.877, df = 244, $P = 0.062$). Proportion of individuals in intermolt stage did not differ between sexes, in any of the host species (*A. cribrarius*: $\chi 2 = 0.620$, $P = 0.431$; *C. danae*: $\chi 2 = 2.601$, $P = 0.107$; *C. ornatus*: $\chi 2 = 2.019$, $P = 0.155$ and *A. spinimanus*: $\chi 2 = 3.601$, $P = 0.058$) (Tab. 1).

In *A. cribrarius*, *C. ornatus* and *A. spinimanus*, infestation (infested or non-infested) was affected by host CW and sex (Tab. 2); in *A. cribrarius* and *A. spinimanus*, the effect of sex was marginally significant; in *C. danae*, CW affected infestation in males only (Tab. 3). In all cases in which CW affected infestation, it was observed that infestation probability increased with size (Fig. 1, Tab. 3). For example, for one-unit increase in size, males of *A. cribrarius* were 1.265 times (26.5%) more likely to be infested.

Infestation prevalence did not differ between males and females in *A. cribrarius* ($\chi 2 = 0.002$, $P = 0.968$), *C. danae* ($\chi 2 = 0.329$, $P = 0.566$) and *A. spinimanus* ($\chi 2 = 0.791$, $P = 0.374$). In contrast, prevalence was higher for females than males in *C. ornatus* ($\chi 2 = 5.281$, $P = 0.022$). Infestation intensity was higher in males than females in *A. cribrarius* (GLM, Deviance = 6.441, d.f. = 1, Residual deviance = 12.393, $P = 0.011$) and *A. spinimanus* (GLM, Deviance = 9.042, d.f. = 1, Residual deviance = 20.910, $P = 0.003$). In *C. ornatus*, the pattern was opposite (GLM, Deviance = 3.975, d.f. = 1, Residual deviance = 149.48, $P = 0.046$), while in *C.*

Table 1. Descriptive variables of portunid crabs and *Octolasmis lowei* infestation by host species and sex (M = male; F = female): Number of individuals (N), Carapace width (mean ± standard deviation in mm), Individuals in intermolt stage (%), Prevalence of infestation (%) and Intensity of infestation (mean ± standard deviation). * Indicates a significant difference between males and females ($P < 0.05$).

Host species	N		Carapace width		Intermolt (%)		Prevalence (%)		Intensity	
	M	F	M	F	M	F	M	F	M	F
A. cribrarius	48	64	*77.5±12.0	70.9±8.9	91.7	96.9	14.6	12.5	*4.7±4.4	1.6±1.1
C. danae	24	140	*77.5±12.4	67.7±7.6	87.5	97.1	29.2	21.4	2.9±2.9	3.4±3.3
C. ornatus	631	687	*56.6±10.0	49.4±6.2	87.2	89.8	*8.7	12.8	*5.9±7.4	8.3±8.9
A. spinimanus	71	175	59.0±14.1	63.2±16.1	77.5	88.0	11.3	6.9	*20.1±23.2	5.0±5.0

Table 2. Analysis of deviance for logistic regression fitted to condition of infestation by *Octolasmis lowei* in each host species. Size and sex of crabs were used as explanatory variables.

Source of variation	*Df*	Deviance	Residual *df*	Residual deviance	$P(>\|\chi^2\|)$
A. cribrarius					
NULL	-	-	111	88.208	-
Size	1	16.596	110	71.613	<0.001
Sex	1	3.887	109	67.725	0.049
Size X Sex	1	0.428	108	67.298	0.513
C. danae					
NULL	-	-	163	175.12	-
Size	1	0.350	162	174.78	0.554
Sex	1	0.403	161	174.37	0.526
Size X Sex	1	7.349	160	167.02	0.007
C. ornatus					
NULL	-	-	1317	905.10	-
Size	1	18.169	1316	886.94	<0.001
Sex	1	27.115	1315	859.82	<0.001
Size X Sex	1	0.882	1314	858.94	0.348
A. spinimanus					
NULL	-	-	245	138.71	-
Size	1	24.428	244	114.28	<0.001
Sex	1	4.266	243	110.02	0.039
Size X Sex	1	2.605	242	107.41	0.107

Table 3. Analysis of deviance for logistic regression fitted to condition of infestation by *Octolasmis lowei*. Odds ratio (OR) and 95% confidence interval (CI) for males and females of host species.

Species	Sex	OR	95% CI	Deviance	$P(>\|\chi^2\|)$
A. cribrarius	Female	1.171	1.04 - 1.39	7.045	0.008
	Male	1.265	1.09 - 1.60	13.763	<0.001
C. danae	Female	0.969	0.92 - 1.02	1.421	0.233
	Male	1.142	1.02 - 1.37	6.012	0.014
C. ornatus	Female	1.069	1.03 - 1.11	11.316	<0.001
	Male	1.098	1.06 - 1.14	29.094	<0.001
A. spinimanus	Female	1.089	1.03 - 1.16	10.853	0.001
	Male	1.211	1.09 - 1.44	19.203	<0.001

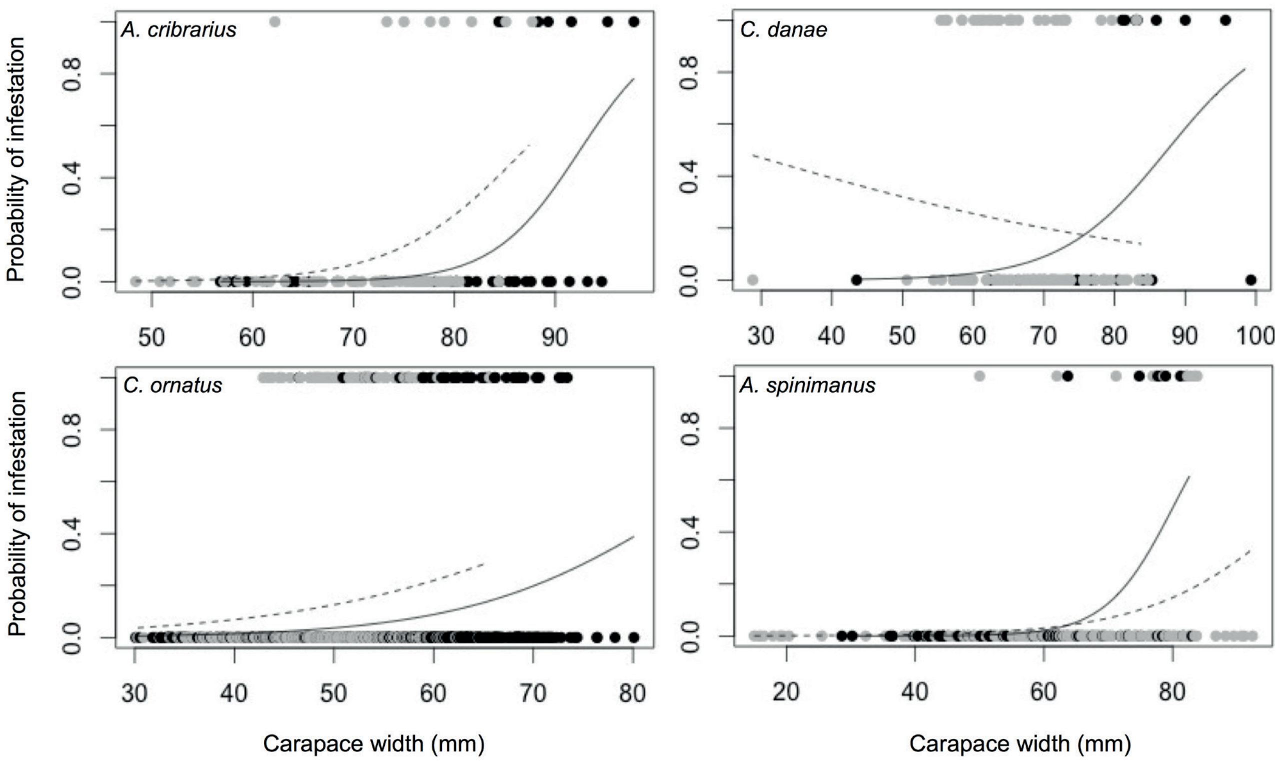

Figure 1. Relationship between probability of being infested by *Octolasmis lowei* and host size by sex. Gray solid circles = Female; Black solid circles = Male. For each species, solid circles on the top and bottom of graph represent the size of infested and no infested individuals, respectively. Solid and dashed lines represent the fitted model for males and females, respectively.

danae infestation intensity did not differ between sexes (GLM, Deviance = 0.219, d.f. = 1, Residual deviance = 34.837, *P* = 0.640) (Tab. 1). Overall, infested crabs were in intermolt stage, except for two *A. spinimanus* individuals that were in pre-molt stage.

Discussion

Portunid crabs have an important role as hosts for *O. lowei*. Infestation by *O. lowei* in portunid crabs was affected by the biological traits of these hosts. We found the probability of infestation by *O. lowei* increased with host carapace width, regardless of host species, as well as that infested crabs were more likely to be adults in intermolt stage. Furthermore, although the prevalence of infestation was similar between females and males (except for *C. ornatus*), the intensity of infestation was influenced by sex for most host species. Overall, infestation by *O. lowei* seems to be restricted to a fraction of the host populations (i.e. adults in intermolt stage), which is in an agreement with other studies that reported epibiont infestation in decapods (Santos and Bueno, 2002; Costa *et al.*, 2010; Machado *et al.*, 2013).

Spatial availability can be a limiting factor for the success of sessile organisms (Connell, 1972). However, the interval during which such space is available is also vital for epibionts on living substrates (Gili *et al.*, 1993). Since molting eliminates epibionts on the carapace surface and within the branchial chambers of crabs and other crustaceans (Walker, 1974; Jeffries and Voris, 1996), the interval between consecutive molting processes, or intermolt period, is often a constraint for epibiont success (Kuris, 1978; Jeffries and Voris, 1996). We found the probability of infestation by *O. lowei* in portunids crabs increases with host carapace width. Also, almost all infested crabs were adults in intermolt stage. These findings support the importance of temporal substrate availability for epibionts, since older and larger crabs molt less frequently than smaller individuals, and are thus more likely to be infested (Li *et al.*, 2014). Similar results have been reported for other decapods infested by *Octolasmis* spp. (Jeffries *et al.*, 1992; Shields, 1992; Machado *et al.*, 2013).

Molt frequency and spatial distribution have been suggested as to promote differences in epibiont infestation between sexes of decapods (Abelló and Macpherson, 1992; Key *et al.*, 1997). For all host species, the proportion of individuals in intermolt stage did not differ between males and females. Since molt activity is related to infestation, such results support the lack of difference in infestation prevalence between sexes for all portunid crabs in the present study, except for *C. ornatus*, in which females had higher infestation prevalence than males. Also, for all host species, males had a larger carapace width than females. However, although a positive relationship was found between host size and probability of infestation for males and females of most host species, the differences in size between sexes alone are unlikely to explain the patterns of infestation prevalence observed for these species.

The differences in infestation prevalence between males and females of *C. ornatus* contrast with previous studies that reported higher infestation prevalence by *O. lowei* in males (Santos and Bueno, 2002; Machado *et al.*, 2013). This may be explained by the differential spatial distribution between sexes of this portunid in the Ubatuba bay. Andrade *et al.* (2013) observed that males inhabit shallower waters, while females are more often found in depths between 15 and 20 m. Our sampling was carried out in a wide range that included both male and female habitats (from 5 to 25 m). It may be that the vulnerability of *C. ornatus* to the infestation by *O. lowei* is higher in deeper waters, where females occur more often. However, our sampling was not properly designed to address robust comparisons among depths and, thus, further studies are required to test if the infestation by *O. lowei* varies throughout a range of depths. In addition, Machado *et al.* (2013) observed higher infestation prevalence by *O. lowei* in females of *C. danae* than males, contrary to our results. A shorter sampling period (5 months) in comparison with other studies may be responsible for such singular results, since infestation can vary temporally. Costa *et al.* (2010) found that *A. cribrarius* presented a lower prevalence of infestation by *O. lowei* and other epibionts during winter. Since the relative contribution of each demographic category (males, non-ovigerous females, ovigerous females and juveniles) to the population of a crab species often varies temporally (Santos *et al.*, 1995; Johnson and Perry, 1999; Carvalho and Couto, 2011; Andrade *et al.*, 2013), these categories might have been represented differently in our sample when compared to those of previous studies, which may explain some divergences in results (e.g. infestation on ovigerous females tend to be higher than non-ovigerous females and males, probably because these females has longer intermolt periods; Costa *et al.*, 2010).

The infestation intensity by *O. lowei* in our study differed between sexes for most host species, but in distinct ways. Males of *Achelous spinimanus* and *Arenaeus cribrarius* presented higher infestation intensity than females. In contrast, females of *C. ornatus* presented higher infestation intensity than males, while no difference was observed between sexes in *C. danae*. Such results suggest the mechanisms involved in avoiding and/or reducing infestation may vary between host sexes and species. For example, Cordeiro and Costa (2010) suggest that an efficient branchial cleaning by females of *Libinia spinosa* H. Milne Edwards, 1834 may result in a lower intensity of infestation than that observed for males. However, this question remains unclear and, thus, further studies are required to explore the causes of inter-specific and sex differences in epibiont infestation. Furthermore, except for *C. danae*, the obtained results contrast with studies that reported a lack of difference in infestation intensity between sexes in portunid crabs (Santos and Bueno, 2002; Costa *et al.*, 2010; Machado *et al.*, 2013). Some divergences in results may be explained by many factors, such as: differences in sampling sites, depth and length among studies. Further studies considering a variety of spatial and temporal scales could contribute to elucidate such divergences.

Octolasmis species have been reported to have low specificity regarding the host use, occurring in a variety of host species (Jeffries *et al.*, 1982; Jeffries and Voris, 1983; Shields, 1992; Walker, 2001; Yan *et al.*, 2004; Kumaravel *et al.*, 2009; Machado *et al.*, 2013), which should be advantageous, since the availability of hard substrate is often a constraint for sessile organisms. In the present study, although *O. lowei* occurred in all portunid species sampled, the infestation by this epibiont seems to vary among their hosts. Both males and females of *A. spinimanus* had much higher intensity of infestation than any other host species, but an infestation prevalence that was comparable to those of other hosts (except *C. danae*). In this case, the abundance of *A. spinimanus* is unlikely to explain the higher infestation intensity, since this portunid species occurred in lower abundance than *C. ornatus*, which had lower infestation intensity. Such result may suggest certain degree of host preference by *O. lowei* towards *A. spinimanus*. In contrast, *C. danae* had the highest infestation prevalence, but lower infestation intensity, which indicates that although a higher proportion of individuals was infested, the average number of *O. lowei* per individual was low. The extent to which the occurrence of *O. lowei* in a variety of host species is related to the preference of this epibiont and/or is a constraint to other factors (e.g. availability of host) requires further investigation. Manipulative experiments with robust designs could improve our understanding about the factors driving the host species and sex preferences by *O. lowei*.

We found that biological traits of portunid crabs, such as carapace width and sex, influence infestation by *O. lowei*, which is in agreement with previous studies (Abelló and Macpherson, 1992; Jeffries *et al.*, 1992; Shields, 1992; Key *et al.*, 1997; Santos and Bueno, 2002; Machado *et al.*, 2013). Some of these traits, such as carapace width, maturity and molt stage, seem to affect *O. lowei* infestation in a similar way for all host species. On the other hand, the effect of sex on infestation varied among host species. In this sense, we suggest a deeper understanding of the factors driving host use by generalist epibionts such as *O. lowei* depends on investigating their occurrence on a variety of potential hosts.

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