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ABSTRACT

Petrolisthes armatus (Gibbes, 1850) life history was evaluated based on growth and reproduction. Specimens were captured at Ubatuba (Brazil), identified, sexed and measured: carapace (CL, length; CW, width), larger cheliped propodus (PL, length; PW, width; and PH, height), and 2th and 5th abdominal somite (AW_2 and AW_5, width). Relative growth was studied using CL as independent variable and its relation with other variables (dependents), to estimate puberty size and morphological maturity. Fecundity was represented by number of eggs *vs*. body size CL, with a better fit using a power function. Considering the 257 specimens analyzed, males were larger than females, and the overall sex ratio was 1:1, with some differences among size classes. Maturity (puberty size) was revealed by: $AW_2 \times CL$ (males: 8.6 mm CL; females: 7.6 mm CL); and $AW_5 \times CL$ (7.1 and 7.6 mm CL, respectively). Reproduction was continuous, but more intense in rainy season and recruitment occurring in dry season. Fecundity of this species was 228 ± 163 eggs, with better fit by a power function ($R^2 = 0.72$). Maturity size and growth differed when a pristine area (Ubatuba) was compared with a polluted area (São Sebastião), in the same Brazilian area (São Paulo State).

Introduction

The porcellanid crab *Petrolisthes armatus* (Gibbes, 1850) is one of the most common anomuran crabs along the Western Atlantic coast of the Americas (Werding et al. 2003). Its geographical distribution covers a wide range of latitudes on Western Atlantic (North Carolina, USA to Brazil), Eastern Atlantic (Senegal to Angola, Ascension Island) and Eastern Pacific coast (Gulf of California, USA to Peru) (Melo 1999 and references therein). Due to this wide geographical distribution, *P. armatus* was considered for a long time as a complex of different species (Werding et al. 2003). However, a recent morphological and genetic study demonstrated that there is no evidence of a *P. armatus* species complex along the American coast (Mantelatto et al. 2011). Therefore, the large population of *P. armatus* along the southwestern Atlantic coast should be considered as a metapopulation (i.e. group of spatially separated populations which interact at some level, according to Levins 1969).

Most of the studies about *P. armatus* have been conducted in Brazilian coast allowing a collection of information about different life-history traits of this species. Among them, there are a series of studies covering several aspects of this species such as population structure, sexual maturity, relative growth, sex ratio, breeding cycle, and larval/adult density (see Oliveira & Masunari 1995; Miranda & Mantelatto 2009, 2010; Oliveira et al. 2013), which supported the use of this species as bioindicator of water quality in marine biotopes (Nicol 1932; Caine 1975; Micheletti-Flores & Negreiros-Fransozo 1999). However, features of the life history might change with a wide latitudinal distribution of *P. armatus*, a fact confirmed by other studies on body size (Atkinson & Sibly 1997; Angilletta & Dunham 2003; Hernáez 2014) and reproductive biology (Hernáez 2001, 2014; Defeo & Cardoso 2002; Brante et al. 2004; Rivadeneira et al. 2010).

Like other decapod crustaceans, *P. armatus* has three postembryonic phases (larval, juvenile, and adult) and transitions among them can be identified (Hartnoll 1974, 1978, 1982; Miranda & Mantelatto 2010). Biometry allows the estimation of brachyuran puberty size using some sexual characters, such as chelar propodus and abdominal
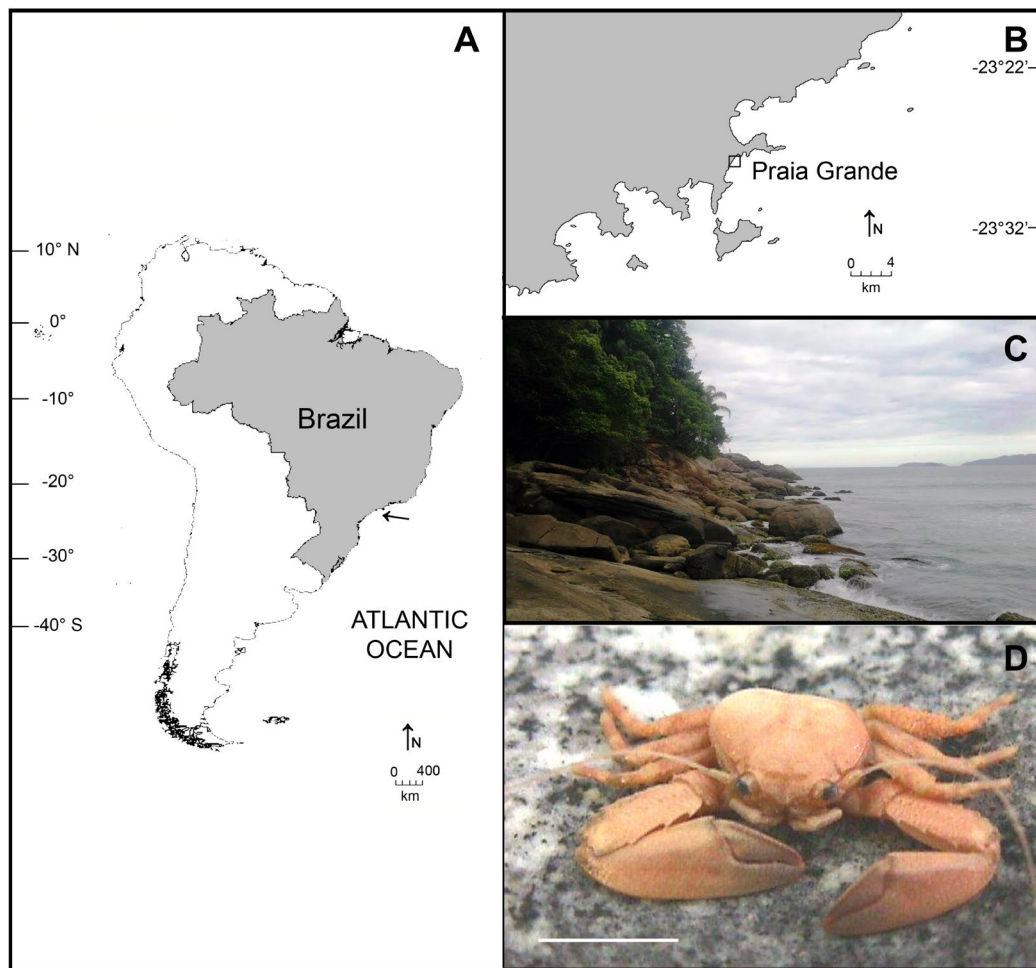
Figure 1. Map of the South America (A), with a geographical detail of the studied area (B); general view of the intertidal north rocky coast of 'Praia Grande' beach (C), Ubatuba, São Paulo State, Brazil; and antero-superior view of an exemplar (male) of *Petrolisthes armatus* (D). (Source: Author).
Note: The size of the scale bar is 10 mm.

segments (Pinheiro & Fransozo 1993). In some crustaceans, these morphological changes are essential to attain sexual maturity (Petriella & Boschi 1997; Souza-Carvalho et al. 2011) and can be revealed by relative growth analysis (Pinheiro & Hattori 2006; Miranda & Mantelatto 2010). In carcinology, this subject is common with species of Brachyuran infraorder (Hartnoll 2001), but a lag is verified with those for Anomuran infraorder, where only a few articles are available about sexual dimorphism (Biagi & Mantelatto 2006; Miranda & Mantelatto 2010; Ferreira 2015).

In this study, we are particularly interested in looking at the population structure, sex ratio as a function of size, relative growth, size at sexual maturity, recruitment intensity, and breeding patterns of *P. armatus* from Northern coast of São Paulo State, Brazil. This kind of information will provide an insight into the life-history traits of this species, comparing our results with those from other porcellanid crabs in order to improve our understanding of population dynamics in marine invertebrates from subtropical regions.

Material and methods

Study area and sampling of crabs

Specimens of *P. armatus* were monthly collected by hand during low tides from August 1996 to July1997 at intertidal zone of Praia Grande beach (23°18′01″S – 45°03′36″W), Ubatuba, Northern coast of São Paulo State, Brazil (Figure 1). Specimens were hand collected under rocks along this rocky coast by three people during one hour. This capture effort (3 h/month) was the same previously tested by Miranda and Mantelatto (2009, 2010) and considered optimum to minimize bias promoted by variability of sampling. This procedure allows different representative sizes of small and adult crabs to be caught in this population.

Animals were carefully rinsed with seawater, placed in a plastic bag and preserved into 70% ethanol until transport to laboratory, where samples were washed with freshwater over a 0.25 mm sieve before sorting. Additionally, we obtained monthly water temperature (WT, ± 0.1 °C) and rainfall (mm) from the dataset of 'Instituto Nacional de Meteorologia' Brazil, while photoperiod data were obtained according to Varejão-Silva and Ceballos (1982), using latitude at the study area (23°18′01″S).

In the laboratory, each crab was identified according to the key for Western Atlantic Porcellanidae of Haig (1956), and the description of *P. armatus* published by Melo (1999). Males have a well-developed gonopods (2th pleomere) and gonopores at the coxae of the 5th pair of pereopods, while females have three paired setose pleopods (3–5th pleomeres) and gonopores at the base of the 3rd pair of pereopods (Osawa & Mclaughlin 2010). Measurements were taken from all collected crabs under a stereomicroscope (Zeiss®Stemi® SV-6): carapace length (CL, from rostrum tip to the posterior margin of the carapace); carapace width (CW, the widest measure between the lateral margins of the carapace); length, width, and height of the largest propodus (PL, PW, and PH, respectively); and width of the second (WA_2) and fifth (WA_5) abdominal somites. Lastly, each female crab was classified according to the presence or absence of embryos carried beneath the pleon (brooding or non-brooding, respectively).

Sexual dimorphism, population structure, and sex ratio

Sexual dimorphism in *P. armatus* was checked by comparison of the average CL between each sex using a *t*-test or Mann–Whitney (*U*), according to homo or heterogeneity, of the variances respectively (Zar 2010). To examine the overall size frequency distribution of *P. armatus*, a size–frequency histograms of the CL was constructed to each sex with 1 mm size classes, with inclusion of brooding females frequency. The normal component of each sex was separated by Bhattacharya method and confirmed by *NormSep* routine (see *FiSAT* software – Gayanilo et al. 1996), with identification of each modal component and mean to each cohort.

Sex ratio along ontogeny was analyzed for *P. armatus* to verify the ratio between sexes and compare with natural ratio (1:1), as a function of size using the patterns proposed by Wenner (1972). For this purpose, sex ratio was estimated as the number of males divided by the total number of individuals in each size class (1 mm) and tested for deviations from an expected 1:1 sex ratio using a binomial test (Wilson & Hardy 2002).

Relative growth and sexual maturity

In Anomuran crabs (Porcellanidae), one of the most noticeable characters is the strong tendency toward asymmetry (e.g. chelipeds in males and pleomeres, in females) (McLaughlin 1980). Each dependent body variable (CW, carapace width; PL, PW, and PH, chelar propodus length, width, and height, respectively; and $AW_2 – AW_5$, abdominal width of the second and fifth somite, also respectively) was related to body size as an independent variable CL. Empirical points were fitted by a power function $Y = aX^b$ (Hartnoll 1978, 1982) using the coefficient of determination (R^2, $p < 0.05$), and the allometric growth was established by constant 'b' (see Somerton 1980). Data were also submitted to the same procedures indicated by Somerton (1980) and Somerton and Macintosh (1983), to identify the size at maturity. The 'segmented' package of '*R*' software – Version 2.5.0 (Ihaka & Gentleman 1996) was used to identify possible break point(s) during ontogeny (puberty size), in males and females, revealing the morphological dimorphism between the developmental stages (juvenile and adult). In each case, the allometric growth rate ('b') was established as isometric ($b = 1$), positive allometric ($b > 1$) or negative allometric ($b < 1$), using a *t*-test to verify a possible difference of *b*-value from the unit ($\alpha = 0.01$). To confirm one or two regression lines for empirical point of each regression analysis, we used a Snedecor's *F*-test ($\alpha = 0.01$) (Sokal & Rohlf 1995), as recommended by Pinheiro and Fransozo (1993). Crabs with missing claws or limbs were excluded from the allometric analyses.

Dynamics of reproduction and recruitment

According to Alvares et al. (2013), South and Southeast Brazilian regions have two well-defined climatic seasons: a dry season (May to October) and a rainy season (November to April). This criterion was used to evaluate possible differences in relation to body size, reproductive activity and intensity of recruitment for *P. armatus*. The proportion of brooding females was estimated as the number of females carrying eggs relative to the total number of females for each season (i.e. excluding juvenile females). Recruitment intensity was described by the presence of small individuals below 5 mm CL (=5th percentile) obtained from the size-frequency histogram of the total crabs collected during the study period (Hernáez & Wehrtmann 2007). We compared the proportion of ovigerous females and recruits among periods using chi-square test and Marascuilo procedure ($\alpha = 0.05$), verifying possible contrasts between and within multinomial proportions (Marascuilo & McSweeney 1977).

Influence of environmental parameters on reproduction

To evaluate the importance of each environmental parameter (water temperature, rainfall, photoperiod and season) on breeding pattern and intensity of recruitment of *P. armatus* (as informed by Sastry 1983), a stepwise multiple regression analysis was used. Regression analysis was implemented with monthly values of each numeric variable. The parameters of the model (β_0: constant, β_1: water temperature, β_2: rainfall, β_3: photoperiod, β_4: season) were obtained through the least square method (Zar 2010). Non-significant predictor variables were removed from the final model. The different assumptions of the multiple regression (i.e. normality of the dependent variable, linearity of predictor variables, homoscedasticity, and independence of residuals) were previously tested before running the analysis.

Fecundity vs. body size

A total of 83 ovigerous females were used to estimate fecundity in *P. armatus*. For this purpose, egg mass was gently detached with forceps from the pleopods of each ovigerous female, embryonic phase established according Hattori and Pinheiro (2001), and the total egg number (EN) of ovigerous females with initial embryonic stages registered in a manual counter under the stereomicroscope (*Zeiss® Stemi® SV-6*). Fecundity was obtained through the relationship of the number of egg (NE) *vs.* CL, with previous outliers removal by Studentized residuals' method. The scatter data were subjected to regression analyses using a power function $Y = aX^b$ (Hartnoll 1978, 1982), which has been previously used in other porcellanid crab species (e.g. Hattori & Pinheiro 2001; Hernáez & Palma 2003). The *b*-value of the *EN*x*CL* relationship was categorized as isometric ($b = 3$), positive allometric ($b > 3$), or negative allometric ($b < 3$) (Somers 1991). Lastly, departures from isometry were tested using independent Student's *t*-tests (Zar 2010).

Results

Sexual dimorphism, population structure, and sex ratio

During this study, 257 specimens of *P. armatus* were captured, comprising 118 males (45.9%) and 139 females (54.1%), including 83 egg-bearing females. The body size CL of males varied between 4.0 and 14.1 mm (mean ± SD, 8.7 ± 2.4 mm), while for females varied between 4.4 and 10.3 mm (7.8 ± 1.39 mm). Ovigerous females ranged from 5.1 to 10.3 mm CL (8.1 ± 1.2 mm). Males were significantly larger than females ($U = 10,354.5$, $p = 0.001$).
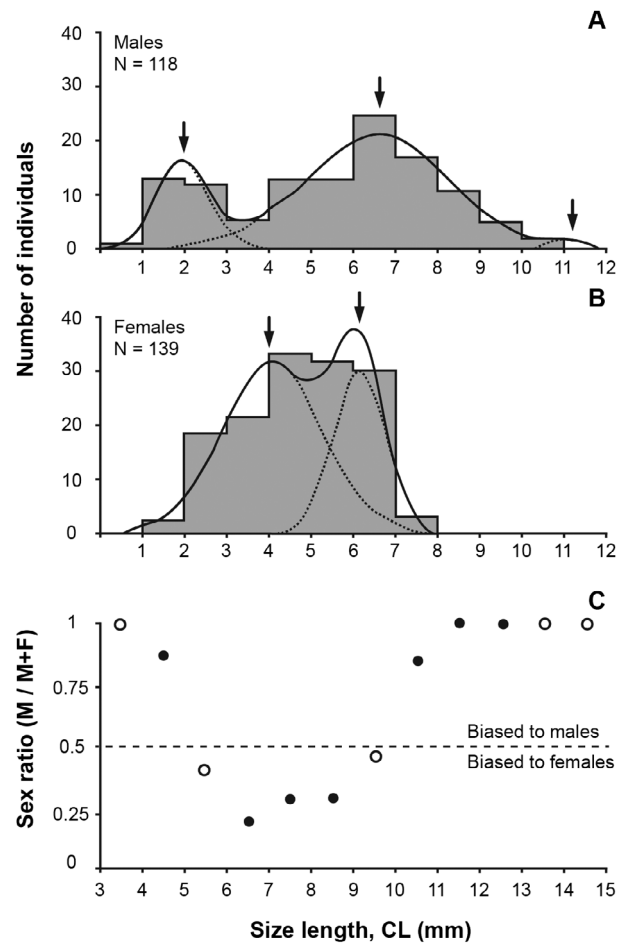

Figure 2. Size-frequency distribution of each sex of *Petrolisthes armatus* (A, males; and B, females); and sex ratio as a function of size (C) at 'Praia Grande, Ubatuba, São Paulo State, Brazil.
Note: Sample size and average (± standard deviation) of the body size (CL) to each population category (males, females without eggs and ovigerous females).

The size structure was asymmetric for both sexes, biased toward smaller individuals in males and females (average << median). Modal progression analysis revealed the presence of three cohorts in males and two cohorts in females (Figure 2A, B).

Overall sex ratio did not differ significantly from 1:1 in the population of *P. armatus*, with a sex ratio proportion of 0.459 ($\chi^2 = 1.72$, $p > 0.05$). Males were more abundant than females in size class smaller than 5.0 mm CL (14 males and 2 females), and between 10.1 and 15.0 mm CL, with a sex ratio biased toward females between 5.1 and 10.0 mm CL (Figure 2C).

Relative growth and sexual maturity

All relationships have significant positive correlation ($p < 0.001$; Table 1) between the variables. No discernible *b*-value change was confirmed when CW and propodus dimensions (PL, PW, and PH) were related to

Table 1. Relative growth in *Petrolisthes armatus* with reference to regression equations, their coefficients of determination (R^2), test to confirmation of one/two line regressions (*F* Snedecor), and test to confirm allometric level (*t*-test), categorizing isometry (0), negative allometry (−) and positive allometry (+). Relationships were based on biometric variables of carapace (CL, length; CW, width), major chelar propodus (PL, length; PW, width; and PH, height) and abdominal width (AW_2, second somite; and AW_5, fifth somite).

Dependent variable	Sex	Stage	N	Equation ($Y = aX^b$)	R^2	F Snedecor	t-test	Allometric level
CW	Male	Total	117	$CW = 0.905\ CL^{1.01}$	0.99*	5.40ns	1.15ns	0
	Female	Total	136	$CW = 0.845\ CL^{1.06}$	0.98*	8.05ns	4.54*	+
PL	Male	Total	94	$PL = 0.798\ CL^{1.31}$	0.98*	9.85ns	14.30*	+
	Female	Total	110	$PL = 0.963\ CL^{1.19}$	0.94*	6.45ns	7.08*	+
PW	Male	Total	95	$PW = 0.153\ CL^{1.29}$	0.95*	7.40ns	12.50*	+
	Female	Total	106	$PW = 0.192\ CL^{1.14}$	0.88*	8.00ns	6.53*	+
PH	Male	Total	94	$PH = 0.242\ CL^{1.41}$	0.90*	9.90ns	6.55*	+
	Female	Total	112	$PH = 0.298\ CL^{1.30}$	0.76*	8.05ns	2.27*	+
AW_2	Male	Juvenile	48	$AW_2 = 0.664\ CL^{1.00}$	0.95*	8.60*	0.01ns	0
		Adult	69	$AW_2 = 0.866\ CL^{0.88}$	0.92*		3.94*	−
	Female	Juvenile	54	$AW_2 = 0.482\ CL^{1.23}$	0.86*	7.60*	3.34*	+
		Adult	84	$AW_2 = 0.860\ CL^{0.95}$	0.68*		0.72ns	0
AW_5	Male	Juvenile	29	$AW_5 = 0.681\ CL^{1.01}$	0.91*	7.10*	0.20ns	0
		Adult	88	$AW_5 = 0.861\ CL^{0.90}$	0.94*		4.31*	−
	Female	Juvenile	52	$AW_5 = 0.467\ CL^{1.29}$	0.86*	7.55*	3.83*	+
		Adult	85	$AW_5 = 0.888\ CL^{0.97}$	0.68*		0.40ns	0

*$p < 0.05$; ns$p > 0.05$.

the independent variable CL for both sex of *P. armatus* (Snedecor test). In contrast, the equations involving abdominal variables (AW_2 and AW_5) *vs.* CL showed differences in *b*-value along the ontogeny of males and females.

The pattern of relative growth to *CWxCL* relationship differed between sexes, with males presenting an isometric growth ($b = 1.01$, $p > 0.05$), while a positive allometry was confirmed for females ($b = 1.06$, $p < 0.05$). All relationships involving measurements of the chelar propodus (PL, PW, and PH) in relation to body size CL, indicated a positive allometry ($p < 0.001$) for both sexes, with a higher degree in males ($1.29 < b < 1.41$) when compared with females ($1.14 < b < 1.30$), but not confirmed during ontogeny of each sex. Otherwise, relationships involving abdominal variables by CL ($AW_2 \times CL$ and $AW_5 \times CL$) revealed an allometric degree change during ontogeny, confirming two phase lines (jv, juvenile; and ad, adult). Both sex showed a reduction of allometric degree between these phases, less pronounced in males ($b_{jv} - b_{ad} = 0.11–0.12$) than females ($b_{jv} - b_{ad} = 0.28–0.32$), but with a change of relative growth from positive allometry to isometry in females (Figure 3, right panel) and isometry to negative allometry in males (Figure 3, left panel). Puberty size in females was 7.6 mm CL for both relationships involving abdominal variables, but in males, the puberty was detected between 7.1 mm CL (AW_5) and 8.6 mm CL (AW_2). Considering the best estimate of size at sexual maturity in males and females, the population of *P. armatus* consisted mainly of adults (60%), with a minor frequency of juveniles (i.e. including recruits) in the overall sample.

Dynamics of reproduction and recruitment

Males were significantly larger than females ($U = 3927.50$, $p = 0.0001$) during rainy season but no during dry season ($U = 1524.0$, $p = 0.808$; Figure 4A). Egg-bearing female of *P. armatus* were found almost continuously throughout the year ($N = 83$); however, a significantly higher number of ovigerous females ($p < 0.001$) were found during rainy season (76%) compared to dry season (34%, Figure 4B). Recruitment intensity showed an inverse seasonal pattern, significantly higher during dry season (14%) than during rainy season (1%) (Figure 4C).

Influence of environmental parameters on reproduction

During dry season, water temperature ranged from 24.1 ± 3.0 to 25.9 ± 2.53 °C, with rainfall varied between 5 and 58 mm, and photoperiod between 10.58 ± 0.03 and 12.58 ± 0.20 h. On the other hand, the variation of these parameters during rainy season ranged from 26.1 ± 3.4 to 30.6 ± 1.9 °C, 74–172 mm, and 11.44 ± 0.19–13.42 ± 0.03 h, respectively (Table 2). Contribution of the parameters 'rainfall' and 'season' on breeding pattern of *P. armatus* was not significant (multiple regression stepwise: rainfall: $t = -1.44$, $p = 0.210$; season: $t = -2.39$, $p = 0.062$); thus, both variables were removed from the final model. The resulting model explained 77.9% of the variability observed, showing a significant relationship between ovigerous females and the temperature/photoperiod (ANOVA test: $F = 12.36$, df = 9, $p = 0.005$). Temperature and photoperiod were related, respectively, in a direct and inverse way to the occurrence of breeding females of *P. armatus*. Indeed, the slopes of these parameters in the resulting multiple regression model showed positive and negative values, respectively (Slopes, temperature: 3.02, photoperiod: −3.69). By contrast, recruitment intensity was not correlated with environmental parameters, accounting for less than 30% of the observed variation in recruits (ANOVA: $F = 0.54$, df = 9, $p = 0.713$).
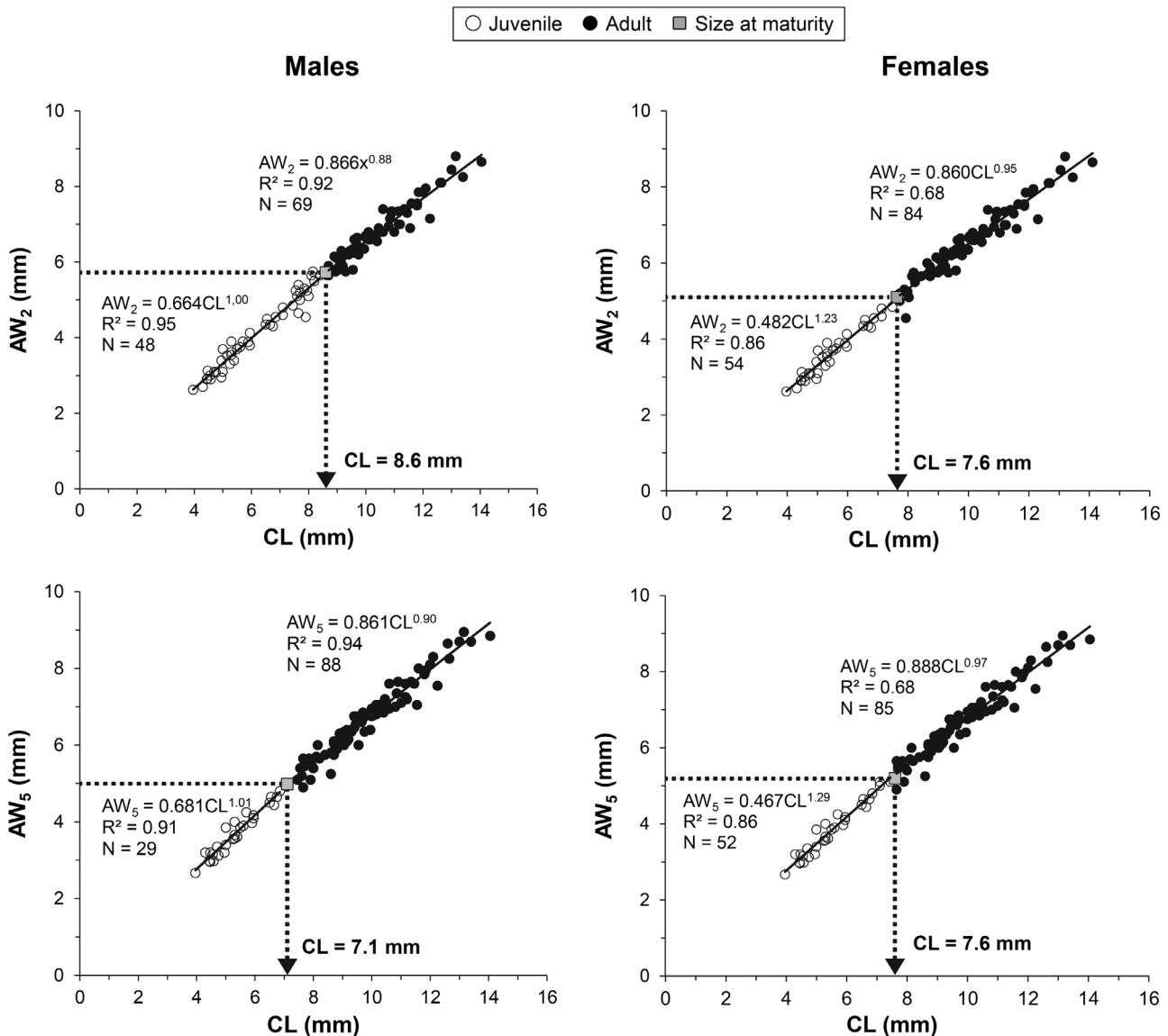
Figure 3. Relationships involving abdominal width (AW2, 2nd segment; and AW5, 5th segment) *vs.* carapace length (CL), in males and females of *Petrolisthes armatus*, and respective equations to each development phase (juvenile and adult), with indicative of the size at morphological maturity.

Fecundity

Fecundity was analyzed for 66 females with eggs in initial embryonic phase out of the 83 ovigerous females collected. In these females, fecundity ranged between 24 and 654 eggs (228 ± 163 eggs). A positive correlation was statistically confirmed between NE and CL in females of *P. armatus* (Pearson correlation: $r = 0.85$, $p = 0.0001$). Indeed, the relationship of $NE \times CL$ gave a good fit to empirical points ($R^2 = 0.72$) in a representative mathematical equation to be used in the conversion between these variables. The slope (*b*) of this relationship was significantly different from three ($t = 12.78$, $p = 0.0001$), which means that fecundity was positive allometric (Figure 5).

Discussion

Ubatuba has been frequently used as natural scenery to study of a series of marine decapod populations from the coast of Brazil (e.g. Pinheiro & Fransozo 1993, 1998, 2002; Bertini & Fransozo 1999; Mantelatto & Martinelli 2001), due to be considered yet an example of a pristine natural area (Mantelatto & Fransozo 2000). Here, we present the first information about the life-history traits of *P. armatus* in Ubatuba Municipality. These results were compared to those obtained from other populations of porcellanid crabs of the South American coast (e.g. Lardies & Wehrtmann 1996; Hattori & Pinheiro 2001; Hernáez 2001; Hernáez & Palma 2003), including other populations of the large

Figure 5. Fecundity relationship involving number of eggs (NE) *vs.* carapace length (CL), of the porcelain crab *Petrolisthes armatus* at Praia Grande, São Paulo State, Brazil.

metapopulation of *P. armatus* along the Brazilian coast, where information about population traits is available (e.g. Miranda & Mantelatto 2009).

Analysis of population structure of *P. armatus* at Ubatuba identifies three and two cohorts for males and females, respectively. This result partially coincides with the bimodal distribution reported by Miranda and Mantelatto (2009) for a population of this species from São Sebastião, about to 80 km at north from Ubatuba. In Ubatuba, *P. armatus* exhibited an unbiased sex ratio, without statistical difference between frequency of males and females in overall sample. This result agrees with the expected pattern under Fisher's theory where natural selection favors an equal frequency of males and females (Fisher 1930). Also, our finding is in agreement with another populations of *P. armatus* from the Brazilian coast where sex ratio did not differ from the expected 1:1 (Oliveira & Masunari 1995; Miranda & Mantelatto 2009). Analysis of sex ratio as a function of size indicated that males outnumber females in the two size classes below 5 mm (14 and 2, respectively). Considering that natural selection favors a 1:1 parental expenditure on offspring of the two sexes (Fisher 1930), our results suggest the possible existence of a differential mortality and/or a differential growth rate between sexes during the early benthic stage in *P. armatus*. According to Wenner (1972), a high mortality rate may affect selectively smaller females, but not males, due to different capabilities to escape, or the females could grow more quickly than males at that size, thus reducing the likelihood of being recorded during processing of the specimens. We assume that the absence of females in smaller size classes is due to natural selection against females during the early benthic stages of *P. armatus*. This assumption is supported by the findings reported by Oliveira and Masunari (1995), where they found a high frequency of males below 5 mm with a sex ratio biased
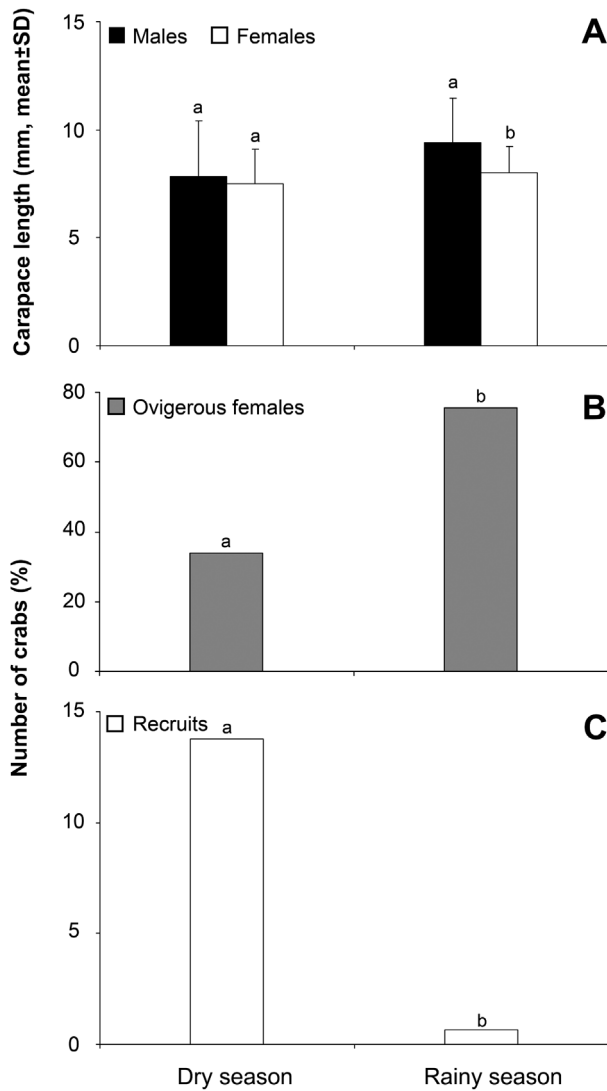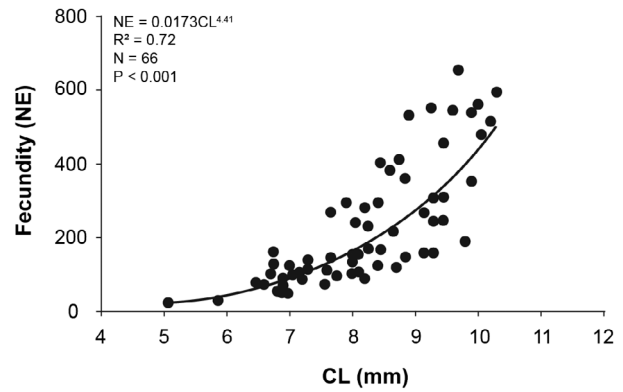

Figure 4. Size of each sex (A), percentage of ovigerous females (B) and recruits (C) in each climatic season (dry: May to October; and rainy: November to April), of the porcelain crab *Petrolisthes armatus* at Praia Grande, São Paulo State, Brazil.

Table 2. Mean values of water temperature, rainfall, and photoperiod in at intertidal zone of Praia Grande, Ubatuba region (SP), Brazil. Values summarize readings obtained from August/l996 to July/1997.

Month/Year	Temperature (°C)	Rainfall (mm)	Photoperiod (h)	Season
August/1996	24.1	5	11.21	Dry
September	25.9	39	11.88	Dry
October	25.8	31	12.58	Dry
November	26.1	74	13.15	Rainy
December	28.3	117	13.42	Rainy
January/1997	27.8	172	13.27	Rainy
February	30.2	120	12.79	Rainy
March	30.6	122	12.14	Rainy
April	28.5	110	11.44	Rainy
May	24.8	33	10.86	Dry
June	24.8	58	10.58	Dry
July	23.5	41	10.71	Dry

toward males for smaller sizes. Also, the present study revealed a prevalence of males in higher size classes than females (14.1 and 10.3 mm CL, respectively). Summarizing, the sex ratio as a function of body size, with the prevalence of males in smaller and higher size classes, and the high proportion of females at intermediate size classes (5.1–10.0 mm CL), followed the Standard pattern (see Wenner 1972), corroborating results previously obtained by Miranda and Mantelatto (2009) for this species.

Hartnoll (1974, 1978, 1982, and 2001) was a pioneer in studies about the relative growth of brachyuran crabs. Patterns revealed by this author have been used as basal information and compared with a few studies available on relative growth for anomurans (Biagi & Mantelatto 2006; Bueno & Shimizu 2009; Hermoso-Salazar & Sanvicente-Añorve 2011; Ríos-Elósegui & Hendrickx 2015), where porcellanid crabs remain as a non representative group, due to their reduced size and minor economic importance. This fact prevents more effective comparisons, particularly for the Porcellanidae family, the same occurring with other populations in relation to reproductive parameters, all useful for conservation purposes.

According to Miranda and Mantelatto (2010), anomurans have a high diversity of relative growth patterns among crustaceans, even when considering the scarce number of studies on Anomura. It is important to highlight that *P. armatus* was previously studied by these authors in other areas of São Paulo State, with divergent points verified between these populations. A common pattern informed by Richard Hartnoll in brachyuran males is a higher propodus chelar size in adults in relation to body size, generally representing a expressive growth rate during ontogeny, which can be used to estimate the size at onset of morphological maturity (Pinheiro & Fransozo 1998). But this fact was not confirmed in males of *P. armatus*, where all measures registered in the chelar segment (PL, PH, and PW) showed a large positive allometry ($1.29 \leq b \leq 1.41$) in relation to body size, but without changes during ontogeny and represented by only one equation to this sex in each chelar biometric relationship. However, a higher allometric growth constant in these chelar propodus variables was registered by Miranda and Mantelatto (2010) in males, revealing a larger size for these appendages. This same growth pattern was reported for other anomuran hermit crabs belonging to Diogenidae (e.g. *Petrochirus diogenes* by Bertini & Fransozo 1999; and *Loxopagurus loxochelis* by Mantelatto & Martinelli 2001). The chelipeds in males of infraorder Brachyura are morphological adaptations to select mates and to manipulate female during copulation (Pinheiro & Fransozo 1993, 1999). The same occurs with crustaceans of the infraorder Anomura, where larger chelipeds are useful during antagonistic interactions with other males, as reported by Turra (2005) for hermit crab *Pagurus criniticornis* (Paguridae), and for the porcellanid

crab *Petrolisthes spinifrons*, according to Baeza and Asorey (2012).

Both relationships of abdominal width (AW_2 and AW_5) present a marked reduction of allometric growth rate, regardless of sex, but with a divergent pattern in males (isometry to negative allometry) when compared to females (positive allometry to isometry). The allometric reduction in porcelain crabs occurs because the abdomen is used for swimming during the juvenile phase, while adults are benthic, living in cavities under rocks, as well as inside galleries found in sandy reefs of sabellariid polychaetes. In addition, the abdomen in anomuran crabs is used similarly as in brachyuran crabs: to fix and protect pleopods (males) or egg mass (females) (Pinheiro & Fransozo 1993). In males, the morphological maturity size based on abdomen variables occurred between 7.1 and 8.6 mm CL, due to the presence of one pleopod pair in the second somite (AW_2) and the absence of pleopods attached to the fifth somite (AW_5), respectively. According, we can indicate 7.1 mm CL as the most reliable measure to represent maturity size in males due to an integrative growth between AW_2 and gonopods in this sex. Therefore, future studies focusing on gonopod measure as a function of size CL could be used to estimate sexual maturity. Otherwise, morphological maturity in females occurred at 7.6 mm CL was very similar to puberty size of males (7.1 mm CL), while ovigerous females started at 5.1 mm CL, indicating a smaller physiological maturity size. A literature review indicates 15.1 mm CL as the maximum body size reached by *P. armatus*, corresponding to 47.0–50.3% of the estimated morphological maturity size obtained in present study. In addition, the present study confirms a similar variation of body size CL for each sex, when compared to values obtained by Miranda and Mantelatto (2010), also representing well the individuals in each size class. However, these authors indicated that chelar propodus relationships could reveal allometric growth changes during ontogeny, a fact not confirmed in the present study, where the same statistical protocol was used to estimate morphological maturity, using three chelar propodus variables (PL, PH, and PW). Furthermore, Miranda and Mantelatto (2010) used CW as independent variable, and the estimated puberty sizes were lower (males: 3.5 mm CW; females: 4.5 mm CW), corresponding to 23.2 and 29.8% of the maximum size in this species, respectively.

P. armatus at Praia Grande (Ubatuba) showed a year-round reproduction with ovigerous females collected throughout the entire study period. Reproductive activity in this species is mainly related to temperature oscillations which is in agreement with the reproductive pattern reported for organisms from tropical to subtropical regions where elevated seawater temperatures favor a continuous gonadal development and embryo production (Sastry 1983; Hartnoll & Gould 1988; Bauer 1989; Costa & Fransozo

2004; Vergamini & Mantelatto 2008; Hernáez et al. 2012; Silva et al. 2016).

Our data also match with the continuous reproductive pattern reported for other populations of *P. armatus* distributed along the Southeast Brazilian coast (Farol Island, Paraná 25°51′S, 48°32′W: Oliveira & Masunari 1995; São Vicente, São Paulo 23°59′S, 46°22′W: Micheletti-Flores & Negreiros-Fransozo 1999; Araçá, São Paulo 23°48′S, 45°24′W: Miranda & Mantelatto 2009), thus revealing the establishment of a common reproductive pattern for all populations of this species in the Brazilian coast. Similarly, our work on breeding periodicity for *P. armatus* follows the reproductive pattern reported in most of the intertidal porcellanid crabs in which the general trend is to breed continuously throughout the year (*Petrolisthes politus*: Scelzo 1985; *P. cinctipes*: Boolootian et al. 1959; *P. elongates*: Jones 1977; *Porcellana sayana*: Meireles 2006).

Even though reproduction was continuous, proportion of brooding females in *P. armatus* were especially high during the rainy season, when temperature, rainfall and photoperiod were greater than dry season. Conversely, recruitment was almost inexistent during rainy season but extremely intense during dry season or when was recorded a notorious diminishing in these environmental parameters. According to information published in literature, this increment allow to initiate/intensify reproductive processes in coastal species of decapods (Hartnoll & Gould 1988; Varadharajan et al. 2013), including an elevation of primary productivity induced by the increment of daylight period and the increasing in water discharge provoked by the intense rainfall. Therefore, in accordance with the previous information, the reproductive activity in *P. armatus* would be mainly induced by the increase of the seawater temperature, rainfall and photoperiod, which also favors the embryos incubation and the subsequent larval releasing in this species.

On the other hand, as has already been mentioned, the recruitment in *P. armatus* would be occurring during the reduction of seawater temperature, rainfall and photoperiod at Ubatuba. According to Gore (1970), *P. armatus* completes their larval development in about to 15–18 days at 28 °C, which in accordance with our information on the presence of brooding females, should reflect in a continuous recruitment pattern for this species in this place. However, our data indicated that recruitment in *P. armatus* is strongly seasonal. Unfortunately, our observations do not allow further conclusions about the environmental cues involved in the recruitment pattern of *P. armatus* at Ubatuba. We argue in favors of additional long-term studies in this species to reveal the environmental factors that induce to the recruitment in *P. armatus*.

Concentration of pollutant can vary according to season, with a reduction of lixiviation of pollutants from terrestrial areas to river, estuaries and to ocean, mainly during the dry season (Islam et al. 2015). The historical anthropogenic region of São Sebastião (SP) can explain the absence of recruits during dry season, as reported by Miranda and Mantelatto (2009), possibly due to a higher concentration of organic pollutants and other xenobiotics commonly used in oil tanks and found in that region. However, in Ubatuba SP, the population of *P. armatus* lives in a pristine habitat, without anthropic activity. Pollutants can affect negatively growth and reproduction of crustaceans, including alteration of sex ratio by organic pollutants, producing abnormal secondary sexual characters in these animals (see review by Rodríguez et al. 2007). The influence of pollutants can explain the size at maturity and modal growth differences verified in this study, when compared with those obtained in polluted area by Miranda and Mantelatto (2009). An increase in fecundity related to female size is a pattern among decapod crustaceans, but in equatorial regions (e.g. Pacific Costa Rica), *P. armatus* can produce three times more eggs when compared to equally sized females from Southern Brazil (Wehrtmann et al. 2012). In respect to production of eggs, *P. armatus* had a high variation of the fecundity since 7.5 mm CL, coincident to maturity size in females, possibly related to primiparous or multiparous females during the studied period. Population biology can reveal interesting information, involving complex responses, which many times are difficult to quantify. In this respect, Ford et al. (2003) conducted studies in the laboratory and in the field, showing that fecundity/fertility can be affected by a variety of different contaminants. This effect was not tested in the present study but indicates other variation source that affects biologic parameters such as metabolic rate, growth and reproduction, need to be evaluated when possible. In this fact, Ubatuba is a Brazilian coastal region where environmental quality is maintained yet, assuring basal characteristics to better population development.

Disclosure statement

No potential conflict of interest was reported by the authors.

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