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Fecundity and reproductive output of the caridean shrimp *Periclimenes paivai* associated with scyphozoan jellyfish

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ABSTRACT

Periclimenes paivai is notable for its symbiotic lifestyle with jellyfish. The objective of this study was to investigate the fecundity and reproductive output of females, and specifically to determine whether females protected in their host have a greater reproductive success than other shrimp species. All anatomical parts of the medusae were analyzed and the *P. paivai* individuals were separated. Among 83 females analyzed, 65 presented embryos in the first developmental stage, and 18 were in the final stage of development. The mean fecundity was 229.08 ± 120.04 in initial-stage embryos and 191 ± 114.76 in final-stage embryos. We observed a positive relationship between the embryo number and the female size; however, the embryo number was not related to the embryonic stage, which indicates that females did not lose their embryos during the incubation period. The weight of brood mass during production is closely related to the female weight according to the results of linear regression, as fecundity increased with female size. In its symbiosis, *P. paivai* can increase the amount of energy used to produce embryos (mean reproductive output = 10.38%) and can elevate the reproductive success.

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medusae; symbiosis;
Palaemonidae

Introduction

The probable benefits of symbiosis include exploration of new resources, occupation of new ecological niches, shelters, higher investment in parental care (protection against predation), and lower energy expenditure in obtaining food resource (Thiel & Baeza 2001; Schiariti et al. 2012). Few families in Caridea are involved in symbiotic associations with benthic organisms such as sponges, sea anemones, echinoderms, other crustaceans, and fish (Bauer 2004; Calado 2008). However, some species of the family Palaemonidae can be found also with pelagic animals such as jellyfish (Bruce 1972). Association with pelagic organisms can bring a higher mobility for symbionts as well as shelter and greater food availability (Nogueira Jr. & Haddad 2005).

Symbiotic lifestyle

Crustaceans of different superfamilies (Palaemonoidea, Majoidea, and Grapsoidea) have symbiotic relationship with *Lychnorhiza lucerna* Haeckel, 1880 medusae (Gonçalves, Wolf, et al. 2016). The nematocysts used as a defense mechanism by these cnidarians do not seem to

affect these crustaceans (Shanks & Graham 1988; Nogueira Jr. & Haddad 2005; Towanda & Thuesen 2006). The Gill epithelium (like other surfaces) of crustaceans is covered with chitin layer which brings protection against physical and chemical damage, and this seems to be a response to most crustaceans to be immune to the parenteral injection of cnidarian toxins (Mebs 2009).

Periclimenes Costa, 1844 is distributed in the Western Atlantic (Bruce 2004) and comprises species with diverse types of symbiotic relationships (Williams Jr. & Williams 1982; Martinelli-Filho et al. 2008; Azofeifa-Solano et al. 2014), and *Periclimenes paivai* Chace 1969 is the only shrimp species reported to associate with the scyphozoan medusoid phase off the Brazilian coast (Criales 1980; Martinelli-Filho et al. 2008; Gonçalves, Wolf, et al. 2016). However, only the first zoeal stage of *P. paivai* has been described (Pantaleão et al. 2013), and our knowledge about its population biology is scarce.

Reproduction

Several studies about the reproductive output (RO) in caridean shrimp have been conducted (Corey & Reid

1991; Anger & Moreira 1998; Azofeifa-Solano et al. 2014; Martínez-Mayén & Román-Contreras 2014), but only Azofeifa-Solano et al. (2014) analyzed this parameter for the symbiotic shrimp *Periclimenes rathbunae* Schmitt, 1924 associated with sea anemones. They found a higher RO in *P. rathbunae* compared to free-living shrimps, which suggests differences in the energy allocation mechanisms in symbiotic species. Azofeifa-Solano et al. (2014) proposed that the benefits of living in association with other invertebrates could provide shrimp increased protection and greater energy reserves used by the females invested in embryo production. The goal of the present study was to determine whether this pattern also occurs in *P. paivai* as a result of its symbiotic lifestyle. Considering the importance to understand the uncommon lifestyle as symbiosis and the lack of information in the literature about living in association, the reproductive biology of the symbiont shrimp *P. paivai* with the scyphomeduse host *L. lucerna* were analyzed. The results obtained allowed a better understanding of the energy invested in reproduction by symbiotic shrimps.

Materials and methods

Sampling

The study area is located at the central coast of the state of São Paulo (23°55'–24°00'S and 46°20'–46°25'W), which includes Santos Bay, and Santos and São Vicente Estuaries. Samples were taken during late winter–early spring 2012 (September and October). The animals were collected with a shrimp fishing boat outfitted with double-rig nets by trawling (30-min duration) at depth between 5 and 15 m. When material of the trawling reached the boat, all jellyfish were immediately separated for analysis to avoid damage of the animals and the loss of associated shrimp.

L. lucerna was identified according to Morandini et al. (2005) and the symbiont shrimps according to Chace (1969) (Figure 1). Females carrying embryos (= fertilized eggs) attached to pleopods were separated, preserved in 70% ethanol and transported to the NEBECC (Group of Studies on Crustacean Biology, Ecology and Culture), Botucatu – São Paulo – Brazil. All anatomical parts of the medusae were carefully examined macroscopically (umbrella, oral arms, oral pillar, gastric cavity, subgenital space, and gonads) to determine the presence of shrimp (Nogueira Jr. & Haddad 2005).

The carapace length (CL) (from the posterior margin of the ocular orbit to posterior end of the carapace) was measured with an accuracy of ± 0.0001 mm using a stereomicroscope (Zeiss Stemi SV6, fitted with a Zeiss Stemi 2000-C image capture system) equipped with a camera and the Axio Visioprogram (vers.4.8). All morphometric measures were performed using this program.



Figure 1. *Periclimenes paivai* under the sub-umbrella of the scyphomedusa *Lychnorhiza lucerna* (Source: Gonçalves, Wolf, et al. 2016).

Fecundity

Fecundity is the total number of offspring produced by a female in a determined period (Ramirez-Llodra 2002). Anger and Moreira (1998) used the definition of 'realized fecundity' instead of 'potential fecundity' for the number of embryos carried by the females on pleopods. For the present study, the fecundity was defined as the total number of embryos carried by females as proposed by Anger and Moreira (1998).

The entire brood mass was removed from female pleopods using a fine forceps. The embryos were counted manually and categorized into two embryonic developmental stages: Stage I, with no eyes formed, and Stage II, with evident eyes formed, as proposed by Corey and Reid (1991).

RO and brood mass volume

Females and embryo mass were dried at 60 °C for 24 h and weighed using a Shimadzu® Aux 220 analytical balance (precision 0.0001 g) to calculate the RO, which is defined as the energy invested in reproduction (Hernández & Wehrtmann 2011). RO was determined only in females carrying recently produced embryos (Stage I). The formula proposed by Clarke et al. (1991) was used to calculate RO: $RO = (\text{Dry weight of the brood mass} / \text{Dry weight of the female without embryos}) \times 100$.

Twenty fertilized eggs were randomly chosen per female to measure both the major and minor axis. The embryo volume for each developmental stage was calculated using the formula $V = 1/6 (\pi D1 \times D2)$, where $D1$ is the major diameter and $D2$ is the minor diameter (Turner & Lawrence 1979). Females in Stage II were used to analyze the possible embryo volume increase.

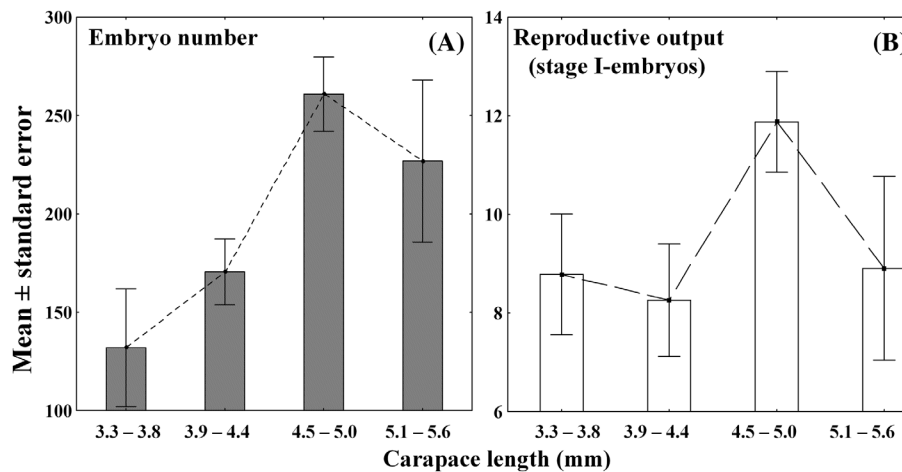


Figure 2. *P. paivai*. Boxplot of size frequency distribution of females carrying embryos, A: relation with embryo number and B: relation with reproductive output (mean \pm standard deviation) in animals from the southeastern Brazilian coast.

Data analysis

Different data transformations were tested with respect to their capacity to improve the normality of the data: $1/x$, \ln , and \sqrt{x} , and the most appropriate transformation was chosen based on the lowest Kolmogorov–Smirnov D. Using this criterion, the number of embryos, CL, embryo volume, female weight, and brood mass weight were \sqrt{x} -transformed. All analyses were performed with a significance level of 5% ($\alpha = 0.05$) (Zar 1999).

Analysis of covariance (ANCOVA) was applied to determine the embryo loss and embryo volume increase during the developmental stage using the number of embryos vs. CL (co-variable = stage of embryonic development) and embryo volume vs. embryonic development (co-variable = female weight), respectively (Hernández & Wehrtmann 2011; da Silva et al. 2016). Linear regressions were tested to observe the relationship between females (CL and female weight) and embryo features (embryo number and brood mass weight) (Anger & Moreira 1998; Terossi et al. 2010).

Results

Fecundity

A total of 83 *P. paivai* females carrying embryos were analyzed, of which 65 were in the initial stage (Stage I) and 18 were in the final stage (Stage II). The CL ranged from 3.42 to 5.62 mm (mean size 4.54 ± 0.48 mm at the Stage I and 4.46 ± 0.45 mm at the Stage II).

The mean number of embryos in Stage I and Stage II were 229 ± 120.04 (minimum 20 and maximum 517) and 191 ± 114.76 (minimum 32 and maximum 540), respectively, representing a mean percentage of embryo loss of 16.6%. However, the number of embryos did not differ with embryo development stages (ANCOVA: $f = 0.63$, $p = 0.43$).

Thus, both embryo stages were grouped together in the linear regression of fecundity analysis.

The number of embryos increased with the CL of females (categorized by class size), except for the last size class (5.1–5.6 mm), which produced fewer embryos than the size class 4.5–5.0 mm CL (Figure 2).

RO and brood mass volume

Females carrying embryos in Stage I weighed 0.02 ± 0.005 mg (0.007–0.029 mg), and their brood mass had a mean weight of 0.0019 ± 0.0013 mg (0.001–0.005 mg). Females carrying embryos in Stage II weighed 0.020 ± 0.005 mg (0.012–0.031 mg), and the embryos weighed 0.0013 ± 0.0009 mg (0.001–0.003 mg).

Embryo volume increased during to the embryogenesis (ANCOVA $f = 14.68$, $p < 0.001$) from 0.0237 mm³ (Stage I) to 0.0307 mm³ (Stage II), representing a volume increase of 29.5%.

The RO (females with embryos in Stage I) ranged from 0.73 to 29.05% (mean = $10.38 \pm 5.60\%$) and increases with the CL of females (categorized by class size) until the second to last size class. The females in the last size class (5.1–5.6 mm) invested less reproductive energy than the 4.5–5.0 mm class (Figure 2). The linear regression analyses revealed a positive relationship between CL and embryo number ($r^2: 0.18$, $p < 0.001$) and female weight and brood mass (=all embryo mass attached on the females pleopods) weight ($r^2: 0.42$, $p < 0.001$) (Figure 3).

Discussion

Fecundity

Caridean shrimp, just as other decapods, have a specific behavior during the incubation period, in which females

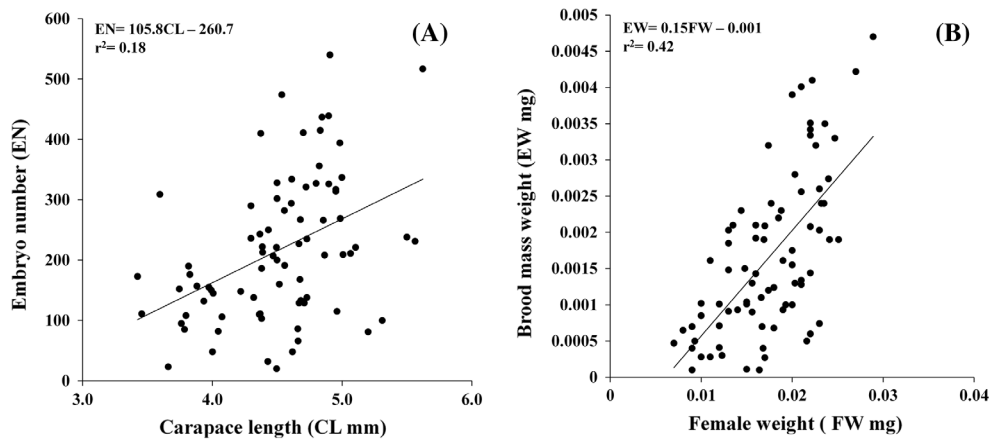


Figure 3. *P. paivai*. Linear regression between A: Embryo number (EN) and carapace length (CL mm), B: Female weight and brood mass weight in animals from the southeastern Brazilian coast.

periodically spend a large amount of time brushing and picking the pleopods with the embryo mass to keep it clean from parasites, ensure its oxygen supply, and carry away wastes produced by embryos (Bauer 2004). This activity is a probable explanation for the relatively low embryo loss in caridean shrimp such as: *P. rathbunae*, 24% (Azofeifa-Solano et al. 2014); *P. longicaudatus* (Stimpson 1860), 24.6% (Corey & Reid 1991); *Macrobrachium acanthurus* (Wiegmann 1836), 23% (Anger & Moreira 1998), and the studied species (16.6%). Furthermore, the lack of a significant embryo loss during embryogenesis maybe related to the shelter and parental care (protection against predation) offered by the host (medusa) as part of the symbiotic lifestyle.

The weights of female *P. paivai* were higher in Stage II than in Stage I, as also observed in another palaemonid shrimp, *Leander paulensis* Ortmann, 1897 (Zimmermann et al. 2015). According to these authors, spawning is a costly activity in the shrimp life cycle because the shrimp uses most of its accumulated energy reserves. At the beginning of the incubation period, females have lower weight and consequently have less accumulated reserves for embryo production. During embryo maturation, an increase in weight occurs in females because the food ingested is used to build up new energy reserves. In addition, post-spawning females need to rebuild their gonads, which will also contribute to increased weight.

The mean embryo volume (EV) of *P. paivai* (0.025 mm^3) was lower than that of other palaemonid shrimps (Table 1), compared to free-living and freshwater species such as *P. longicaudatus*, *Cuapetes americanus* (Kingsley 1878), *Macrobrachium ohione* (Smith 1874), and *Macrobrachium olfersii* (Wiegmann 1836). Even species that have symbiotic relationships, with those of *P. rathbunae* and *Periclimenes pandionis* Holthuis, 1951, have a greater embryo volume than the studied species. When we compared our results

with those of the sea anemone with caridean *P. rathbunae*, which have a similar size, the total embryo number and the embryo volume of *P. paivai* are smaller than those of *P. rathbunae*. This different pattern maybe related with the host type and the association model. Bauer (2004) explains that caridean shrimps are intense influenced by environment, host and other factors can influence the mating, brooding, and reproduction in life to these animals. Despite theoretical affirmations, others studies should be carried out, including laboratory experiments to discover if the host really influences the size and number of caridean's offspring.

In general, palaemonid shrimps with an extended larval development produce small embryos (Wear 1974). Until now, only the first zoeal stage has been known and compared between other *Periclimenes* shrimps and *P. paivai* to demonstrate the morphological differences and similarities among the group (Pantaleão et al. 2013); however, laboratory studies identified eight zoeal stages in similar species (*Periclimenes sagittifer* (Norman, 1861)) (Santos et al. 2004).

An increase in embryonic volume during the ontogeny seems to be common in Decapoda Crustacea (Lardies & Wehrtmann 1997; Terossi et al. 2010; Antunes et al. 2014; Azofeifa-Solano et al. 2014) because the crustacean embryos absorb water and consequently increase in water content (presenting an increasing size) (Pandian 1970). Wear (1974) suggested a close relationship between the increase in embryo volume produced by females during the ontogeny and the number of embryonic and larval stages presented by the species. This relationship suggests that the increase in water volume is lower in species with numerous larval stages, while a higher increase in water volume is observed in species with fewer larval stages. In addition to the embryonic volume, senescence seems to be a common factor in Crustacea reproduction. Vogt (2014)

Table 1. Number of palaemonid species analyzed, minimum and maximum female carapace length (CL), fecundity (embryo number), mean embryo volume, minimum and maximum reproductive output (RO) in Stage I, and habitat of the species (modified from Corey & Reid 1991 and Azofeifa-Solano et al. (2014)). NA = No data available.

Species	Number of Individuals	CL (mm) (min-max)	Fecundity	Embryo mass (mm ³)	RO (%) (min-max)	Habitat	Reference
<i>Periclimenes paivai</i> (Chace 1969)	65	3.42–5.62	20–540	0.025	0.73–29.05	Scyphozoa Jellyfish	Present Study
<i>Periclimenes rathbunae</i> (Schmitt 1924)	70	2.25–5.25	80–605	0.038	0.094–24	Sea anemone	Azofeifa-Solano et al. (2014)
<i>Periclimenes pandionis</i> (Holthuis 1951)	5	2.84–4.0	67–259	0.050	NA	Coral reef	Corey and Reid (1991)
<i>Periclimenes longicaudatus</i> (Stimpson 1860)	24	2.16–3.04	49–149	0.049	NA	Free Living	Corey and Reid (1991)
<i>Periclimenes ornatus</i> (Bruce 1969)	NA	3.0–6.0	10–1000	0.49	NA	Sea Anemone	Omori et al. (1994)
<i>Palaemon northropi</i> (Rankin 1898)	13	5.52–7.84	128–755	0.2	8.9–19.3	Free living	Corey and Reid (1991)
<i>Palaemon gravieri</i> (Yu 1930)	NA	5.34–16.63	306–6160	NA	NA	Free Living	Kim and Hong (2004)
<i>Leander tenuicornis</i> (Say 1818)	13	5.20–7.52	181–640	0.093	NA	Free Living	Corey and Reid (1991)
<i>Leander paulensis</i> (Ortmann 1897)	46	4.27–6.92	227–1360	0.013–0.055	4.8–28.5	Red-Algae	Zimmermann et al. (2015)
<i>Macrobrachium ohione</i> (Smith 1874))	12	11.88–18.17	3577–12,353	0.080	NA	Free Living Freshwater	Corey and Reid (1991)
<i>Macrobrachium olfersii</i> (Wiegmann 1836)	8	9.40–12.25	1966–4683	0.076	NA	Free Living Freshwater	Corey and Reid (1991)
<i>Cuapetes americanus</i> (Kingsley 1878)	345	1.55–3.22	19–164	0.034–0.058	NA	Submerge vegetation	Martínez-Mayén and Román-Contreras (2014)

explained that senescence is closely related to changes in structure, physiology, and behavior in animals. In terms of reproduction, senescence can influence the speed and pattern changes in reproduction after the first release of offspring. In this study, we suggest that senescence occurs in *P. paivai*, where a decrease in the fecundity and RO in the largest ovigerous females is observed (Figure 2). This event is reported to other caridean shrimp (Bauer 1991; Torres et al. 2007). Future studies focusing on reproductive biology of *P. paivai* and other *Periclimenes* species are needed to test this senescence hypothesis.

A symbiotic lifestyle may influence the percentage of RO, where *P. paivai* shows a higher range in RO than do other palaemonid shrimp, with mean of $10.38 \pm 5.60\%$ reaching 29% (see table 1). We believe that the symbiotic lifestyle may be the most important factor determining the higher values of RO and lower embryo loss in *P. paivai*. According to Azofeifa-Solano et al. (2014), the protection offered by the host would be the main reason to reach reproductive potential in symbiotic shrimp species. The jellyfish host forms a protective structure for pelagic crustacean symbionts during a most vulnerable phases of their life cycles (females carrying embryos). This association provides shrimps with food and shelter from predators, so *P. paivai* can spend more energy in reproduction, growth, and embryo production.

Because of the lack of information available, more studies about this symbiosis are necessary to better understand the type of relationship between these species and their ecological role in the marine environment. The population

density of the hosts can cause direct and indirect effects on populations of symbiont animals. Anthropogenic activities such as habitat destruction, fisheries, and exotic species introduction have negatively influenced the relationship of symbiotic organisms, causing alterations in the communities (Kiers et al. 2010). On the south-eastern coast of Brazil, jellyfish are accidentally captured as bycatch by trawl-fishing for other target species and they are mostly discarded (Gonçalves, Bolla Jr., et al. 2016). It is noteworthy that the incidental capture of jellyfish dramatically affects the species that live with them symbiotically (Mianzan & Cornelius 1999). Therefore, future studies involving *L. lucerna* and *P. paivai* should consider the anthropogenic influences experienced by *L. lucerna*.

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Disclosure statement


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