

## Population biology of the green porcelain crab *Petrolisthes armatus* (Crustacea: Porcellanidae) in a tropical estuarine bay of northeastern Brazil

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**Abstract:** The aim of this study was to investigate the population biology of the green porcelain crab *Petrolisthes armatus* in an estuarine area of northeastern Brazil. Individuals were monthly sampled (February 2011-January 2012) during the spring low tide. Four transects, 10 m apart from each other and perpendicular to the shoreline were delimited in the rocky zone of a beach, comprising an area of approximately 861 m<sup>2</sup>. Crab sampling was carried out using 0.25-m<sup>2</sup> plots (10 equally spaced plots were sampled from each transect per month). A total of 836 individuals were collected: 401 males (48%), 220 non-ovigerous females (26.3%), and 215 ovigerous females (25.7%). Ovigerous females were significantly larger than males and non-ovigerous females, while males were significantly larger than non-ovigerous females. The overall sex ratio of 1:0.9 did not differ significantly from the expected 1:1. The highest abundance (19.8 ind.m<sup>-2</sup>) was observed in transect 3, in the mid-intertidal, suggesting zonation and edge effect. Ovigerous females were recorded in all months except in May 2011, suggesting continuous reproduction and the mean fecundity was 145 ± 121 embryos. There was a significant correlation between carapace width and number of embryos. Although the study area showed some signs of disturbance caused by anthropogenic action, the population of *P. armatus* was stable in its natural environment.

**Résumé :** *Biologie de la population du crabe porcelaine vert Petrolisthes armatus (Crustacea : Porcellanidae) d'un estuaire tropical du nord-est du Brésil.* Le but de cette étude était d'étudier la biologie de la population du crabe porcelaine vert *Petrolisthes armatus* dans une zone estuarienne du nord-est du Brésil. Les individus ont été échantillonnés tous les

mois (février 2011 à janvier 2012) pendant la marée basse du printemps. Quatre transects, distants de 10 m et perpendiculaires à la ligne d'eau, ont été délimités dans la zone rocheuse d'une plage, d'une superficie d'environ 861 m<sup>2</sup>. L'échantillonnage des crabes a été effectué en utilisant des parcelles de 0,25 m<sup>2</sup> (10 parcelles équidistantes ont été échantillonnées dans chaque transect par mois). Un total de 836 individus a été recueilli : 401 mâles (48%), 220 femelles non ovigères (26,3%) et 215 femelles ovigères (25,7%). Les femelles ovigères étaient significativement plus grandes que les mâles et les femelles non ovigères et les mâles significativement plus gros que les femelles non ovigères. Le sex-ratio de 1:0,9 ne différait pas significativement de 1:1 attendu. La densité totale a été estimée à 6,9 ind. m<sup>-2</sup>. L'abondance la plus élevée a été observée dans le transect 3, au milieu de la zone intertidale, ce qui suggère une zonation et un effet de bordure. Les femelles ovigères ont été observées tous les mois sauf en mai 2011, ce qui suggère une reproduction continue. La fécondité moyenne au stade initial du développement était de 145 ± 121 embryons. Il y avait une corrélation significative entre la largeur de la carapace et le nombre d'embryons. Bien que la zone d'étude ait montré des signes de perturbation causés par l'action anthropique, la population de *P. armatus* était stable dans son environnement naturel.

**Keywords:** Anomura • Porcelain crab • Population structure • Reproductive biology • Estuary • Bahia state

## Introduction

The family Porcellanidae comprises 30 genera and approximately 280 species of decapods known as porcelain crabs. These crabs occur in a wide variety of tropical and temperate marine habitats, including intertidal and subtidal zones (Rodríguez et al., 2005; Osawa & McLaughlin, 2010). Porcellanids are usually free-living organisms that inhabit rocky shores, mangroves, and coral reefs (Gore, 1974). Some species live symbiotically with other marine macroinvertebrates such as asteroids, sea anemones, and sea urchins (Gore, 1974; Baeza, 2007).

The genus *Petrolisthes* is globally distributed and comprises approximately 100 valid species (Rodríguez et al., 2005), with five occurring along the Brazilian coast (Ferreira & Melo, 2016). Among these species, the green porcelain crab *Petrolisthes armatus* (Gibbes, 1850) has the widest distribution, occurring in the intertidal of the Atlantic and Pacific Coasts. In the Western Atlantic, *P. armatus* occurs from North Carolina to Florida, Gulf of Mexico, Antilles, Colombia, and Brazil (Ferreira & Melo, 2016). In the Eastern Atlantic, the species is distributed from Senegal to Angola and in the Central Atlantic it occurs in the Ascension Island (Ferreira & Melo, 2016). In the Eastern Pacific, it is distributed from the Gulf of California to Costa Rica, Galapagos Islands, and Peru (Ferreira & Melo, 2016). Due to its recent occurrence north of Cape Canaveral, FL, *P. armatus* is considered an invasive species in estuaries of Georgia and South Carolina, where it has reached high densities within a few months after colonization (Knott et al., 2000). Hollebhone & Hay (2007) found mean densities of 1,000 crabs.m<sup>-2</sup>, suggesting that *P.*

*armatus* may significantly impact oyster reef communities throughout the South Atlantic Bight. More recently, Wassick et al. (2017) estimated a maximum density of 11,542 ind.m<sup>-2</sup> at Trask Landing (Bluffton, South Carolina, USA).

*Petrolisthes armatus* is considered to be euryhaline since adults are found under rocks mainly in estuarine and coastal ecosystems (Coelho, 2000). The population biology of *P. armatus* has been studied in the United States eastern coast, where it is considered as an invasive species (Knott et al., 2000; Hollebhone & Hay, 2007; Wassick et al., 2017), and in the Pacific coast of Costa Rica (Diaz-Ferguson & Vargas-Zamora, 2001). In Brazil, Oliveira & Masunari (1995 & 1998) addressed its population structure as well as its parasite *Aporobopyrus curtatus* (Richardson, 1904) in Farol Island, Paraná (southern Brazil). Micheletti-Flores & Negreiros-Fransozo (1999) studied the composition of a population associated with a colony of the polychaete *Phragmatopoma lapidosa* Kinberg, 1867 in São Vicente, southern coast of São Paulo state. Miranda & Mantelatto (2009 & 2010) studied its population structure, reproductive period, relative growth, and sexual maturity in two mangroves (one disturbed and one pristine) in Araçá, São Sebastião municipality, northern coast of São Paulo (southeastern Brazil). Oliveira et al. (2013) studied the density of larvae and adults, mainly ovigerous females, in the estuary of the Marapanim River, Pará state, Amazon region. Pinheiro et al. (2017) evaluated the life history based on growth and reproduction in Praia Grande, Ubatuba municipality, northern coast of São Paulo (southeastern Brazil). Finally, Wehrtmann et al. (2012) compared the reproductive patterns of populations from São Paulo (Brazil) and Costa Rica.

*Petrolisthes armatus* is quite common in estuaries of the northern portion of South America; however, there is only one study focusing population aspects (Oliveira et al., 2013) in this tropical point of its occurrence. The lack of information about the crustacean fauna of this region is a cause of concern. In the last few years there have been increasing environmental changes due to overfishing, pollution of rivers, estuaries, and marine environments, as well as mangrove deforestation. In this context, to contribute to the knowledge on the population biology of *P. armatus* in its native distribution range, we investigated (1) the density of the species in its native area and along its tidal distribution; (2) the species' spatial and temporal distribution; (3) the demographic patterns (including sex ratio, mean size, and size-frequency distribution); and (4) the reproductive patterns of the species. Regarding spatial distribution, we investigated the existence of zonation and edge effect, i.e. if the discontinuity of land cover could

influenced the spatial distribution of the individuals once the edge effect alter physical gradients, species distribution and many ecological and ecosystem processes (Laurance et al., 2002).

## Material and Methods

### Study area

Fieldwork took place in the intertidal of Pontal Bay, near the mouth of Cachoeira River, Ilhéus, Bahia state, northeastern Brazil ( $14^{\circ}48'28''\text{S}$ - $39^{\circ}01'33''\text{W}$ ) (Fig. 1). The rocky area was surrounded by fine sand and sandy-muddy sediment. The study area is under the influence of both the Cachoeira River and oceanic conditions, providing ideal conditions for the occurrence of *P. armatus*.

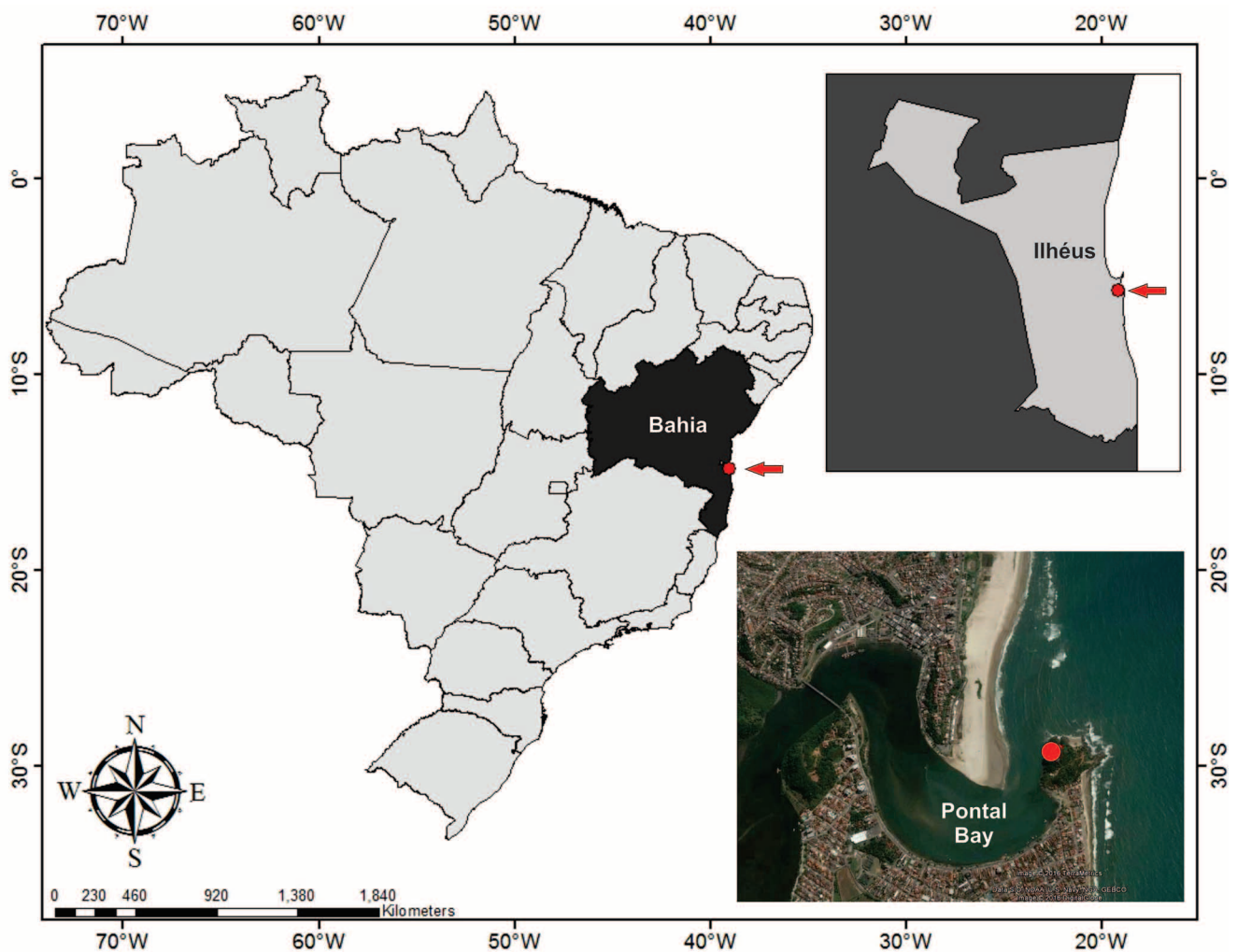


Figure 1. *Petrolisthes armatus*. Location of the study area, Pontal Bay, Ilhéus, Bahia, northeastern Brazil.

### *Sampling methods*

Individuals were sampled monthly during spring low tide, from February 2011 to January 2012. Four transects, perpendicular to the shoreline, were delimited in the rocky zone, comprising an area of 860.6 m<sup>2</sup>. Ten plots measuring 0.5 m × 0.5 m (0.25 m<sup>2</sup>) were equally spaced in each transect. Transects ran from the high to the low intertidal, in order to sample the entire habitat and record the total abundance in each transect. The crabs were manually collected from under the rocks and from dead shells of the oyster *Crassostrea mangle* Amaral & Simone, 2014. Individuals were anesthetized with ice, preserved in 70% ethanol, labeled, and stored until further analyses.

At every collection event, salinity was measured with an optical refractometer and the water and air temperature were obtained using a mercury thermometer. Rainfall data from February 2011 to January 2012 were obtained from the meteorological station of SBIL/INFRAERO/Ilhéus.

### *Laboratory analysis*

In the laboratory, individuals were identified and sexed based on presence (females) or absence (males) of gonopores on coxae of third pereopods (Melo, 1999). Even the smallest females of our samples could be recognized based on that character. Moreover, they were checked for the presence of embryo masses attached to the females' pleopods. Carapace width (CW) was measured to the nearest 0.01 mm using a vernier caliper.

### *Population structure*

Population structure was analysed through size-frequency distribution of all individuals collected during the study period. Individuals were grouped in 1 mm size-class intervals from 1 to 10 mm of CW. Significant differences from 1:1 in overall sex ratio (male:female) and monthly sex ratio were evaluated using the chi-square test ( $\chi^2$ ) and the Fisher test (z), respectively. Overall size-frequency distributions were tested for normality using Kolmogorov-Smirnov (KS) test, and mean size of males, non-ovigerous females and ovigerous females was compared using the one-way ANOVA with a post-hoc test of Tukey. The relationships between the monthly density and monthly climate conditions (temperature and precipitation) was tested using Pearson correlation coefficient ( $\alpha = 5\%$ ).

### *Reproductive biology*

The breeding season was defined as the period when ovigerous females were observed. The average size at the onset of functional maturity was determined based on the CW at which 50% of total females sampled were considered sexually mature, i.e., were ovigerous. The

average size at the onset of functional maturity was estimated as the CW at which 50% of females were adults by interpolating the equation obtained through a logistic regression (Pagano & Gauvreau, 2006) of the individual's maturation stage (immature = 0; mature = 1) vs. CW (e. g. Chiquetto-Machado et al., 2016; Rocha & Barbosa, 2017) using the software PAST (Hammer et al., 2001). The male secondary sexual characters were not observed. The pleopods and the entire embryo mass of each ovigerous female were removed and placed in Petri dishes filled with seawater. The embryos were gently detached from the pleopods with a small brush or tweezers. Embryos were examined under a stereomicroscope and classified according to their stage of embryonic development based on Hernáez & Palma (2003) and Wehrtmann et al. (2012). Fecundity was estimated with 30 females bearing embryos at stage I (initial) to avoid underestimation due to embryo loss during incubation (adapted from Litulo, 2005). The relationship between fecundity and female body size was tested using Pearson correlation coefficient ( $\alpha = 5\%$ ).

### *Spatial distribution*

The spatial distribution was evaluated by estimating the population density in the plots along the transects, with plots 1 and 2 considered as high intertidal, 5 and 6 as mid intertidal, and 9 and 10 as low intertidal. The remaining plots were excluded from this analysis due to we are aiming to evaluate the main effect of intertidal zone on the population density. Thus, including data of transitional plots possibly would bias this effect.

Additionally, the number of crabs per transect was quantified and transects were grouped into edge (transects 1 and 4) and center (transects 2 and 3) to verify any "edge effect" in the spatial distribution of the individuals. Transects 1 and 4 were near the lateral edge of the sampling area, where sandy-muddy sediment and smaller rocks prevail, while transects 2 and 3 had larger rocks and constant humidity (A.O. Almeida, pers. obs.).

One-way ANOVA and the post-hoc test of Tukey were used to test the difference between i) the three intertidal zones (i.e., low, mid, and high intertidal); ii) the four transects; and iii) males and females, using the total number of individuals as the response variable.

## **Results**

### *Abiotic factors*

During the study period air temperature ranged from 21°C in August 2011 to 34°C in February 2011 (mean ± SD: 26.1 ± 3.5°C). The lowest water temperature was recorded in June 2011 (24°C) and the maximum in February 2011



(31°C) ( $26.8 \pm 2.0^\circ\text{C}$ ). Salinity ranged from 3.5 to 36.5 ( $23.1 \pm 12.0$ ). Minimum and maximum salinity were recorded in October and February 2011, respectively. Rainfall varied from 73.5 mm in January 2012 to 971.8 mm in November 2011 ( $591.2 \pm 289.2$  mm) (Table 1).

#### Population structure

A total of 836 crabs were sampled, 401 males (48%), 220 non-ovigerous females (26.3%), and 215 ovigerous females (25.7%). Their size ranged from 1.9 to 9.3 mm (mean  $\pm$  SD:  $5.6 \pm 1.6$  mm) in males; 1.0 to 8.1 mm ( $4.5 \pm 1.3$  mm) in non-ovigerous females; and 3.8 to 8.8 mm ( $6.2 \pm 0.9$  mm) in ovigerous females. The latter were significantly larger than males and non-ovigerous females (Table 2 & Fig. 2). Males were significantly larger than non-ovigerous females (Table 2 & Fig. 2).

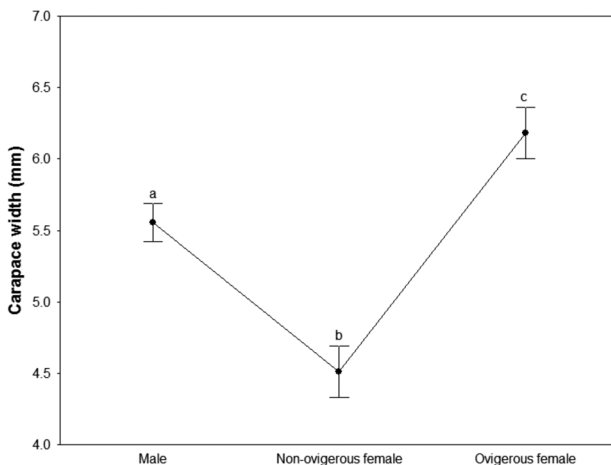
The size-frequency distribution was normal for males (KS = 0.046,  $p > 0.05$ ) and females (ovigerous and non-ovigerous) (KS = 0.041,  $p > 0.05$ ). Males were more abundant in size classes 4-

**Table 1.** *Petrolisthes armatus*. Monthly air and water temperatures, salinity and mean rainfall at Pontal Bay, Ilhéus, Bahia, from February 2011 to January 2012.

Months	Air temperature (°C)	Water temperature (°C)	Salinity	Mean rainfall (mm)
February	34	31	36.5	302.9
March	28.3	28.2	7.5	584.6
April	25.5	28	10.5	891.5
May	25.5	27	29	745.4
June	23.5	24	32.5	544.0
July	24.2	26	32.5	741.5
August	21	25.5	31.5	713.7
September	22	24	35	563.5
October	27	26	3.5	830.8
November	28.5	27	9	971.8
December	25	26	25	131
January	28.5	29	24.5	73.5
<b>Annual Mean <math>\pm</math> SD</b>	<b>26.1 <math>\pm</math> 3.5</b>	<b>26.8 <math>\pm</math> 2.0</b>	<b>23.1 <math>\pm</math> 12.0</b>	<b>591.2 <math>\pm</math> 289.2</b>

**Table 2.** *Petrolisthes armatus*. Sum of squares (S.S.), degrees of freedom (D.F.), mean squares (M.S.), F, and p value of one-way ANOVA using the carapace width (mm) as response variable and their sex (male, non-ovigerous female, and ovigerous female) as categorical variable.

	S.S.	D.F.	M.S.	F	p
Sex	313.37	2	156.68	85.72	0.0001
Residuals	1522.60	833	1.83		

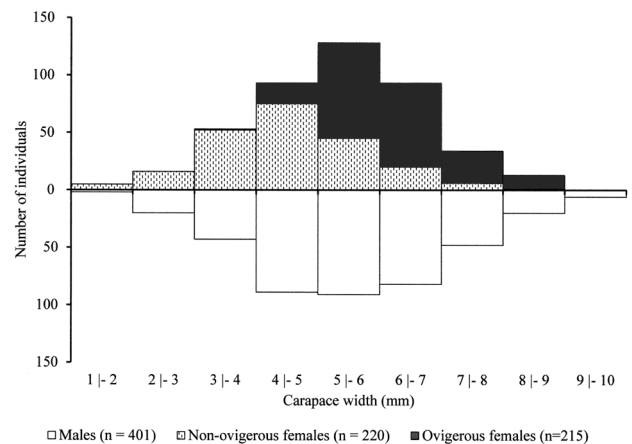


**Figure 2.** *Petrolisthes armatus*. Carapace width (mm) mean (circles) and confidence interval at 95% level (bars) of males, non-ovigerous females, and ovigerous females. Different letters indicate statistical differences.

5 mm ( $n = 89$ ) and 5-6 mm ( $n = 91$ ). Non-ovigerous females were more abundant in the class 4-5 mm ( $n = 75$ ), while ovigerous females appeared in size class 3-4 ( $n = 1$ ) and were more abundant in the class 5-6 ( $n = 83$ ). Only males were present in the class 9-10 mm (Fig. 3).

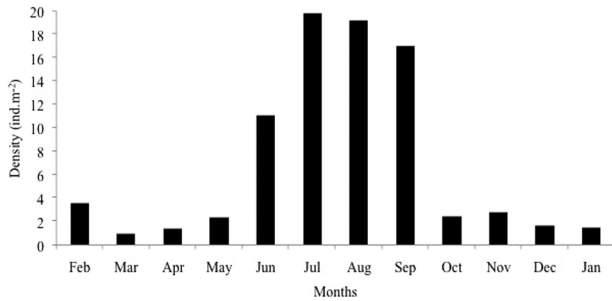
#### Density

The highest density was observed in July 2011 (19.8 ind.m<sup>-2</sup>), while March 2011 showed the lowest density (0.9



**Figure 3.** *Petrolisthes armatus*. Overall size-frequency distribution of males, non-ovigerous females, and ovigerous females.

ind.m<sup>-2</sup>) (Fig. 4). Monthly density was negatively correlated with mean monthly temperature ( $r = -0.58$ ,  $p = 0.046$ ). On the other hand, there was no correlation with mean monthly rainfall ( $r = 0.33$ ,  $p = 0.30$ ) and salinity ( $r = 0.46$ ,  $p = 0.13$ ).



**Figure 4.** *Petrolisthes armatus*. Monthly density of all individuals sampled from February 2011 to January 2012 at Pontal Bay, Ilheus, Bahia.

#### Sex ratio

The overall sex ratio was 0.9:1 (M:F), which did not differ from the expected 1:1 ratio ( $\chi^2 = 0.6127$ ,  $p = 0.4338$ ). Similarly, the monthly sex ratio did not differ from the Mendelian proportion (z test,  $p$  from 0.380 to 0.867) (Table 3). No differences in the sex ratio were found in each size class (z test,  $p$  from 0.277 to 1.000) (Table 4). Finally,

**Table 3.** *Petrolisthes armatus*. Number of individuals per month and monthly sex ratio from February 2011 to January 2012 at Pontal Bay, Ilheus, Bahia.

Months	Males		Females (ovigerous and non-ovigerous)		Ratio
	n	% per month	n	% per month	
February	15	1.8	21	2.5	0.71
March	3	0.3	6	0.7	0.50
April	9	1.1	5	0.6	1.80
May	13	1.6	10	1.2	0.72
June	51	6.1	60	7.2	0.85
July	98	11.7	100	12.0	0.98
August	87	10.4	105	12.5	0.87
September	76	9.1	94	11.2	0.81
October	16	1.9	8	1.0	2.00
November	118	2.2	10	1.2	1.8
December	8	0.7	10	1.2	0.6
January	9	1.1	6	0.7	1.5
<b>TOTAL</b>	<b>401</b>	<b>48</b>	<b>435</b>	<b>52</b>	<b>0.9</b>

**Table 4.** *Petrolisthes armatus*. Sex ratio per size class and results of the z test for individuals sampled from February 2011 to January 2012 at Pontal Bay, Ilheus, Bahia.

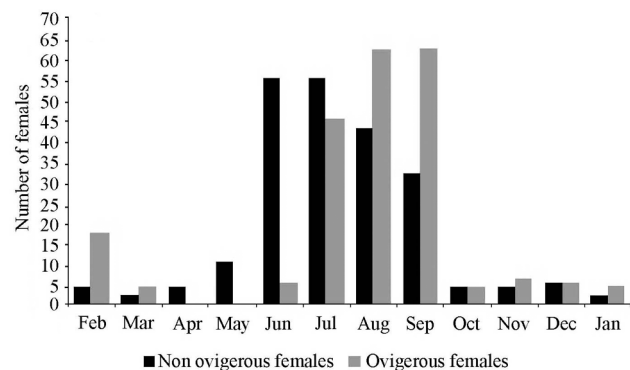
Size classes	Proportion (M:F)	p
1   2	0.4	0.5921
2   3	1.1	1.0000
3   4	0.8	0.4650
4   5	0.9	0.8326
5   6	0.7	0.0644
6   7	1.0	0.9134
7   8	1.3	0.4159
8   9	2.1	0.2772
9   10	0.0	0.1667

the number of males and females did not differ between transects ( $F = 0.024$ ,  $p = 0.883$ ) and plots ( $F = 0.126$ ,  $p = 0.730$ ).

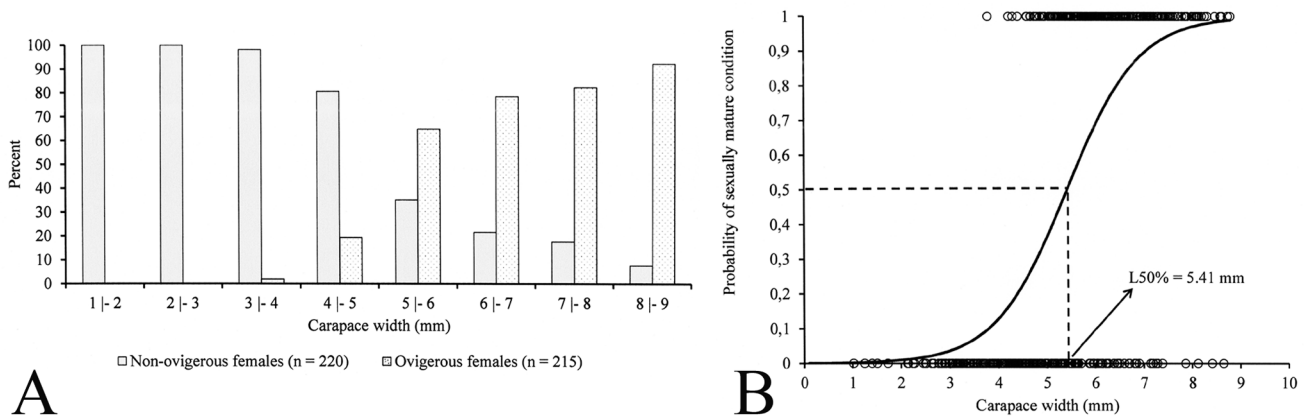
#### Reproductive biology

Ovigerous females occurred every month except for May 2011. The number of ovigerous females ranged from one (April 2011) to 62 (August and September 2011) (Fig. 5). The highest frequencies of ovigerous females were observed from July 2011 to September 2011, characterizing the population reproductive peak. Ovigerous females comprised 49.4% of all females. The smallest ovigerous female measured 3.8 mm of CW, corresponding to the size class 3.0-4.0. From this size class onwards, the proportion of ovigerous females gradually increased. Thus, we estimated the average size at the onset of functional maturity (L50%) at 5.41 mm of CW (Fig. 6).

Fecundity ranged from 21 to 426 embryos (mean  $\pm$  SD:  $145 \pm 121$ ) and it was positively correlated with female size ( $r = 0.5362$ ,  $p = 0.0023$ ).



**Figure 5.** *Petrolisthes armatus*. Number of non-ovigerous and ovigerous females per month from February 2011 to January 2012 at Pontal Bay, Ilheus, Bahia..



**Figure 6.** *Petrolisthes armatus*. **A.** Frequency distribution by size classes of females (non-ovigerous and ovigerous stages discriminated). **B.** Size at the onset of functional maturity of females estimated by logistic regression based on the non-ovigerous (0) or ovigerous (1) condition plotted against carapace length.

*Spatial distribution*

The spatial distribution was unequal along the intertidal zone and among transects. The highest abundance was found in the mid intertidal (n = 211), followed by the low intertidal (n = 165) and high intertidal (n = 48). The number of individuals did not differ significantly between the mid and low intertidal and between the low and high intertidal (Fig. 7A & Table 5). Considering each transect, the highest abundance was seen in transect 3 (n = 412) and the lowest in transect 1 (n = 32). A one-way ANOVA with Tukey post-hoc test showed that there were more individuals in transect 3 than in the others. Transect 1 had the lowest abundance, while there was no statistical difference between transects 2 and 4 (Fig. 7B & Table 6).

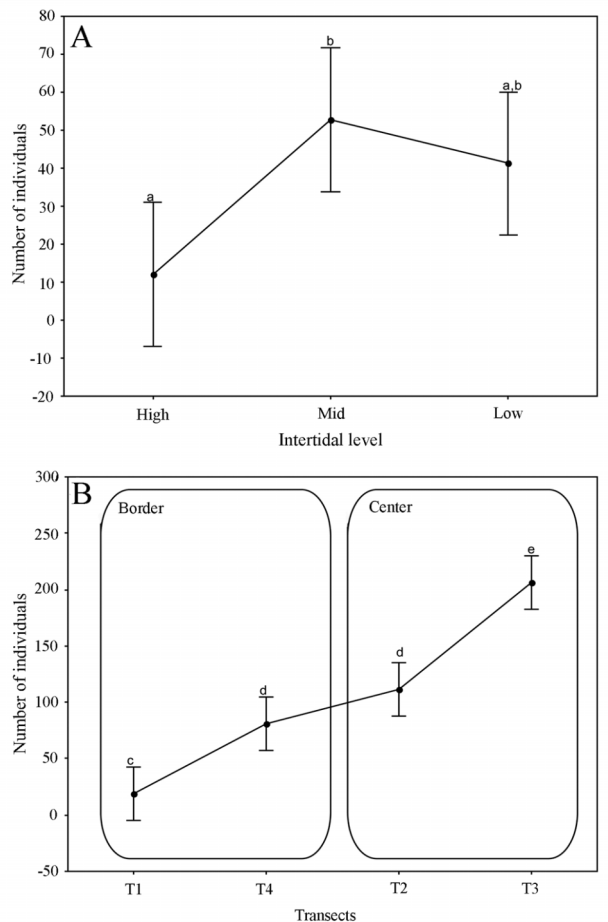
**Table 5.** *Petrolisthes armatus*. Sum of squares (S.S.), degrees of freedom (D.F.), mean squares (M.S.), F, and p value of one-way ANOVA using the number of individuals as response variable and the three different intertidal levels as categorical variable.

	S.S.	D.F.	M.S.	F	P
Intertidal levels	3531.17	2	1765.58	6.312	0.019
Residuals	2517.50	9	279.72		

**Discussion**

*Population structure*

Males were significantly larger than non-ovigerous females in the studied population. This result corroborates the data obtained for the same species in two states in Brazil, Paraná



**Figure 7.** *Petrolisthes armatus* **A.** Distribution of individuals regarding intertidal level. **B.** Distribution of individuals regarding transects. Different letters indicates statistical differences.

**Table 6.** *Petrolisthes armatus*. Sum of squares (S.S.), degrees of freedom (D.F.), mean squares (M.S.), F, and p value of one-way ANOVA using the number of individuals as response variable and the four different transects as categorical variable.

	S.S.	D.F.	M.S.	F	p
Transect	36442	3	12147.33	83.487	0.0005
Residuals	582	4	145.50		

and São Paulo (Oliveira & Masunari, 1995; Miranda & Mantelatto, 2009 & 2010; Pinheiro et al., 2017). According to Miranda & Mantelatto (2009), the larger size attained by males can be advantageous as it allows a higher reproductive potential and fertilization of a higher number of females. Moreover, larger males have higher chances to copulate due to their advantage during competition with conspecifics, as observed in brachyuran crabs (Christy, 1987).

In populations of *P. armatus* from Paraná and São Paulo, the maximum size of individuals was 13.5 and 14.1 mm of CW, respectively (Oliveira & Masunari, 1995; Miranda & Mantelatto, 2009; Pinheiro et al., 2017), which is much higher than that found in this study (9.3 mm). The mean size from the studied population was 5.3 mm, while the population from São Paulo had a mean of 7.5 mm (Miranda & Mantelatto, 2009). The four populations here discussed are from different latitudes, south (Paraná), southeastern (São Paulo), and northeastern (Bahia) Brazil. The high annual mean temperature recorded during this study might explain the difference in size between populations. Higher temperatures at lower latitudes might stimulate growth and reproduction; therefore, individuals might reach sexual maturity earlier and be smaller than those inhabiting higher latitudes (Lardies et al., 1998; Wehrtmann et al., 2012).

The frequency distribution of the entire population (males and females) by size class was unimodal, the same distribution was seen when only males and only females were considered. The unimodal distribution is a common feature in decapod crustacean populations from tropical regions, where seasonal climate changes are not very strong (Ribeiro et al., 2012). On the other hand, the sub-tropical population from São Paulo showed a bimodal distribution, which might be a consequence of the intense recruitment in certain periods due to seasonal climate changes (Miranda & Mantelatto, 2009; Pinheiro et al., 2017).

#### Sex ratio

The sex ratio found in this study was similar to that reported by other authors who have studied populations of *P. armatus* at different locations. No statistical differences in the total and monthly sex ratios were observed in the populations of *P. armatus* from South Georgia (Hollebone

& Hay, 2007), São Sebastião, São Paulo (Miranda & Mantelatto, 2009), Ubatuba, São Paulo (Pinheiro et al., 2017) and southeastern USA (Georgia, North Carolina and South Carolina) (Wassick et al., 2017). Populations of *P. armatus* from two beaches of the Gulf of Nicoya, Pacific coast of Costa Rica, had a sex ratio equal to 1:1.6; however, the authors did not mention if it differed significantly from 1:1 (Diaz-Ferguson & Vargas-Zamora, 2001). The 1:1 sex ratio is a common pattern in decapod crustaceans that live in heterosexual pairs (see Lardies et al., 1998), and in porcellanid crabs this pattern is also frequent (Ahmed & Mustaquim, 1974; Gebauer et al., 2007; Baeza et al., 2013; Pinheiro et al., 2017).

#### Density

Our data corroborates the findings of Micheletti-Flores & Negreiros-Fransozo (1999) that observed high densities of *P. armatus* in banks of the polychaete *P. lapidosa* during winter in São Sebastião, São Paulo state. On the other hand, Masunari & Oliveira (1995) reported the highest densities during summer, when higher temperatures occur. Similarly, Hollebone & Hay (2007) found densities of 15 to 3900 ind.m<sup>-2</sup> during the warmer months and densities of only 400 ind.m<sup>-2</sup> after the colder months, in South Georgia, United States. Oliveira et al. (2013) found two peaks of density in an Amazon estuary, one in August (dry season) and one in February (rainy season). Rainfall also seems to affect the population density of *P. armatus*, as it was observed during the rainy season in São Sebastião, when animals reached higher abundances (Miranda & Mantelatto, 2009). However, our results showed no correlation between density and rainfall, corroborating the patterns of *P. armatus* populations from Costa Rica (Diaz-Ferguson & Vargas Zamora, 2001). In Ilhéus, the abundant rainfall is equally distributed throughout the year (mainly from March to November), thus dry and wet seasons are loosely delimited (Lima et al., 2010).

Miranda & Mantelatto (2009) found no correlation between the occurrence of *P. armatus* and temperature or salinity; these parameters varied little during the study period. However, in our study, the water temperature varied from 31°C (February 2011) to 24°C (June 2012), and this variation was sufficient to influence the density of *P. armatus*. Due to heavy rainfall that occurred before sampling, salinity was very low in March 2011, April 2011, and October 2011, however, it did not influence the density of *P. armatus* in Pontal Bay.

#### Reproductive biology

The size of the smallest ovigerous female is usually used to estimate the smallest size at which individual maturity is reached (Ahmed & Mustaquim, 1974). Considering this



criterion, we reported the second earliest sexual maturity (3.8 mm of CW) among all populations of *P. armatus* studied to date (Oliveira & Masunari, 1995; Miranda & Mantelatto, 2009; Wehrtmann et al., 2012; Pinheiro et al., 2017), except Wassick et al. (2017) that based on logistic regression and 50% ovigerity rates estimated the size at maturity to be 2.4-3.7 mm of CW.

The size of ovigerous females sampled in São Sebastião, Ubatuba and Farol Island ranged from 4.0 to 11.9 mm of CW (Miranda & Mantelatto, 2009), from 5.1 to 10.3 (Pinheiro et al., 2017), and from 4.5 to 12.5 mm of CW (Oliveira & Masunari, 1995), respectively. Miranda & Mantelatto (2010) estimated a size ranging from 3.5 to 4.5 mm for the morphometric maturity of *P. armatus*, and Pinheiro et al. (2017) estimated a size ranging from 7.1 to 8.6 mm for males and 7.6 for females. Our estimate of the average size at the onset of functional maturity was only similar to that reported by Wehrtmann (2012) for a population from Araçá region, São Sebastião, Brazil. However, it is important to note that in that study the size of the smallest ovigerous female was also considered as the size at the onset of maturity.

Wehrtmann et al. (2012) compared the populations of *P. armatus* from southeastern Brazil (São Sebastião) and Costa Rica (Punta Morales, Pacific side). The authors observed that the smallest ovigerous female and the mean size of ovigerous females from Costa Rica were smaller than those from Brazil. This pattern supports the fact that environmental factors, particularly temperature, salinity, food availability, and pollution are responsible for latitudinal variations in some reproductive traits (e.g. size at onset maturity). These different patterns are population responses to different environmental conditions that occur along the geographic distribution of a given species. Higher temperatures at low latitudes stimulate growth and induce early sexual maturation when compared with high latitude regions (Lardies et al., 1998; Wehrtmann et al., 2012). Therefore, females of *P. armatus* from Costa Rica can reproduce earlier than those from São Paulo (Wehrtmann et al., 2012). In the same way, females from Ilhéus also attain smaller sizes and begin to produce embryos earlier than those from São Paulo and Paraná (Miranda & Mantelatto, 2009; Oliveira & Masunari, 1995; Pinheiro et al., 2017).

The continuous reproductive pattern of *P. armatus* from Pontal Bay, Ilhéus corroborates the pattern observed in other populations of the species (Oliveira & Masunari, 1995; Diaz-Ferguson & Vargas-Zamora, 2001; Miranda & Mantelatto, 2009; Pinheiro et al., 2017). Oliveira et al. (2013) observed ovigerous females throughout the year in the Marapanim River, Pará; however, two peaks of abundance were observed, one in June (end of rainy season) and one in August (dry season). On the other hand, a large proportion of ovigerous females were recorded in the

warmer months (June to September) in South Georgia (Hollebone & Hay, 2007). According to Litulo (2005), the presence of ovigerous females throughout the year ensures a constant recruitment of juveniles and a stable population of adults.

The presence of individuals in the smaller size classes over the entire study period indicates a continuous recruitment, as observed by Miranda & Mantelatto (2009) in São Sebastião. On the other hand, Oliveira & Masunari (1995) and Pinheiro et al. (2017) recorded two distinct recruitment periods (one in summer and one in winter) during a one-year study in the Farol Island and Ubatuba, respectively. Hollebone & Hay (2007) recorded recruitment occurring mainly during the warmer months in South Georgia. Finally, earlier recruitment was observed in southern sites compared to northern sites in a 400-kilometer range in the Atlantic waters of the southeastern USA (Wassick et al., 2017).

Species inhabiting low latitude (tropical climate) regions that have less variation in temperature frequently show longer reproductive periods than those inhabiting temperate areas (high latitude) (Lomolino et al., 2010; Wassick et al., 2017). In fact, ovigerous females were absent following the coldest months in South Georgia (Hollebone & Hay, 2007). In addition, other factors such as food availability and the synchrony between sexual maturity, mating, and embryo incubation, play an important role on the reproductive activity of marine crustaceans (Sastry, 1983).

The mean number of embryos (438) of *P. armatus* in Costa Rica (Wehrtmann et al., 2012) and in Ubatuba, São Paulo ( $228 \pm 163$ ) (Pinheiro et al., 2017) was higher than that seen here (145). According to Wehrtmann et al. (2012), *P. armatus* produces more embryos compared to other species of the same genus, due to its small individual embryo volume. Among all species of *Petrolisthes*, only *Petrolisthes tuberculatus* (Guérin, 1835), which is a much larger species, produces more embryos than *P. armatus* (Hernández & Palma, 2003).

The relationship between the carapace length of females and the number of embryos was positively correlated, corroborating the study by Wehrtmann et al. (2012), Pinheiro et al. (2017) and Wassick et al. (2017). Such pattern is also common in other decapods, as mentioned by Lardies & Castilla (2001), Lardies & Wehrtmann (2001) and Pavanelli et al. (2010). However, females of *P. armatus* from Costa Rica produce more embryos than the Brazilian populations. According to Wehrtmann et al. (2012), environmental conditions, such as temperature, food availability, salinity, and pollution, exert a significant influence on the reproduction of different populations of the same species.

#### *Spatial distribution*

Individuals of *P. armatus* were present in all three intertidal

levels, but the higher density was seen in the mid and lower intertidal zones. Organisms that inhabit the intertidal zone may spend more than 50% of their lives in the semi-terrestrial environment, facing prolonged air exposure and high temperatures (Stillman & Somero, 1996). Porcellanids are common in this environment and are physiologically and biochemically adapted to tolerate variations in temperature and salinity, as well as low humidity (Stillman & Somero, 1996; Lagos et al., 2011).

In general, the distribution of organisms along the intertidal is a consequence of the interaction between environmental factors, which are more important in the high intertidal, and biotic factors (e.g. competition and predation), which predominate in the low intertidal (Stillman & Somero, 1996; Stillman, 2002; Lagos et al., 2011). In this context, our results demonstrated that *P. armatus* inhabits preferentially the mid intertidal, and occasionally uses the low intertidal zone. However, individuals seem to avoid the high intertidal, even though the distribution in this zone was not statistically different from the low intertidal zone. The higher number of individuals in the low intertidal suggests that environmental factors, rather than biotic factors, influence the distribution of *P. armatus*. Therefore, *P. armatus* probably has a lower tolerance to the environmental conditions of the high intertidal of Pontal Bay. The small number of individuals found in this zone, particularly when compared to the mid intertidal zone, corroborate this assumption.

By grouping transects into "edge" and "center", our results showed that individuals of *P. armatus* were more abundant in the center, suggesting the occurrence of an edge effect. Transects 1 and 4 were more susceptible to deposition/removal of small rocks due to the increase in river flow during the rainiest periods, as observed during fieldwork. These unstable conditions might explain the lower abundance of individuals in these two transects. On the other hand, inner transects (particularly transect 3) provided more stable conditions for *P. armatus*.

In conclusion, the maximum density of 19.8 ind.m<sup>-2</sup> was much lower than that observed in a non-native area (e.g. United States; Hollebone & Hay, 2007) and similar to those found in other areas of Brazil (e.g. Oliveira et al., 2013). The highest abundance was found in transect 3 in the mid intertidal suggesting zonation and edge effect. The higher density was observed in July 2011, while March 2011 had the lowest density. The unimodal distribution and the presence of ovigerous females throughout the year suggest that the reproductive pattern of the studied population is continuous, similar to other populations of *P. armatus*. The demographic patterns indicated that males achieve significantly larger size than non-ovigerous females. Additionally, the 1:1 sex ratio suggests that the population of *P. armatus* in Pontal Bay is physiologically and

behaviorally adapted to its habitat. Finally, the mean number of embryos (145 ± 121) was lower than in other studies. Although the Pontal Bay is disturbed by anthropogenic effects such as urbanization and sewage discharge (see Souza et al., 2009), the population of *P. armatus* seems to be stable in its natural environment.

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