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Spatio-temporal variation of the population structure and density of the shore crab *Pachygrapsus gracilis* (Grapsidae) in an estuary on the Brazilian Amazon coast

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Abstract

The present study investigates the spatio-temporal variation in the density of the adults and larvae of the shore crab *Pachygrapsus gracilis* and identifies the reproductive period and the population structure of the species in the Marapanim estuary, in northern Brazil, in order to describe the biological characteristics of this equatorial population on the Atlantic coast. Specimens were collected manually every month over the course of a year. Adults were collected at four rocky outcrops in the upper and lower mid-littoral. Larvae were sampled at six points using horizontal trawls of the surface water. The sampling points represent the inner and outer estuary, its two margins, and varying gradients of salinity. The density of the zoea I and adults were higher on the margins with the highest sediment deposition rates and salinity. Only the density of the adults correlated significantly with salinity. Although ovigerous females were only collected in the rainiest periods, the presence of juveniles throughout the year indicates that the species reproduces continuously. The population parameters indicate that the density of *P. gracilis* was related to salinity, and that part of the life cycle of these crabs is completed in the Marapanim estuary. This species reproduces in the estuary, exports zoea I to the coastal waters and then probably returns as megalopae, responding to local conditions through systematic shifts in its distribution and abundance over time and space. The population was relatively stable and able to adjust to the considerable variation in abiotic factors that are typical of this estuary.

Keywords

Brachyura, ecology, equatorial estuary, reproduction, rocky substrate, salinity

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INTRODUCTION

Variation in the abundance and spatial distribution of a species permit the adjustment of population traits (such as growth, mortality, and reproduction) to the characteristics of the environment (Gerhart and Bert, 2008; Almeida *et al.*, 2010). Crab populations may present distinct patterns of distribution within the coastal zone, which are affected by survival rates, body size, and sex or age (Menendez, 1987; Cannicci *et al.*, 1999; Almeida *et al.*, 2008). In some crabs, the juveniles tend to congregate more in the lower portion of the mid-littoral in comparison to the adults, to avoid desiccation. Abundance may also be affected by the availability of food, while the females may prefer the upper portion close to the waterline, to optimize their reproductive activities (Vergamini and Mantelatto, 2008). Salinity is one of the principal factors influencing the distribution of brachyurans in estuaries, and the success of the population of a given species will depend on the extent to which its life stages are adapted to variations in salinity (Charmantier *et al.*, 1998).

The crabs of the superfamily Grapsoidea MacLeay, 1838 have an initial planktonic phase and are among the most abundant of intertidal organisms, due to their physiological, morphological, and behavioral adaptations for a semi-terrestrial lifestyle (Schubart *et al.*, 2000). Most grapsoid species are distributed in a variety of habitats in temperate and tropical seas, which accounts for the considerable versatility of their life cycle (Flores and Paula, 2002).

Few studies have focused on the larval development of the crabs of the family Grapsidae MacLeay, 1838, which inhabit tropical estuaries. The larval development has been described in several species from six of the seven (WoRMS, 2020) grapsid genera: *Geograpsus* Stimpson, 1858, *Grapsus* Lamarck, 1801 (Guerão *et al.*, 2001), *Goniopsis* De Haan, 1833 (Fransozo *et al.*, 1998), *Metopograpsus* H. Milne Edwards, 1853 (Kakati, 1982), *Pachygrapsus* Randall, 1840 (Ingle, 1987), and *Planes* Bowdich, 1825 (Konishi and Minagawa, 1990). Grapsids have a prolonged larval development cycle, with a large number of larval stages, as observed in *Pachygrapsus marmoratus* (Fabricius, 1787) (Cuesta and Rodríguez, 2000), which has six larval stages, *Pachygrapsus transversus* (Gibbes, 1850) (Brossi-Garcia and Rodrigues, 1997), with seven larval stages, and *Geograpsus lividus* (H. Milne Edwards, 1837) (Cuesta *et al.*, 2011), which has eight larval stages. Brossi-Garcia and Rodrigues (1993) observed approximately 13 zoeal stages in *Pachygrapsus gracilis* (de Saussure, 1857) reared under laboratory conditions. However, studies of the spatiotemporal distribution of grapsids in the wild are rare, despite the abundance and the importance of the ecological role of these crabs in tropical benthic communities.

Pachygrapsus gracilis is a small, widely-distributed crab which occurs throughout the Americas between southern Florida and southern Brazil, as well as the eastern Pacific and the eastern Atlantic (Melo, 1996; Poupin *et al.*, 2005). This species has been recorded in a variety of habitats, ranging from algae and sponges associated with mangrove roots to hollow tree trunks, sandy beaches, and in particular, rocky substrates (Hartnoll, 2006). In an Amazon estuary, *P. gracilis* and other brachyurans (principally ocypodids and grapsoids) suffer high rates of predation by the Pemecou sea catfish *Sciades herzbergii* (Bloch, 1794), known locally as the guribu, which uses Amazonian mangroves as nurseries and feeds predominantly on brachyurans throughout its life cycle (Giarrizzo and Saint-Paul, 2008). The available data on *P. gracilis* include studies of the development of its larvae (Ingle, 1987; Brossi-Garcia and Rodrigues, 1993), megalopae (Cházaro-Olvera and Rocha-Ramírez, 2007) juveniles (Arruda and Abrunhosa, 2011), megalopal transport mechanisms (Cházaro-Olvera *et al.*, 2007), the abundance of the larvae (Vieira, 2006), the production of spermatophores and seminal fluid (Tiseo *et al.*, 2014; 2017), hull fouling (Cuesta *et al.*, 2016) and general occurrence records (Hartnoll, 1965; Powers, 1977; Coelho and Ramos-Porto, 1980; Melo, 1996; Almeida and Coelho, 2008; Melo, 2008; Gain *et al.*, 2017; Briones-Fourzan *et al.*, 2020).

Only one study has focused on the population structure of *P. gracilis* (Souza and Fontoura, 1993), and it revealed distinct patterns of body length and relative growth in the males and females, with the females being larger in size; which indicates differential mortality rates in the adult population (Souza and Fontoura, 1993).

The objective of the present study is to investigate the spatio-temporal variation and density of *P. gracilis* adults and larvae in a tropical Amazonian estuary, including the description of the population structure of the species in order to test the hypothesis of greater density of this species in the high estuary, with continuous reproduction and presence of larvae and adults throughout the year.

MATERIAL AND METHODS

Study area

The estuary of the Marapanim River, in the northeastern extreme of the Brazilian state of Pará, is partially mixed, and it is located to the east of the mouth of the Amazon River. The estuary is linked directly to the Atlantic Ocean, with high tidal (about 5m) and fluvial energy, and tidal creeks with wide mouths (Silva *et al.*, 2009) (Fig. 1).

This location is influenced by the local rainy (January to June) and dry (July to December) seasons (Moraes *et al.*, 2005). However, based on the precipitation records from the National Waters Agency (ANA) for Marapanim, rainfall in January during the present study period was substantially lower (94.53 %) than the historical mean value for this month. Given this, the month of January was grouped with the dry season months for analysis in the present study.

The region's climate is humid equatorial, with a mean air temperature of 27 °C, rising to 30 °C during the dry season (Berrêdo *et al.*, 2008). The semi-diurnal local macrotidal regime, associated with the discharge of water and sediments from the Amazon River, contributes to the formation of an environment characterized by considerable atmospheric circulation and mixing of the water, which has a major influence on the local coastal dynamics, as well as the morphology of the estuarine channel (Berrêdo *et al.*, 2008).

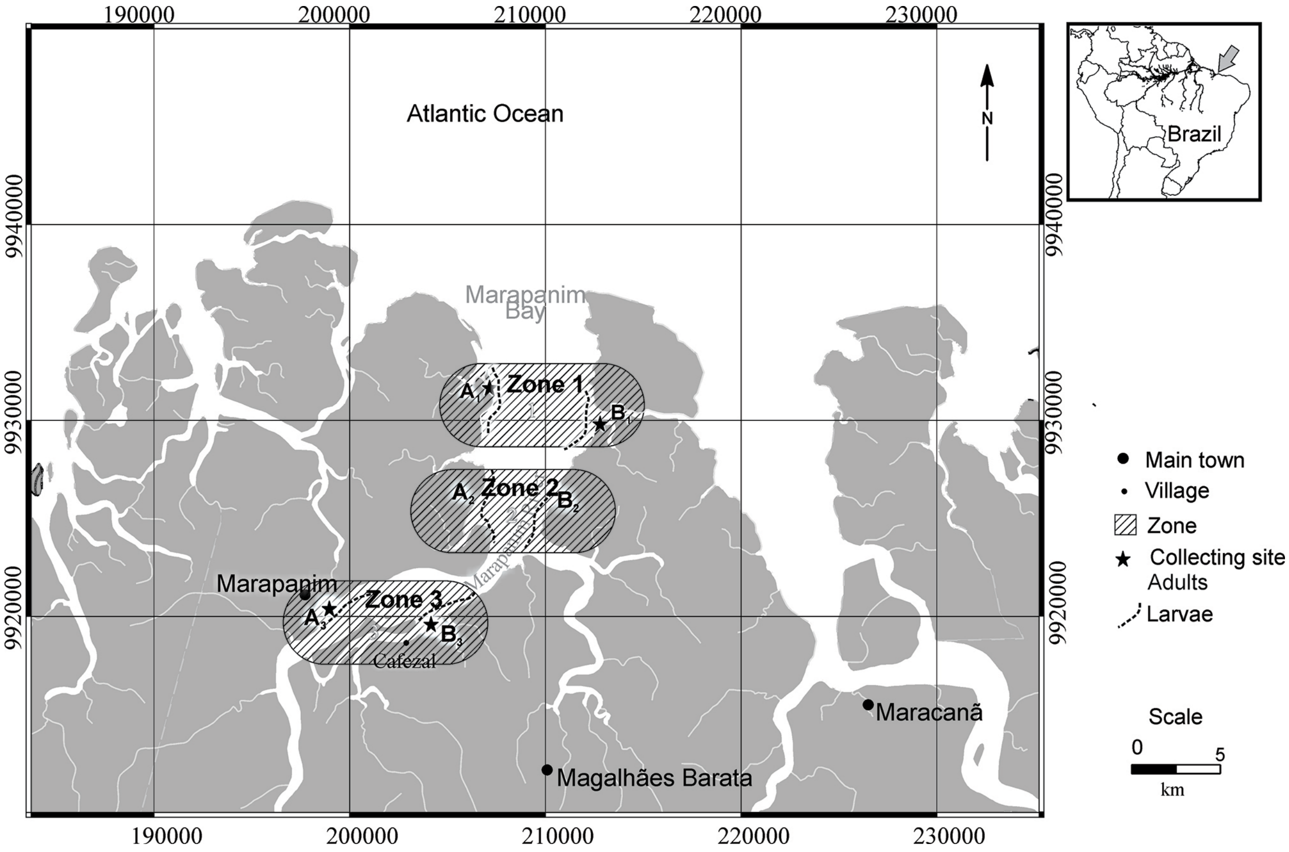

Figure 1. Map of the study area in the Marapanim estuary, Pará (Brazil), showing the three areas in which *Pachygrapsus gracilis* adults and larvae were sampled between August, 2006, and July, 2007.

The Marapanim estuary is characterized by a diversity of natural features, with substrates varying from sandy sediments to rocky outcrops (Silva *et al.*, 2009). The region's rocky outcrops are composed of laterized silt-clay of varying grain sizes, colors, and ferruginous characteristics, even though they are derived from the same geological source, that is, the Barreiras formation.

Collection of larvae

Larvae of *P. gracilis* were collected from six sites in the Marapanim estuary, representing the two margins, and the inner, middle, and outer zones of the estuary (Fig. 1). The left or western margin (profile A) is characterized by a higher degree of human occupation, as well as a predominance of clay substrates, reflecting the deposition of sediments, whereas the right or eastern margin (profile B) is less densely populated, and has a greater proportion of medium silt with less clay, indicating higher levels of erosion and turbulence (Berrêdo *et al.*, 2008). The zones were defined based on the gradient of salinity, with the outer estuary (zone 1) having the highest salinity, and the inner zone (3) having the lowest salinity (Oliveira *et al.*, 2012) (Fig. 1).

The zooplankton samples were collected from the surface water during three-minute horizontal trawls at a velocity of approximately one to 1.5 knots with a conical-cylindrical net (200 µm mesh and 0.50 m diameter at the opening). A calibrated flowmeter (Hydrobios) was attached to the mouth of the net in order to calculate the volume of water filtered. The larvae collected were fixed in a 4 % formaldehyde solution neutralized with sodium tetraborate. The samples were collected monthly between August, 2006, and July, 2007, resulting in a total of 144 samples.

The salinity of the water was measured in the laboratory using an optical refractometer (Atago), while the temperature was taken a few minutes (5–10') before each trawl, using a YSI multiparameter analyzer. A Folsom type sample splitter was used to divide each 1 L plankton sample, with a 250 mL subsample being obtained for analysis, which contained representatives of all the larval taxa contained in the whole sample. The larvae were separated from the zooplankton samples, analyzed under a Zeiss optic microscope, dissected, and identified based on the studies of Brossi-Garcia and Rodrigues (1993) and Souza *et al.* (2013). The larval vouchers were deposited in the Museu Paraense Emílio Goeldi (MPEG).

Collection of adults

Adult specimens were collected from rocky outcrops at four of the study sites: A1 (0°38'S 47°38'W), A3 (0°42'S 47°41'W), B1 (0°38'S 47°34'W), and B3 (0°43'S 47°38'W). While the sites have the same general substrates (2013 letter from JF Berrêdo; unreferenced), the outcrops vary in their size and density. The largest and densest rocks are found at sites A1 and B1. By contrast, site A3 contains much smaller fragments of rock, only slightly larger than gravel, as well as being partly covered with mud, silt and clay (Silva and Martinelli-Lemos, 2012).

Two portions of the mid-littoral (the upper and lower halves of the tidal range) were sampled at each of the four sites. The upper portion was defined on the basis of the maximum limit of the tides in the estuary, while the lower portion was defined by the minimum level of the tide. Three replicate samples were collected from each portion, chosen at random. A total of 288 samples (4 sites × 2 portions × 3 replicates × 12 months) were obtained. All samples were collected during the daytime, at low tide during the new moon, with the same number of quadrats per margins, zone and month.

Sample quadrats of 0.25 m^2 were distributed randomly at each study site, and the crabs found within each quadrat were collected manually. The specimens were placed in sieves (0.02 mm mesh) inside buckets and washed with water from the estuary to separate the organisms from the rocks. At each site, the salinity of the water found among the rocks adjacent to the quadrat was measured using an optical refractometer.

The specimens were kept on ice for transportation to the laboratory, where they were stored in a freezer until processing, when they were defrosted at room temperature and identified. The sex of each specimen was determined by the morphological examination of its sexual appendages (Melo, 1996) and the abdomen. The specimens were measured with a digital caliper (Mitutoyo, 0.01 mm precision) to obtain the carapace width (CW), defined as the greatest horizontal width of the cephalothorax, and abdomen width (AW), which was measured at the interval between the fourth and fifth abdominal somites. Voucher adult specimens were deposited in the carcinological collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the Goeldi Museum, in Belém.

Relationships between the occurrence of adults and larvae and prevailing environmental conditions

The density of the larvae was calculated by dividing the number of larvae by the volume of water sampled, and presented as the number of individuals per cubic meter (ind./m^3). The volume of water filtered by the trawl was estimated by $V = A*R*C$, where V = the volume of water filtered, in m^3, A = area of the net mouth in square meters (for the 0.5 m diameter net, $A = 0.19625\ m^2$), R = number of rotations of the flowmeter before and after each trawl, and C = a standardization factor obtained from the calibration of the flowmeter ($C = 0.32$). The abundance of adults is presented as a density, calculated by dividing the number of individuals (ind.) by the sample area (0.25 m^2).

The densities of *P. gracilis* adults and larvae were not distributed normally, even after transformation. In this case, differences in density between zones, margins (profiles), and seasons were evaluated using the nonparametric Mann-Whitney (*U*) test, while the Kruskal-Wallis nonparametric analysis of variance (*H*) was used to assess the variation in density, temperature, and salinity over the different months of the study period. The *t* test was used to evaluate the hypothesis of equality in size (CW) between the sexes. The significance of the relationships between the sum of density (of the adults and larvae) and the mean salinity and temperature was evaluated using Spearman's correlation coefficient.

Adult population structure

The specimens were grouped in 2-mm size classes for the analysis of the variation in carapace width. The normality of the distribution of these data was evaluated for the whole data set and for the males and females separately using the Kolmogorov-Smirnov (KS) test. Deviations in the sex ratio for the months when at least 20 specimens were collected were evaluated using Chi-square (χ^2). The specimens of undetermined sex were excluded from this analysis.

Size estimates at the onset of sexual maturity

Carapace width at first sexual maturity was estimated by analyzing the breakpoints of the regressions of abdomen width (dependent variable) *vs.* carapace width (independent variable). The length of morphological sexual maturity was also identified by the break point method. The regression was adjusted using the linear equation $\ln Y = \ln a + b.\ln X$, where a = the intersection of the Y axis when $X = 0$, and b = the slope of the regression or the constant rate of variation of Y in relation to X. The data were log-transformed. All the analyses considered an α value of 5 % (Zar, 2010). Statistical analyses were performed using the Statistica® v.6 Software.

RESULTS

Environmental variables

The temperature of the water was lowest in February (27.5 °C) and highest (29.7 °C) in August (Fig. 2), and the mean temperature was similar between seasons (dry: 28.8 ± 0.4; rainy: 27.9 ± 0.4). The mean salinity of the running (dry: 25.8 ± 5.8; rainy: 9.5 ± 4.9) and interstitial water (dry: 23.9 ± 5.6; rainy: 9.6 ± 5.3) was also higher during the dry season (Fig. 2). The lowest salinity (0) was recorded in March, and the highest (44) in October. The mean salinity was similar in both areas, with a slightly higher value being recorded in the running water (19.0 ± 9.4) in comparison with the main channel (17.9 ± 8.7).

Density of adults and larvae

Pachygrapsus gracilis larvae were observed throughout the year, with no significant seasonal variation being found in the larval abundance (Mann-Whitney $U = 255$, $p = 0.56$), that is, between the rainy (mean abundance = 2.36 ± 1.65 ind./m^2) and dry seasons (mean = 2.07 ± 0.94 ind./m^2). Similarly, while the median density varied from 0.33 ind./m^2 in March to 4 ind./m^2 in May (Fig. 2), there was no significant variation among months (Kruskal-Wallis $H_{(11;48)} = 2.42$, $p = 0.99$).

All the larvae were found only in the first zoeal stage. The zoea I presented similar patterns of density, with no significant difference being recorded between seasons (U = 4449, *p* = 0.68), that is, between the rainy (23.58 ± 15.64 ind./m^3) and dry seasons (15.15 ± 10.15 ind./m^3). May was also the month with the highest density of zoea I (44.31 ind./m^3), while June had the lowest density (3.13 ind./m^3). Median monthly density was 18.66 ± 12.73 ind./m^3 (Fig. 2), with no significant variation among months (H=18.011, *p* = 0.0813). Zoea I were captured when salinity was between 3 and 35, while adults were only encountered when salinity was 8–35.

The *P. gracilis* zoea I (U = 707, *p* = 0.001) and adults (U = 205.5, *p* = 0.00002) were both significantly more abundant in zone 1 than in zone 2 (Fig. 3). Both groups were also more abundant on margin A, although the difference was only significant for the adults (adults: U = 94, *p* = 0.004; zoea I: U = 2459, *p* = 0.59). This pattern was maintained across sites, with the density of both adults and zoea I being highest at site A1, followed by A3, B1, and then B3 (Fig. 3). The study species was found primarily (98.7 %) in the upper mid-littoral, with only two specimens (1.3 %) being collected in the lower portion.

Population structure

A total of 158 adults were collected, of which 61 (38.6 %) were males, 56 (35.44 %) were females, 20 (12.65 %) were ovigerous females, and 21 (10.16 %) were of undetermined sex. Ovigerous females were only collected between January and July (except February), with a peak in July; the only month in which the number of ovigerous females was higher than that of the non-ovigerous ones (Fig. 4). A total of 2,768 *P. gracilis* zoea I was collected during the study period.

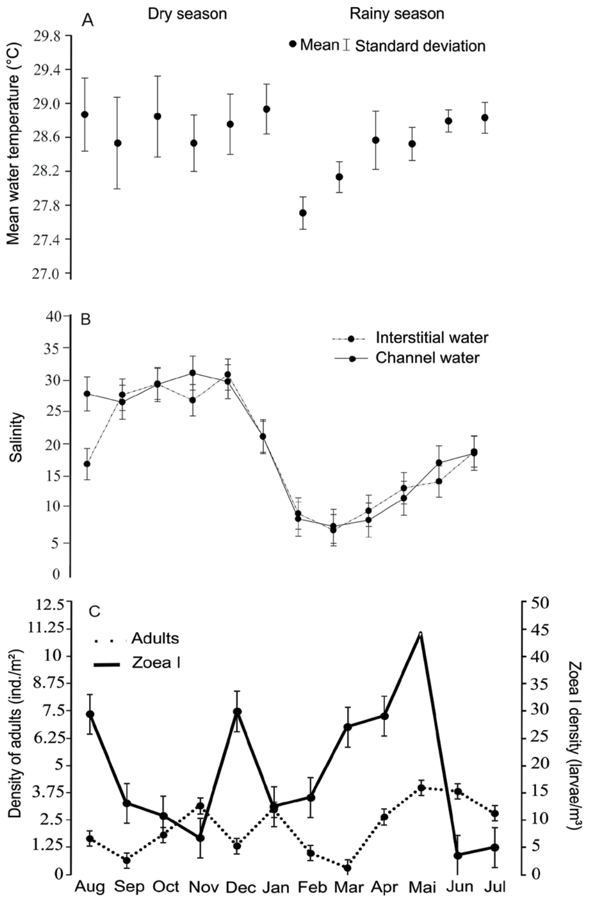

Figure 2. Mean water temperatures, salinity (± Standard deviation), and sum of densities of adult and larval *Pachygrapsus gracilis* recorded each month in the Marapanim estuary between August, 2006, and July, 2007.

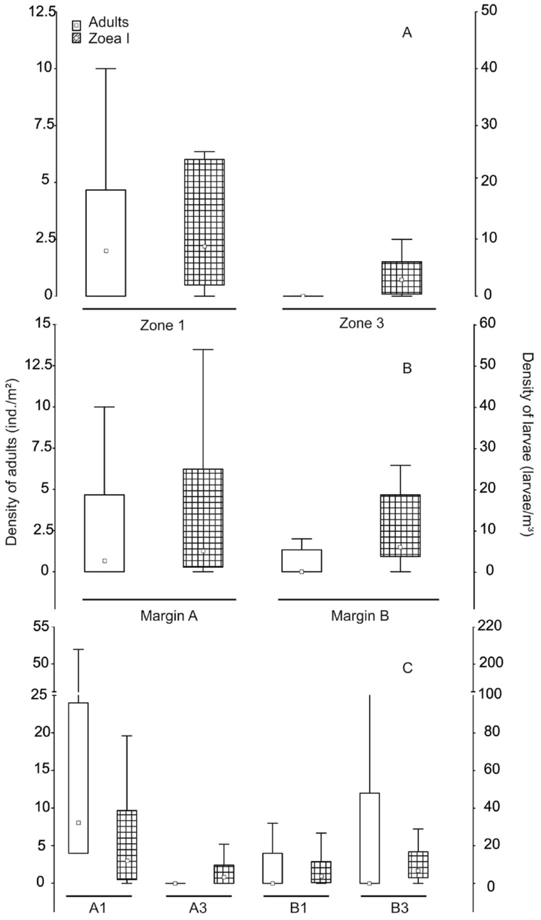

Figure 3. Median and quartiles (25–75 %) of density of *Pachygrapsus gracilis* adults and larvae in different (A) zones, (B) profiles, and (C) sites in the Marapanim estuary.

Site A1 presented the greatest abundance of females, ovigerous females, and zoea I. Site A3 was the only site at which practically no adults – only a single male – were found, although the abundance of zoea I was the second highest recorded at the different sites (Fig. 5).

The same breakpoint pattern was observed in the data on carapace and abdomen width (Fig. 6), that is, at a carapace width of 8 mm in both sexes, which indicates that this is the size at which *P. gracilis* matures morphologically. This criterion was used to distinguish juveniles from adults in all subsequent analyses. The regression statistics for each sex are shown in Tab. 1. Juvenile recruitment was continuous throughout the year, except for March and September (Fig. 7).

The *P. gracilis* size classes were distributed normally in the dataset as a whole (KS = 0.23, $p = 0.21$), as well as in the males (KS = 0.1279, $p > 0.05$) and females (KS = 0.045, $p > 0.05$), when analyzed separately. A unimodal distribution was found for both sexes, with a peak at 4–6 mm in the males and 8–10 mm in the females (Fig. 8).

The sex ratio was female-biased (1:1.24), but was not significantly different ($\chi^2 = 1.64, p = 0.2$) from 1:1. The mean (± SD) carapace width was 10.78 ± 2.23 mm in the ovigerous females, 8.91 ± 3.74 mm in males, and 8.77 ± 2.95 in females, although, once again, these differences are not significant ($t = 0.74$; $p = 0.45$). The carapace width data are summarized in Tab. 2. A significant correlation was found between adult density and salinity (R = 0.43, $p = 0.004$), although there was no relationship with water temperature (R = 0.10, $p = 0.51$), nor between the density of zoea I and either of these environmental factors (salinity: R = 0.08, $p = 0.42$; temperature: R = 0.09, $p = 0.42$).

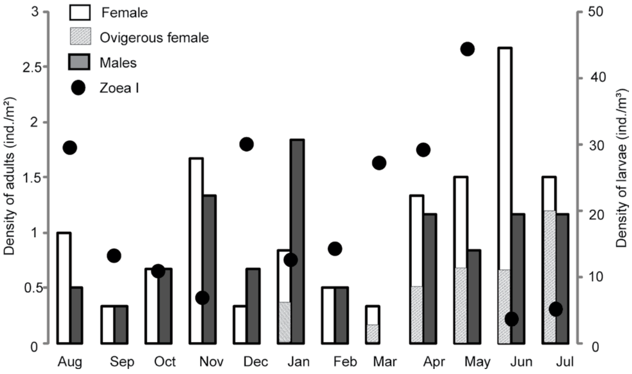

Figure 4. Temporal variation in the total density of males (gray columns), non-reproductive females (white), ovigerous females (black) *Pachygrapsus gracilis* adults and larvae (dots) collected from the Marapanim estuary between August 2006, and July 2007.

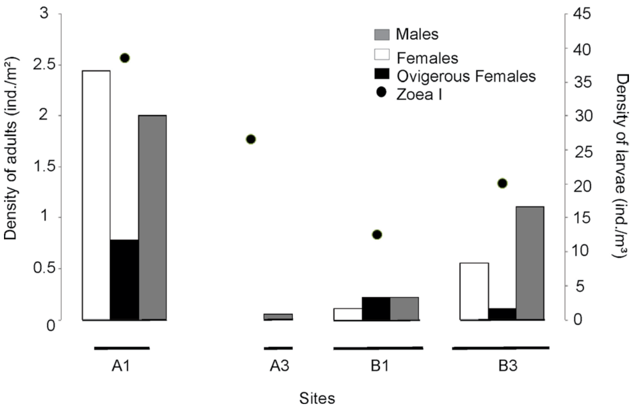

Figure 5. Spatial variation in the total density of males (gray columns), non-reproductive females (white), ovigerous females (black) *Pachygrapsus gracilis* adults and larvae (dots) collected from different sites in the Marapanim estuary.

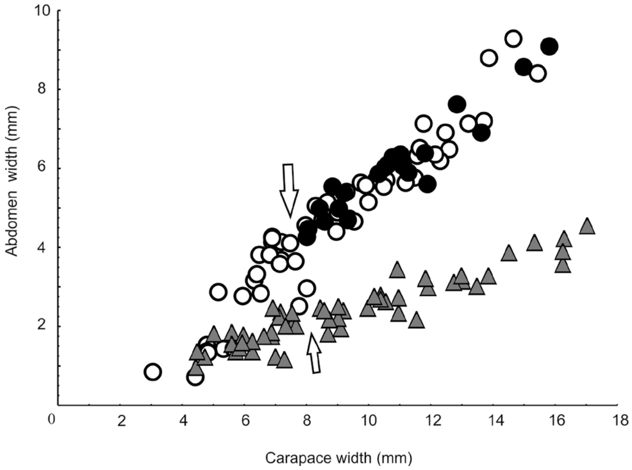

Figure 6. Regression between the carapace width and abdomen width in the *Pachygrapsus gracilis* specimens collected in the Marapanim estuary. White circles = non-reproductive females; black circles = ovigerous females, and triangles = males. The arrows indicate the breakpoints that represent the body size at morphological sexual maturity. Abdomen width is measured between fourth and fifth abdominal segment.

Table 1. Regression equations for the *Pachygrapsus gracilis* specimens collected in the Marapanim estuary (Pará, Brazil) between August 2006, and July 2007. F = female, OF: ovigerous female, M = male, N = number of individuals, AW = abdomen width (mm), CW = carapace width (mm), R^2 = coefficient of determination.

Sex	N	Equation	R^2
F	56	ln AW = -1.1946 + 0.6561*ln CW	0.91
OF	20	ln AW = 0.0806 + 0.5477* ln CW	0.90
M	61	ln AW = 0.2274 + 0.2301* ln CW	0.86

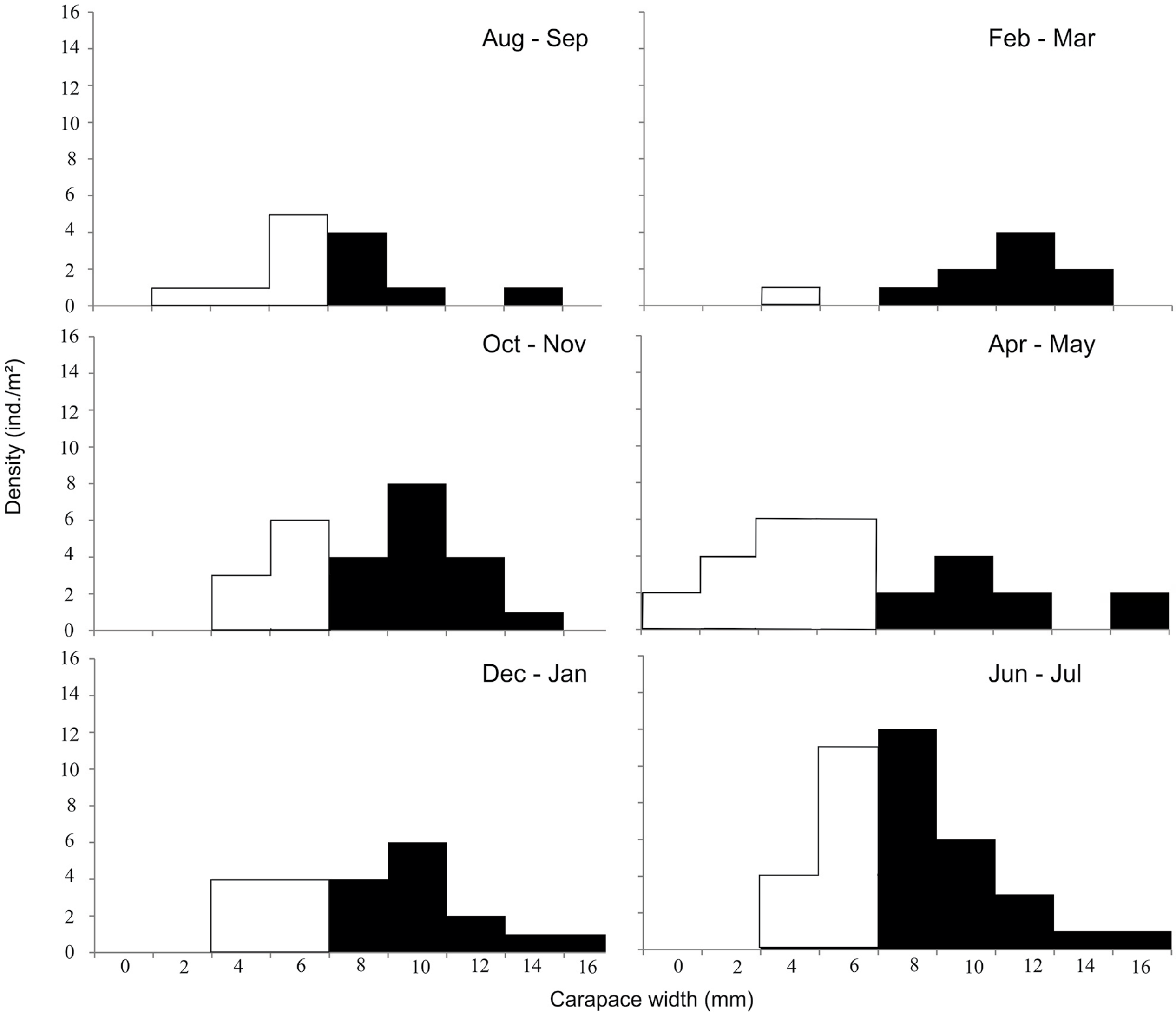

Figure 7. Structure size analysis (carapace width, CW) of the *Pachygrapsus gracilis* specimens recorded each month between August 2006, and July 2007, in the Marapanim estuary. The black bars represent the adults, and the white bars represent the juveniles.

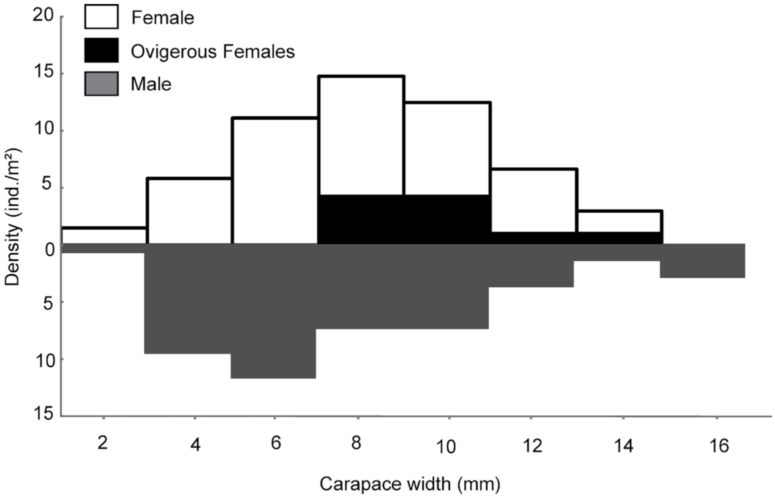

Figure 8. Relative frequency of the carapace widths of the male and female *Pachygrapsus gracilis* specimens collected in the Marapanim estuary.

Table 2. Minimum, maximum and mean (± Standard deviation, SD) carapace width (mm) of the male and female *Pachygrapsus gracilis* specimens collected from the Marapanim estuary in Pará, Brazil, from August 2006, to July 2007.

Sex	Minimum	Maximum	Mean	SD
Female	3.04	15.46	8.77	2.95
Ovigerous Female	8.02	15.81	10.78	2.24
Male	3.70	17.06	8.91	3.48

Discussion

The zoea I and adults of *P. gracilis* presented similar patterns of distribution and density over time and in space, indicating a degree of interdependence between the different life stages of this species. The principal pattern was the occurrence of higher densities in the more saline zones. Despite the fact that ovigerous females were only collected during the rainy season, probably due to the rather small sample sizes, zoea I and juveniles were observed throughout the year, indicating that reproduction is continuous in the Marapanim estuary, as observed in most other tropical (Hartnoll, 2006; Bessa *et al.*, 2010) and subtropical (Peiró and Mantelatto, 2011) crab species, with peaks of larval abundance between March and May, and August and December. The same pattern was observed in *Lepidophthalmus siriboia* Felder and Rodrigues, 1993 and *Upogebia vasquezi* Ngoc-Ho, 1989 (Oliveira *et al.*, 2012), *Panopeus lacustris* Desbonne in Desbonne and Schramm, 1867, *Uca maracoani* (Latreille, 1802), and *Leptuca cumulanta* (Crane, 1943) (Lima *et al.*, 2019) in Marapanim estuary.

This pattern may be related to reproduction occurring in adjacent intertidal habitats, such as mangroves and other muddy environments, as recorded by Souza and Fontoura (1993) in Rio Grande do Sul (Brazil). Leme and Negreiros-Fransozo (1998) recorded a similar pattern for *Aratus pisonii* (H. Milne Edwards, 1837) in southeastern Brazil. This emphasizes the influence of larval transportation mechanisms on the planktonic dynamics of the species (Cházaro-Olvera *et al.*, 2007; Murphy and Iken, 2014).

The presence of ovigerous *P. gracilis* females in the dry season was recorded only in July and January, the latter being an atypical month, since it is normally characterized by high precipitation rates. Despite this, the data reinforce the seasonal distribution of the females and emphasize the importance of rainfall for the reproduction of this species. In tropical areas, the reproductive activity of grapsoids tends to be highest during the rainy season (Dittel and Epifanio, 1990), as also verified in *P. gracilis* in the Tramandaí River (Souza and Fontoura, 1993), and the estuary of the Patos Lagoon, in Rio Grande do Sul, where larvae were observed during the rainy season (Vieira and Calazans, 2010). This pattern may reflect the more favorable conditions generated by the input of rainwater, such as the expansion of areas in which to disperse, providing access to a wider range of feeding resources and potential shelters (Litulo *et al.*, 2005; Vergamini and Mantelatto, 2008).

The presence of larvae in the zoea I stage indicates that the reproduction of the species occurs in the estuary, while the absence of late-stage larvae indicates a migratory pattern. This larval export strategy has already been verified in other species of the genus, such as *Pachygrapsus crassipes* Randall, 1840 (DiBacco *et al.*, 2001) and *P. marmoratus* (Drake *et al.*, 1998). The lack of any relationship between the density of zoea I and ovigerous females in the different sectors of the study area may reflect this transportation of the larvae by the tidal and fluvial currents. This conclusion is emphasized by the data from the low salinity site A2, which returned the second highest number of zoea I, without any ovigerous females being recorded. This question is especially important in the case of *P. gracilis*, given its prolonged larval development period, which allows the larvae time to disperse over long distances (Díaz-Cabrera *et al.*, 2012), and contributes to the lack of synchrony between the abundance of the adults and the larvae.

Larger densities of *P. gracilis* zoea I and adults were found on margin A of the estuary, characterized not only by anthropogenic features, but also by higher levels of sediment deposition. The higher proportion of ovigerous females found at site B1 may reflect a specific reproductive strategy of this species, given the greater degree of conservation of this area, and the fact that most brachyurans seek more stable environments in which to reproduce (Mantelatto and Fransozo, 2000; DiNuzzo *et al.*, 2020).

However, relatively low or high temperatures may hinder settlement, as observed in *P. gracilis* in Jamaica (Hartnoll, 1965) and in the Caeté estuary, in Pará (Diele *et al.*, 2010), where the species suffered metabolic stress at temperatures of between 30 °C and 32 °C. However, in the Marapanim estuary the temperature variation was minimal, which is typical of equatorial regions (Carvalho and Couto, 2011), with no significant correlation found between the density of the species and water temperature.

The occurrence of *P. gracilis* in the upper portion of the intertidal zone is consistent with the pattern observed in *P. transversus* in Portugal, which may be accounted for primarily by the ability of these species to exploit a diversity of habitats, as well as their tolerance of conditions that may provoke metabolic stress (Flores and Paula, 2002). This distribution pattern may be specific to rocky substrates, however, given that *P. gracilis* is found throughout the mangroves of the Caeté River in Pará (Diele *et al.*, 2010). The catfish *S. herzbergii* preys on grapsids primarily on unconsolidated substrates during the rainy season, given that the vision-oriented anti-predator defense strategy of these crabs is hampered by the increased turbidity of the water during this period (Giarrizzo and Saint-Paul, 2008).

The considerable amplitude of the size classes observed in the present study indicates that, in this species, the juveniles and adults share the same space. This indicates a partial or total lack of competition for resources between these different age classes, at least in the rocky outcrops surveyed. This may also reflect a pattern of social behavior or grouping that enhances protection against predators and allows for the formation of a microhabitat favorable to the species (Deudero *et al.*, 2005).

The unimodal distribution of the carapace width frequencies indicates a stable *P. gracilis* population structure in the study area, reflecting the balance between birth and mortality rates (Hartnoll and Bryant, 1990). Other grapsoids, such as *P. transversus* (see Flores and Negreiros-Fransozo, 1999), *Sesarma recta* (Randall, 1840) (Castiglioni *et al.*, 2010), *P. marmoratus* (see Flores and Paula, 2002), and *Helograpsus haswellianus* (Whitelegge, 1890) (Katrak and Dittmann, 2011), also present a unimodal distribution pattern. The balanced sex ratio of *P. gracilis* recorded here indicates that the males and females in the study population have a similar spatio-temporal distribution, and birth, mortality, and predation rates (Johnson, 2003).

These results nevertheless diverge from those recorded for *P. gracilis* in Rio Grande do Sul, where the females predominated in the larger body length classes (Souza and Fontoura, 1993). They also contrast with the pattern found in other grapsoids, such as *P. transversus* (see Abele *et al.*, 1986), *Aratus pisonii* (see Leme and Negreiros-Fransozo, 1998), and *Goniopsis cruentata* Latreille, 1803 (Silva and Oshiro, 2002). In general, males suffer higher mortality rates, due to their aggressive territorial behavior, which leaves them more exposed to predators, whereas the females tend to be more cryptic (Abele *et al.*, 1986). However, these factors do not appear to have played a prominent role in the characteristics of the *P. gracilis* population analyzed here.

Despite the lack of any significant variation in the size of the carapace between the male and female *P. gracilis* analyzed in the present study, the generally larger size of the females was consistent with the findings of previous studies (Hartnoll, 1965; Souza and Fontoura, 1993) and the pattern observed in other grapsoid crabs (Clores and Ramos, 2013). Even so, the mean lengths of both males and females were shorter than those recorded in Rio Grande do Sul (10.3 mm and 11.4 mm, respectively) by Souza and Fontoura (1993). In the neighboring Caeté estuary, carapace lengths ranged from 7 mm to 14 mm (Diele *et al.*, 2010), that is, the minimum length was substantially longer, and the maximum, shorter than those recorded in the Marapanim estuary. The differences in size that the same, widely-distributed species presents at different sites may be related to the influence of salinity, which can restrict growth due to the energy necessary for osmoregulation (Camargo *et al.*, 2017).

The results of the present study indicate that *P. gracilis* develops part of its life cycle in the Marapanim estuary, where it reproduces, exports zoea I to the coastal waters of the ocean, and returns, probably in the form of megalopae, to develop its benthic phase, responding to local conditions through systematic shifts in distribution and abundance over time and space. The parameters recorded in the present study indicate that the population was relatively stable and able to adjust to the considerable variations in abiotic factors that are typical of this estuary, reinforcing the need for its conservation. As little data is available on this species, further research into abundance and growth patterns, distribution, population structure, reproduction, and physiology will be essential for a more reliable understanding of its life cycle and its ecological role in this ecosystem.

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