



Reproductive biology of the shrimp *Palaemon northropi* (Rankin, 1898) (Caridea: Palaemonidae) from an estuary in the Brazilian northeastern

Biologia reprodutiva do camarão *Palaemon northropi* (Rankin, 1898) (Caridea: Palaemonidae) de um estuário no nordeste brasileiro

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(Recebido em 05 de março de 2019; aceito em 17 de setembro de 2019)

The objective of this study was to evaluate aspects of the reproductive biology of *Palaemon northropi*, a shrimp of the northeastern Brazilian estuarine region. The specimens were sampled between July and November 2017, with a hand net, and were identified to species level and sexed. We measured the carapace length (CL) of males and females and the second pleura length (PL) of females. A total of 85 individuals were collected, including 36 males and 49 females (24 non-ovigerous and 25 ovigerous). The sex ratio was 0.42, with a non-significant departure from the 1:1 ratio. Mean sizes (\pm SD) of males and females were 3.41 ± 0.54 and 4.98 ± 1.33 mm CL, respectively. The mean size of the PL (\pm SD) of females was 2.67 ± 1.03 mm CL. Mean fecundity was 255 ± 57.84 embryos. The CL was positively associated with fecundity, but the fecundity did not vary between embryo developmental stages. *Palaemon northropi* shows sexual dimorphism, with females being larger than males. The results indicate that the embryonic development of *P. northropi* occurs normally, even in an estuarine region, such as that of present study, since there was no significant loss of embryos during development. This study contributes to knowledge of the reproductive biology of *P. northropi* and help in our understanding of the ecological relevance of these shrimps in estuarine environments.

Keywords: Decapoda, estuary, fecundity.

O objetivo deste estudo foi avaliar aspectos da biologia reprodutiva de *Palaemon northropi*, um camarão da região estuarina do nordeste brasileiro. Os espécimes foram capturados entre Julho e Novembro/2017 com uma rede de mão, e foram identificados quanto ao nível de e sexados. Nós mensuramos o comprimento da carapaça (CC) de machos e fêmeas e o comprimento da segunda pleura (CP) das fêmeas. Um total de 85 indivíduos foram coletados, incluindo 36 machos e 49 fêmeas (24 não-ovígeras e 25 ovígeras). A razão sexual foi de 0.42, com um desvio não significativo na proporção de 1:1. Os tamanhos médios (\pm DP) dos machos e das fêmeas foi de 3.41 ± 0.54 e 4.95 ± 1.32 mm CC, respectivamente. O tamanho médio de CP (\pm DP) para as fêmeas foi de 2.67 ± 1.03 mm CP. A fecundidade média foi de 255 ± 57.84 embriões. O CC está associado positivamente com a fecundidade, porém a fecundidade não varia entre os estágios de desenvolvimento embrionário. *Palaemon northropi* apresenta dimorfismo sexual, com fêmeas maiores do que os machos. Os resultados indicam que o desenvolvimento embrionário de *P. northropi* ocorre normalmente, mesmo em uma região estuarina, como no presente estudo, visto que não foi verificada perda significativa dos embriões durante o desenvolvimento. Este estudo contribui para o conhecimento da biologia reprodutiva de *P. northropi* e auxilia na compreensão da relevância ecológica destes camarões em ambientes estuarinos.

Palavras-chave: Decapoda, estuário, fecundidade.

1. INTRODUCTION

The genus *Palaemon* Weber, 1795 is the third richest of the Palaemonidae family Rafinesque, 1815 and is represented by about 90 species, which can be found in marine, estuarine, and freshwater environments [1]. The shrimp of this family are an important part of the food chain, and they also have commercial value, as they are used as ornamental, fishing bait, and food [2, 3]. Reproductive strategies of palaemonid shrimp are an essential part of the population dynamics and life cycles of the species [4]. Therefore, knowledge of the reproductive biology of these shrimp is important when defining criteria for biodiversity preservation in estuarine areas [5]. According to Stearns (1976) [6], some critical aspects of shrimp reproductive biology are considered to be key life-history traits, such as the breeding period, estimated by the presence of ovigerous females in the population (continuous or seasonal) [4]; fecundity, described as the number of embryos attached under the pleon [7]; embryo size and volume, which indicate the effect of various selective pressures on reproductive output and larval development [8]; and size at the onset of maturity, i.e., defining the minimum size for sexually mature females [9, 10].

Several species of the genus *Palaemon* were studied with regard to their reproductive biology, such as: *Palaemon northropi* (Rankin, 1898) [7, 11], *Palaemon pandaliformis* (Stimpson, 1871) [12]; *Palaemon longirostris* H. Milne Edwards, 1837 [4, 13]; *Palaemon gravieri* (Yu, 1930) [14]; and *Palaemon elegans* Rathke, 1837 [15]. However, considering the diversity of species, life habits, and environments occupied by the species of this genus, it is still not possible to understand how parameters of their reproductive biology can vary inter- and intra-specifically.

The species *Palaemon northropi* has a wide geographic distribution and can be found along the eastern coast of the Americas, from the USA (Florida) to Uruguay (and from the States of Ceará to Santa Catarina in Brazil) [16]. This species is a marine palaemonid shrimp that commonly occurs in stressful environments with wide variations of temperature and salinity, including intertidal sand and mudflat pools, reef pools during low tide, and the lower portions of estuaries near mangrove areas [7].

Anger & Moreira (1998) [7] and Pralon & Negreiros-Fransozo (2006) [11] studied the reproductive biology of *P. northropi*, with emphasis on its fecundity, embryo size, and development, as well as the relationship between body size and fecundity. Considering the variation in some of the reproductive parameters (e.g., fecundity) of *P. northropi* found in these previous studies, the aim of this study was to analyze various reproductive parameters of a *P. northropi* population in an estuarine area of Sergipe State, Brazil. In addition, we analyzed the body size, sex ratio, size of females at the onset of morphological sexual maturity, and fecundity (number, volume, and stage of embryo development) in a sample of individuals.

2. MATERIAL AND METHODS

2.1 Study area and sampling methods

The *P. northropi* specimens were sampled from July to November 2017, in Croa do Goré (11°05'47"S; 37°09'30"W) in the municipality of Aracaju, located approximately 5 km from the mouth of the Vaza-Barris estuary, one of the main estuarine systems in Sergipe State, northeastern Brazil (Figure 1). This estuary extends for approximately 20 km along the coast, and its mangrove forest is composed mainly of trees of the genera *Rhizophora*, *Laguncularia*, and *Avicennia* [17, 18]. Individual *P. northropi* were caught during low tide, under the marginal roots of the mangrove canopy, using a 2 mm mesh hand net. All sampling in this study were performed in accordance to applicable state and federal laws regarding capture of wild animals. This study did not involve endangered or protected species.

For all sampling, one transect of approximately 20 m was outlined, parallel to the fringe of the mangrove canopy. All shrimp collected in this transect were isolated in plastic bags containing

seawater. After that, the bags were placed in a thermal box and transported to the Laboratory of Carcinology of the Universidade Federal de Sergipe.



Figure 1: Sergipe State, northeastern coast of Brazil, red arrow shows the Vaza-Barris estuary region.
Fonte: Os autores

2.2 Laboratorial procedure

In the laboratory, the shrimp were identified to species level according to the pertinent literature [19, 20]. Specimens of *P. northropi* were conserved with 70% ethanol and deposited into the scientific collection of the Laboratory of Carcinology of the Universidade Federal de Sergipe (CARCINO). Individuals were sexed by the presence or absence of the appendix masculina in the endopod of the second pleopod in males or females, respectively [4]. We measured the carapace length (CL) of males and females based on the distance of the posterior margin of the eye orbit to the posterior margin of the carapace; the length of the second pleura (PL) was measured only for females. The measurements were performed under a stereomicroscope (Leica M205C), using the imaging software Leica Application Suite (LAS) version 4.4, with an accuracy of 0.05 mm.

We recovered all embryos attached to the pleopods of ovigerous females, and counted the total number of embryos under a stereomicroscope (Leica M205 C). Embryos carried by ovigerous females were classified, based on Wehrtmann & Lardies (1999) [21], into three different groups: Stage I, round egg with uniformly distributed yolk and no visible eye pigments; Stage II, ovoid egg and embryo with elongated eye pigments; and Stage III, ovoid egg and embryo with well-developed eyes and a free pleon.

2.3 Data analysis

The model assumptions of homoscedasticity (Levene's test) and normality (Shapiro-Wilk's test) of the distribution of size within the population were initially tested [22]. Individuals were distributed into 10 size classes, from 1.9 to 7.9 mm CL, in increments of 0.6 mm. The mean CL

size was compared between males and females by a non-parametric Mann-Whitney test ($\alpha < 0.05$) [20]. The sex ratio was estimated as the quotient between the number of males and the total number of individuals. Therefore, a sex ratio higher or lower than 0.5 indicates if a population is skewed toward males or females, respectively. For each size class, we tested deviations from the 1:1 sex ratio using a binomial test [23]. The onset of sexual maturity, indicated by the carapace length (CL) when 50% of the female shrimp are morphologically mature, was estimated by means adjustment of the data to a logistic function (CL_{50}). Embryo volume (EV) of a sample of embryos ($N = 10$) was also calculated for each female, following the same criteria used in previous studies of decapods [24, 25, 26]. The largest (L) and smallest (S) diameter of each embryo was measured using the Leica Application Suite software. Embryo volume (EV) was calculated using the formula: $EV = 1/6(LS^2\pi)$ [27].

Analysis of covariance (ANCOVA) was conducted to test if fecundity differed between embryo stages (with eggs with embryo development at stage I, II, or III, as independent factor) and shrimp body size (CL as covariate) [22]. We conducted multiple comparisons of means (among groups at different embryo stages) using the Tukey test ($\alpha < 0.05$) [22]. Finally, analysis of covariance (ANCOVA) was conducted to test if fecundity differed between embryo volume (as independent factor) and shrimp body size (CL, as covariate) [22]. We conducted multiple comparisons of means (between embryo volume) using the Tukey test ($\alpha < 0.05$) [22].

3. RESULTS

A total of 85 specimens of the shrimp *Palaemon northropi* were obtained, including 36 males (42.3%) and 49 females (57.7%), 25 of which were ovigerous. Specimens of *P. northropi* were distributed into 10 size classes, from 1.9 to 7.9 mm CL, in increments of 0.6 mm CL (Figure 2A). Only females were observed in the largest size classes (4.3-4.9 to 7.3-7.9 mm CL), except in the 6.7-7.3 mm CL size class, in which no individual was registered (Figure 2A). The mean size (\pm SD) of females was 4.98 ± 1.33 mm CL, ranging from 1.56 to 7.69 mm CL. The mean size (\pm SD) of males was 3.41 ± 0.54 mm CL, ranging from 2.15 to 4.29 mm CL. Significant differences were observed between the size of female and male *P. northropi* (Mann-Whitney; $U = 277.55$; d.f. = 83; $p < 0.001$), with females being larger than males. The overall sex ratio in the study was 0.42, with a non-significant departure from the 1:1 ratio (Binomial; $p = 0.177$). Sex ratio was biased in favor of males in the size classes 3.1-3.7 and 3.7-4.3 mm CL and in the other classes only females were observed (Figure 2B). The mean (\pm SD) pleura length of females was 2.67 ± 1.03 mm PL, ranging from 0.80 to 5.51 mm PL.

We estimated morphological sexual maturity for females at 4.57 mm CL (Figure 3). The smallest ovigerous female measured 5.07 mm CL. Fecundity varied from 109 to 362 embryos, with a mean (\pm SD) of 239.64 ± 72.21 embryos per female. For females carrying Stage I embryos ($N = 12$), fecundity varied from 181 to 362 embryos, with a mean (\pm SD) of 255.00 ± 57.94 embryos. For females carrying Stage II embryos ($N = 2$), the number of embryos varied from 230 to 303 with a mean (\pm SD) of 266.50 ± 51.62 embryos. For females carrying Stage III embryos ($N = 11$), the number of embryos varied from 109 to 340, with a mean (\pm SD) of 218.00 ± 87.25 embryos. ANCOVA did not detect any effect of embryo stage (I, II, or III) on fecundity ($F = 0.497$; d.f. = 1, 23; $p = 0.615$). On the other hand, fecundity is directly related to female CL; larger females carried more embryos than smaller females ($F = 6.035$; d.f. = 1, 23; $p = 0.023$) (Figure 4). The interaction term of the ANCOVA was not significant ($F = 0.970$; d.f. = 1, 23; $p = 0.336$). Therefore, neither large nor small females lost embryos during embryo development. The slope of the positive relationship between CL and fecundity differed significantly (Linear regression; $F = 7.573$; d.f. = 23; $p = 0.011$).

Embryo volume varied from 0.032 to 0.345 mm³, with a mean (\pm SD) of 0.084 ± 0.02 mm³, for Stage I; 0.081 ± 0.02 mm³ for Stage II; and 0.159 ± 0.06 mm³ for Stage III. An ANCOVA test indicated an effect of embryo stage on embryo volume ($F = 75.49$; d.f. = 1, 23; $p < 0.001$). On the other hand, CL did not affect embryo volume ($F = 0.12$; d.f. = 1, 23; $p = 0.723$). The interaction term of the ANCOVA was significant ($F = 11.897$; d.f. = 1, 23; $p = 0.001$). The slope of the positive

relationship between CL and embryo volume differed significantly among stages (Linear regression; $F = 21.863$; d.f. = 23; $p < 0.001$).

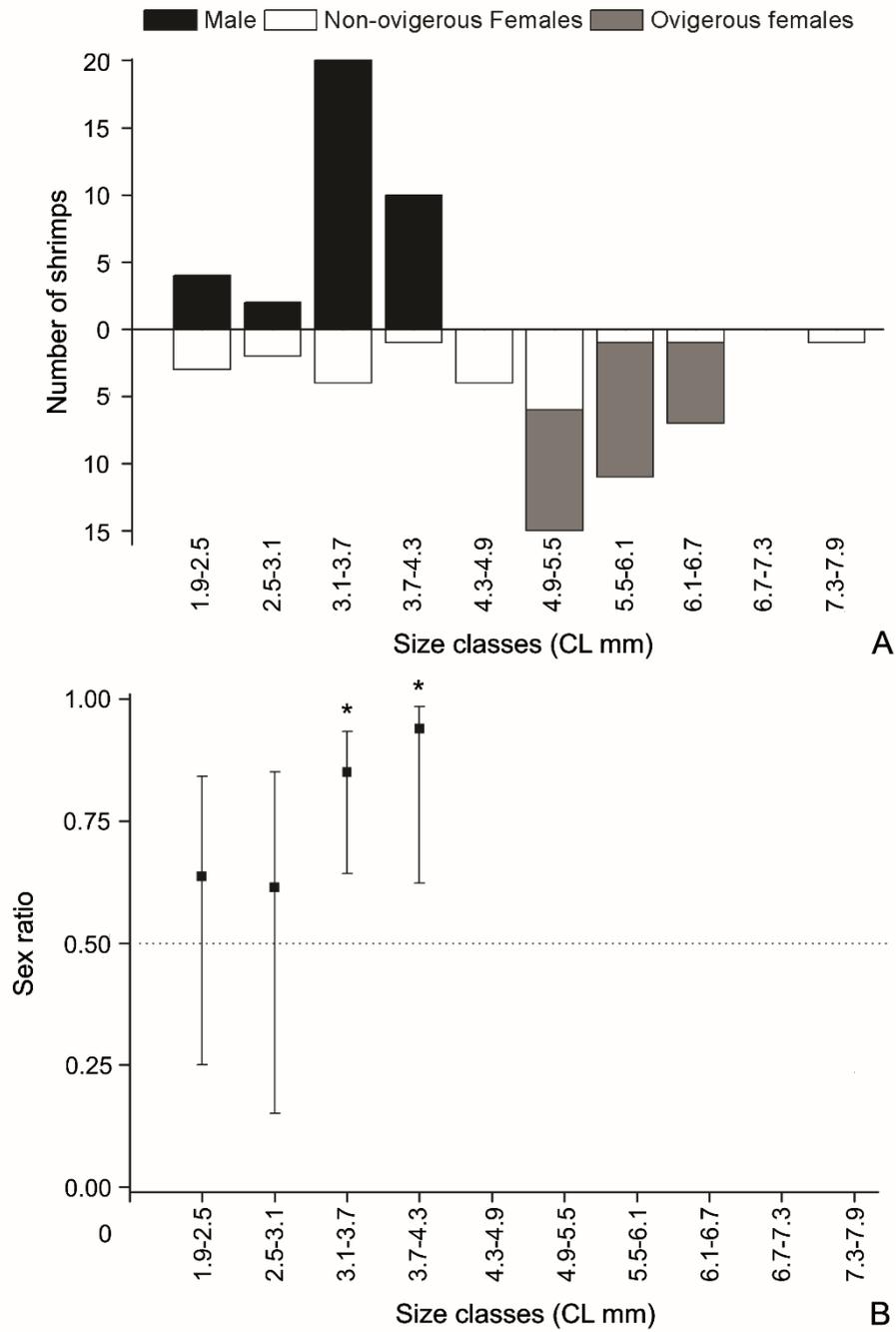


Figure 2: *Palaeomon northropi* (Rankin, 1898). (A) Size frequency distribution of body size (CL mm); (B) Sex ratio (estimate ± SE) by size class (CL mm). Fonte: Os autores.

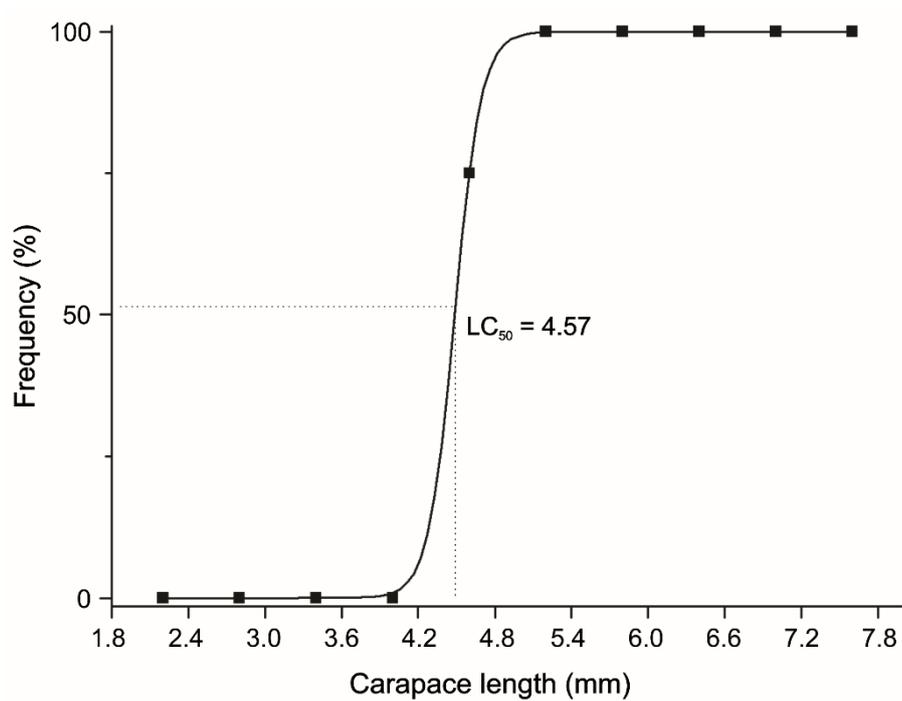


Figure 3: *Palaeomon northropi* (Rankin, 1898). Adjustment of the logistic function, indicating the carapace length (CL) when 50% of female shrimp are morphologically mature. Fonte: Os autores.

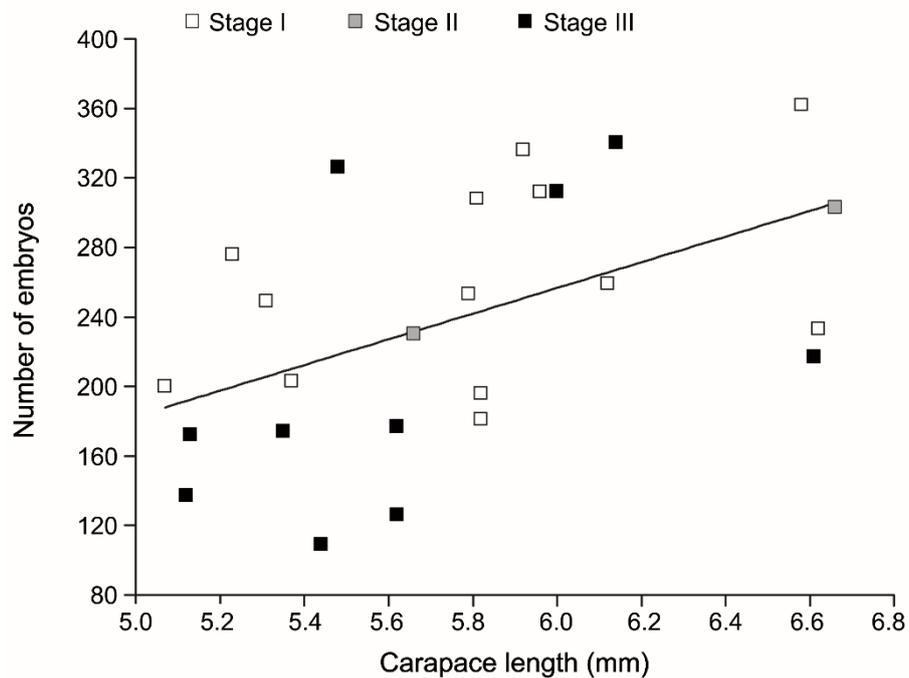


Figure 4: *Palaeomon northropi* (Rankin, 1898). Relationship between the number of embryos and carapace length (CL), according to embryo stage. Fonte: Os autores.

4. DISCUSSION

In this study, the sex ratio of *P. northropi* was slightly biased in favor of females but did not differ significantly from 1:1. Kim (2005) [28] also observed a sex ratio in *P. gravieri* that was biased in favor of females. However, the predominance of males was observed for other

Palaemonidae, such as *P. northropi*, *Palaemon adspersus* Rathke, 1937, and *Macrobrachium borelli* (Nobili, 1896) [11, 29, 30]. According to Fisher (1958) [31], natural selection favors the 1:1 proportion. However, variation in, for example, longevity, differential migration, locality, competition, climate, mortality, and growth rate [32], may occur in some species to cause a deviation from the expected proportion. Our results do not agree with the study by Pralon & Negreiros-Fransozo (2006) [11], in which there was a higher proportion of males in the population. These authors considered the higher proportion of males to be a reproductive strategy of *P. northropi*. However, this species may adopt different reproductive strategies depending on the habitat or region.

Sexual dimorphism of size was pronounced in *P. northropi*, with females reaching larger sizes than males. The same pattern was observed in a *P. northropi* population in São Paulo State, Brazil by Pralon & Negreiros-Fransozo (2006) [11]. Moreover, larger females have been observed in other species of the genus *Palaemon*, such as *Palaemon xiphias* Risso, 1816 from the Spanish Mediterranean coast [33], *P. pandaliformis* from the north coast of São Paulo, Brazil [7], and *P. longirostris* from the Mira River estuary, Portugal [13]. According to Sanz (1987) [34], the difference in growth rates of male and female *P. elegans* is related to gonadal development. Sexual dimorphism is also commonly observed in other Pleocyemata (e.g., [35, 36, 37, 38]). In this case, females allocate most of their energy to somatic growth, resulting in a larger body size, which allows them to carry larger gonads and to incubate more embryos during the reproductive period [39]. There is a reduction in energy invested in growth by males that may reduce the risk of predation [29]. However, the opposite pattern is observed in other Palaemonidae shrimp of the genus *Macrobrachium* Spence Bate, 1868, in which males reach larger sizes than females, such as for *Macrobrachium acanthurus* (Wiegmann, 1836) [7], *Macrobrachium olfersi* (Wiegmann, 1836) [40], *Macrobrachium iheringi* (Ortmann, 1897) [41], and *Macrobrachium brasiliense* (Heller, 1862) [42]. According to Mantelatto & Barbosa (2005) [42], this pattern is a function of the male domain over females, which is not observed for the genus *Palaemon*.

Size at the onset of female morphological sexual maturity, recorded in this study, was closer to the size of the smallest ovigerous females sampled in this period (see Table 1). The estimated value of female morphological sexual maturity was similar to that found by Pralon & Negreiros-Fransozo (2006) [11] for a population of *P. northropi* from Ubatuba, São Paulo, Brazil and by Rosa et al. (2015) [46] for *P. pandaliformis* from the Bay of Paranaguá, Paraná, Brazil (Table 1). On the other hand, the body size of females at sexual maturity was higher than observed in *P. longirostris* [4] (Table 1). In addition, we verified in the present study that the body size (carapace length) of *P. northropi* females is positively related to fecundity. This pattern agrees with studies on other caridean shrimp (e.g., [39, 48, 49]). In this sense, a relationship between brood and female size suggests that selective forces or constraints act on the reproductive output of the species [8, 50, 51]. However, in *P. gravieri* [12], there was no significant relationship between embryo size and female carapace length, despite this being a general trend of crustacean species.

The estimated fecundity for *P. northropi*, in this study, was lower than for other species of the genus *Palaemon*, such as *P. elegans* [43], *P. gravieri* [14], and *P. longirostris* [4] (Table 1). However, since fecundity varies with female body size, it is expected that larger species, such as those mentioned above, present a higher fecundity compared to *P. northropi* (Table 1). Therefore, it is of no surprise that the fecundity of *P. northropi* is equivalent to the similarly sized *P. pandaliformis* [45, 46, 47]. Compared to other populations of *P. northropi*, the fecundity recorded in this study was higher than for *P. northropi* from the region of Ubatuba, Brazil [11] (Table 1). However, the fecundity was lower compared to a population of *P. northropi* from a southern region of the United States studied by Corey & Reid (1991) [44] and similar to the fecundity recorded by Anger & Moreira (1998) [7] for a population of *P. northropi* from the São Sebastião coast, Brazil (Table 1). The differences observed in the fecundity of populations of the same species may be related to size variation [52]. Also, this difference may be related to the latitudinal gradient in which individuals of the species were sampled (see Table 1). According to Thorson (1950) [53], Fransozo & Costa (2004) [54], and Costa et al. (2010) [55], the latitudinal gradient is usually a factor in shrimp reproductive strategies, which is often referred to as the “classic paradigm”. However, it is important to highlight the need for more studies comparing differences in the fecundity of *P. northropi* populations found at various latitudes.

Table 1: Descriptive data for species of the genus *Palaemon* Weber, 1795. Maximum female carapace length (CL), female sexual maturity size, carapace length of the smallest ovigerous female (< OF), fecundity (embryo number per female), embryo volume (mm³), and latitude of the sample region. NA = no data available. Fonte: Os autores.

Species	Max CL (mm)	Size maturity sexual (mm)	CL (mm) < OF	Fecundity	Embryo volume (mm ³)	Latitude	Reference
<i>P. elegans</i> Rathke, 1837	23.8	NA	NA	306-1704	NA	40°54'S (Turkey)	Başçınar et al. (2002) [43]
<i>P. gravieri</i> (Yu, 1930)	16.6	NA	5.3	306-6160	0.05-0.14	34°49'S (Korea)	Kim & Hong (2004) [14]
<i>P. longirostris</i> (Milne Edwards, 1837)	14.6	7.7	7.1	78-1391	NA	45°20'S (France)	Béguer et al. (2010) [4]
<i>P. northropi</i> (Rankin, 1898)	NA	NA	NA	172-418	NA	23°48'S (Brazil)	Anger & Moreira (1998) [7]
<i>P. northropi</i> (Rankin, 1898)	7.8	NA	NA	128-755	0.20	28°80'S (United States)	Corey & Reid (1991) [44]
<i>P. northropi</i> (Rankin, 1898)	9.6	4.4	4.5	34-267	NA	23°20'S (Brazil)	Pralon & Negreiros-Fransozo (2006) [11]
<i>P. northropi</i> (Rankin, 1898)	7.7	4.5	5.1	109-362	0.03-0.34	11°05'S (Brazil)	Present study
<i>P. pandaliformis</i> (Stimpson, 1871)	7.8	NA	4.1	103-412	0.10	23°29'S (Brazil)	Mortari et al. (2009) [45]
<i>P. pandaliformis</i> (Stimpson, 1871)	8.3	NA	3.0	75-207	0.10	23°20'S (Brazil)	Mortari et al. (2009) [45]
<i>P. pandaliformis</i> (Stimpson, 1871)	NA	4.2	4.2	27-393	NA	25°42'S (Brazil)	Rosa et al. (2015) [46]
<i>P. pandaliformis</i> (Stimpson, 1871)	13.2	NA	3.8	34-250	0.09-0.26	15°42'S (Brazil)	Paschoal et al. (2016) [47]

In this study, we found that female *P. northropi* did not lose embryos during embryonic development, even while inhabiting estuarine environments with stressful conditions, like daily variations of salinity and temperature. Caridean shrimps and other decapods adopt a specific behavior during the incubation period, in which females spend some time brushing the embryo mass to remove parasites and to ensure good oxygen supply [56]. This activity is a possible explanation for the low embryo loss in caridean shrimp, such as *Periclimenes rathbunae* (Schmitt, 1942) [57] and *M. acanthurus* [7], among others. In this study, the mean embryo volume of *P. northropi* increased as embryo development proceeded from Stage I to Stage III. However, an increase in embryonic volume during ontogeny is common in decapods [e.g., 57, 58, 59, 60]. This is because crustacean embryos are able to absorb water and, consequently, increase in size [61]. The mean embryos volume was similar to that in a population of *P. northropi* studied by Corey & Reid (1991) [44] and to other species of *Palaemon*, such as *P. gravieri* [12] and *P. longirostris* [2] (Table 1). On the other hand, the embryo volume was higher compared to other Palaemonidae shrimp, such as *Cuapetes americanus* (Kingsley, 1878) [62] and shrimp of the genus *Periclimenes*

(Costa, 1844) [44, 49, 57, 63]. Differences in embryo volume may be related to differences in the environmental conditions, particularly salinity, of the species' habitats [64].

In short, our results indicate that the reproductive biology of an estuarine population of *P. northropi* differs from other populations of the same species, mainly in regards to fecundity. Such differences appear to be influenced by habitat conditions, intrinsic factors within each population, and the latitudinal gradient. In this sense, further studies on how reproductive strategies vary along the latitudinal gradient might provide a better understanding of the potential adaptations of this species to different environments.

5. CONCLUSION

This study evaluated some reproductive biological aspects of the shrimp *Palaemon northropi*, in an estuarine region of the State of Sergipe, northeastern Brazil, such as population structure, sex ratio, fecundity, size of females at the onset of morphological sexual maturity, and the relationship between female size and fecundity. We observed a 1:1 sex ratio for this population and sexual dimorphism between males and females: females were, on average, larger, which may allow them to carry larger gonads and to incubate a greater number of embryos. In addition, we found an increase in fecundity with increasing female body size and that females did not lose eggs during the developmental stage. This information is important and relevant to the understanding of *P. northropi* reproduction biology, as well as ecological patterns of estuarine environments.

6. ACKNOWLEDGMENT

Authors are grateful to the colleagues Y. T. Reis and C. R. P. Guimarães (University of Sergipe, Department of Biology) for allowing us to use their laboratory equipment and anonymous reviewers for critically reviewing the manuscript. We sincerely appreciate the research opportunity provided by the Federal University of Sergipe and to the members of the "Laboratório de Carcinologia da UFS" for support with the logistical assistance that helped to make this study possible.

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