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## Biological aspects of the marine crab *Plagusia depressa* (Fabricius, 1775) on the northeast coast of Brazil

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### ABSTRACT

The marine crab *Plagusia depressa*, despite its broad geographic range, is not well known. Here, we attempt to fill this gap by studying several aspects of its biology. We sampled *P. depressa* in the reefs of Coruripe, Brazil and investigated the sex ratio, body size, maturity, the allometric growth of the gonopod in males and of the abdomen in females, the reproductive effort, the breeding season and the influence of environmental variables. We found that 1) the sex ratio, overall, does not deviate from 1:1; 2) females (33.71±10.62 mm) are larger than males (30.45±9.94 mm;  $t_{1,764} = -4.40$ ,  $p < 0.001$ ); 3) males (23.42±0.24 mm) mature at smaller sizes than females (26.78±0.19 mm); 4) the growth of the gonopod is positive allometric in juveniles (slope = 1.66±0.04), but negative allometric in adolescents (0.93±0.02) and adults (slope = 0.86±0.03). In females, the abdomen undergoes a positive allometry in juveniles (slope = 1.74±0.04) and adolescents (slope = 1.97±0.09), but an isometric growth in adults (slope = 0.99±0.04); 5) the breeding period is continuous and not influenced by rainfall, water temperature and salinity; 6) egg mass strongly increases with body mass (slope = 1.56,  $R^2 = 0.84$ ,  $p < 0.001$ ).

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## Introduction

Crustaceans have long been known for their extremely high diversity and diversified morphology, life-history, and habitats that they occupy (Melo 1996; Ng et al. 2008; Grave et al. 2009). Brachyuran crabs contribute a great deal to this diversity as they comprise 5000 species inhabiting terrestrial, freshwater, intertidal, and marine environments (Melo 1996; Grave et al. 2009). However, the general biology of many brachyuran species remains unknown. Here, we attempt to partially fill this gap by investigating several biological aspects of the understudied marine crab *Plagusia depressa* (Fabricius, 1775).

Biological aspects play a ubiquitous role in the population dynamics of a species. Such aspects represent a set of adapted traits that co-evolved to maximize offspring survival and, therefore, maximize the fitness of individuals in their local habitats (Stearns 1976). This is mostly shaped by how natural populations respond to local environmental conditions (Sastry 1983; Lardies et al. 2010; Lira et al. 2015). However, severe disturbances might undermine the

ability of species to survive and reproduce, which can ultimately lead to species loss. Therefore, efforts to improve our knowledge on the biology of species are critical to our comprehension of how they can cope with such disturbances.

In this context, we believe that *P. depressa* is a species of particular relevance due to its grazing and predation activity, and so is likely to have a pronounced effect in the structure of ecological communities (Webb and Eyre 2004; Alberti et al. 2007; Angelini et al. 2018; White et al. 2018). Second, coastal ecosystems are extremely sensitive to environmental change. With the increasing effects of climate change, these environments will most likely suffer unprecedented and irreversible changes in their structure (Glibert et al. 2014; Spalding et al. 2014), directly affecting crabs inhabiting these areas. Third, the biological aspects of a species are important information for its sustainable management, which is especially important for *P. depressa* as it is commonly used as a food source by fishing communities along the coast of Brazil (Coelho et al. 2004; Freitas and Santos 2007).

*Plagusia depressa* (Brachyura: Plagusiidae) is a marine decapod with a broad geographic distribution, occurring in the Western Atlantic, from South Carolina in the United States to the south of Bahia State, Brazil, and in the Eastern Atlantic, in the Azores archipelago and from Senegal to Angola (Melo 1996). This species can be found in crevices of rocks, shallow subtidal zones, and coral reefs in intertidal zones (Melo 1996). Despite its wide geographic distribution, studies on the biology of *P. depressa* are limited to a few studies encompassing its feeding habits (Hartnoll 1965), swimming ability and morphology (Hartnoll 1971), larval development (Wilson and Gore 1980; Schubart et al. 2001), growth (Coelho et al. 2004), and population biology (Freitas and Santos 2002, 2007).

With these aspects in mind, we here studied multiple biological traits of the tropical marine crab *P. depressa* on the northeastern coast of Brazil. Specifically, we assessed the body size in males and females, the sex ratio, the sexual maturity, the breeding season, the reproductive effort, and the allometric growth of body traits related to reproduction, i.e. the gonopod, the copulatory organ of males, and the abdomen in females, which function as an incubatory chamber for the eggs. Moreover, we evaluated whether environmental factors play a role in the reproductive period of this species.

## Material and methods

### Area of study, field sampling, and laboratory procedures

The area of study is located at Coruripe, Alagoas, Brazil (Figure 1), a region characterized by its extensive limestone reefs. The climate in this area is of type 'As', described as Equatorial Savannah with dry summer – rainfall below 60 mm in the summer (Kottek et al. 2006).

Field collections were conducted from January to December 2011 in seven sites (5–10 metres apart from each other) in the limestone reefs in Coruripe. At night, crabs were manually collected by three people at low tide for two hours. To do so, we used a landing net and flashlights. The light diminishes the vision of the crabs and facilitates their sampling. We then transported all crabs in containers with 70% ethanol to our laboratory, and later cataloged and stored them in the Carcinological collection from the Federal University of Alagoas, Brazil. Moreover, we measured water temperature and salinity and obtained rainfall data from the State Department for the Environment and Water Resources from Alagoas. Temperature was measured with a toluene thermometer during field

sampling, and water samples were transported in a cooler to our laboratory at the Federal University of Alagoas in order to measure the salinity using a refractometer.

In the laboratory, the crabs were sexed based on the shape of the abdomen – which is round in females and triangular in males (Melo 1996) – measured for carapace width, abdomen width (females), and gonopod length (males) with a caliper to the nearest 0.05 mm. Moreover, their wet weight (g) was obtained with a digital scale to the nearest 0.01 g. Crabs with malformed body parts or that have molted recently were not measured to avoid inaccurate measurements. The females incubating eggs were separated from other crabs for subsequent assessment of number and mass of eggs, which was conducted following the procedures adopted by Lira and Calado (2013). Only females incubating eggs in the initial stage of development (i.e. yolk occupying the whole internal volume of the eggs and no evidence of cleavage or cellular differentiation – Brante et al. 2003) were considered for further analysis.

### Statistical analysis

Although we sampled crabs in seven different sites, we pooled the data for our analyzes. We sampled in different sites to merely standardize our sampling and to maximize our chances of obtaining the most representative sample from the local *P. depressa* population; specifically, our intention was (1) to maximize the size range of individuals and ovigerous females and (2) to maximize the number of ovigerous females that were sampled. Most importantly, we adopted this procedure because there are no apparent environmental differences among sites and, therefore, we do not expect any differences among individuals from different sites.

All the statistical analyses were performed in R statistical software (R Development Core Team 2018). To evaluate whether the sex ratio differs from the expected 1:1 ratio, both within months and within sizes classes, we performed a chi-square test ( $\chi^2$ ). To investigate whether the frequency of males and females fluctuate through time, we compared the monthly sex ratios also by implementing a chi-square test, and a post-hoc chi-square test with Bonferroni correction for multiple comparisons using the package *fifer* (Fife 2017). Moreover, we used a two-tailed *t*-test to investigate whether males and females differ in body size.

To test for differences among the monthly proportions of ovigerous females, we also used a chi-



**Figure 1.** Location of the area of study in Alagoas, Brazil.

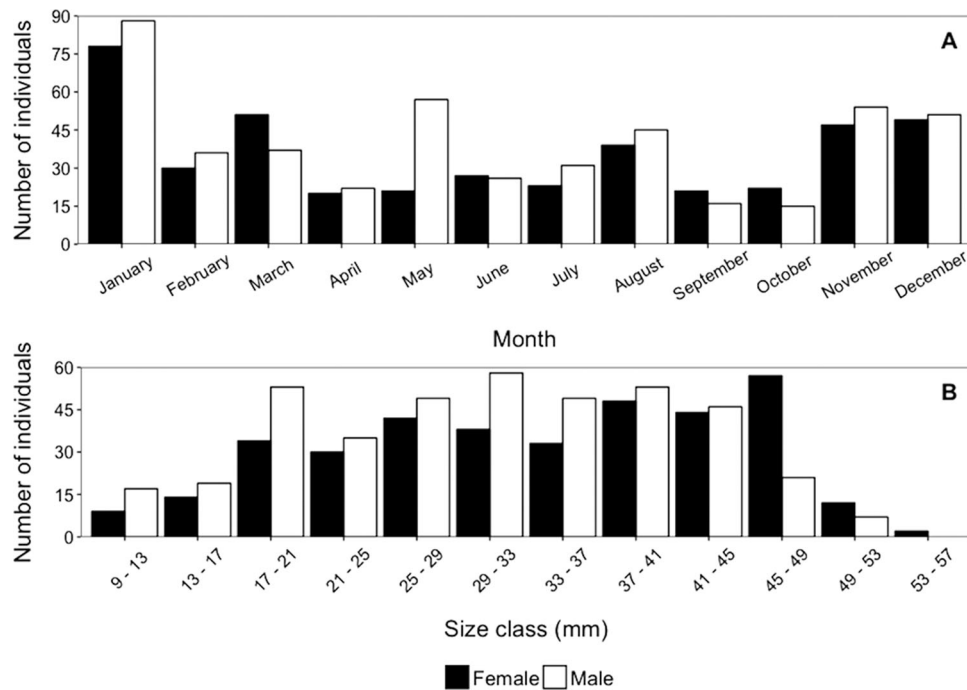
square test and a post-hoc chi-square test with Bonferroni correction. To assess the association between the environmental factors and the breeding activity of *Plagusia depressa*, we applied a Generalized Linear Model (GLM) with binomial error and logit link function for overdispersed data in the R package *dispmod* (Scrucca 2018). The proportion of ovigerous females was used as the response variable and the environmental factors as explanatory variables. In addition, we evaluated the relationship between female body mass and egg mass by implementing a linear regression model.

We also investigated whether *P. depressa* presents different allometric growth patterns during ontogenetic development. Such differences usually occur between immature and mature individuals (Hartnoll 1982) and have been widely used for inferring morphologic sexual maturity in crustaceans (Hartnoll 1982; Fernández-Vergaz et al. 2000). To do so, we first applied a nonhierarchical K-means classification method based on the relationship between gonopod length and abdomen width with body size, for males and females, respectively. In this procedure, individuals are grouped in different clusters such that variation between clusters is maximized but variation within each cluster is minimized (adapted from Sampedro et al. 1999). We then tested the data with two and three pre-assigned number of clusters. For both males and females, the explanatory power of the test was higher for the three-group option, and we thus adopted these three distinct groups for further analysis. Then, we applied a logistic regression followed by a

dose–response test ( $L_{50\%}$  curve) to estimate the size in which 50% of the individuals have transitioned to another stage of development (cluster). Subsequently, we grouped individuals according to the size range of each stage and classified them as either juveniles, adolescents, or adults. We, therefore, assumed that the pattern of allometric growth differs between these stages of development. To evaluate this assumption, we applied an Analysis of Covariance using gonopod length and abdomen width as the response variables, body size as the explanatory variable, and the stage of development as the grouping variable. All data were log-transformed to meet the assumptions of normal distribution and homogenous distribution of residuals. We defined the pattern of allometric growth based on the slope ( $b$ ) of the linear regressions applied to the logs of gonopod length, abdomen width, and body size. This was implemented for each stage of development for both sexes. Specifically, growth is isometric when  $b = 1$ , negative allometric when  $b < 1$ , and positive allometric when  $b > 1$  (Hartnoll 1982, Fernández-Vergaz et al. 2000).

## Results

A total of 403 males and 363 females were collected, resulting in a 1.11:1 unbiased sex ratio. Overall, the sex ratio did not differ from unity within months – except for May ( $\chi^2 = 16.6$ , d.f. = 1,  $p < 0.001$ ; Figure 2a). However, there was a difference in ratios among months ( $\chi^2 = 21.55$ , d.f. = 11,  $p = 0.028$ ), which was driven by the difference between March (0.72:1) and



**Figure 2.** The monthly distribution (a) and the size class distribution (b) of males and females of *Plagusia depressa* from Coruripe, Alagoas, Brazil.

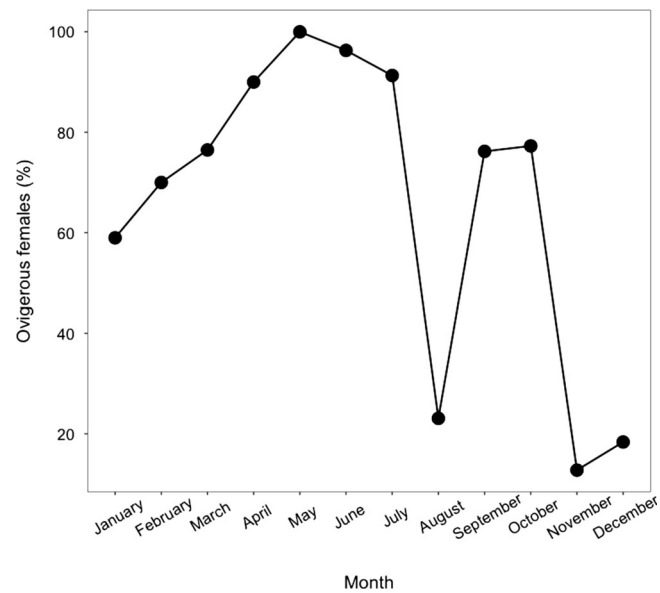
May (2.71:1;  $p = 0.005$ ). Regarding the sex ratio among size classes (Figure 2b), the contrast detected by the chi-square test ( $\chi^2 = 33.4$ , d.f. = 11,  $p < 0.001$ ) was driven by differences among the size class 45 | 49 (0.37:1) and the classes 17 | 21 (1.56:1,  $p = 0.001$ ), 25 | 29 (1.16:1,  $p = 0.035$ ), 29 | 33 (1.52:1,  $p = 0.001$ ), 33 | 37 (1.48:1,  $p = 0.02$ ), and 37 | 41 (1.1:1,  $p = 0.048$ ) – the difference was marginally significant with class 9 | 13 (1.88:1;  $p = 0.052$ ). Within each size class, however, ratios were predominantly unbiased – except for the classes 17 | 21 ( $\chi^2 = 4.15$ ,  $p = 0.04$ ), 29 | 33 ( $\chi^2 = 4.16$ ,  $p = 0.04$ ), and 45 | 49 ( $\chi^2 = 16.6$ ,  $p < 0.001$ ). Moreover, females were larger than males (females =  $33.71 \pm 10.62$  mm, males =  $30.45 \pm 9.94$  mm;  $t_{1,764} = -4.40$ ,  $p < 0.001$ ).

The breeding season was continuous throughout the year, with a peak from April to July (Figure 3). The frequency of ovigerous females from January to July and from September and October differed from the ones in August, November, and December, the months in which the frequency of ovigerous females are the ( $\chi^2 = 156.27$ ,  $p < 0.001$ ; Tukey test  $< 0.001$ ). We, however, did not find any influence of the environmental factors on such variation (in all possible interactions:  $1.22 > \chi^2 > -1.14$ ,  $p > 0.06$ ). Also, we found that egg mass was positively and strongly correlated with the body mass of females and evidenced that egg mass increases at a substantially higher rate than body mass (Figure 4).

The size in which 50% of male crabs have developed from juveniles to adolescents was  $23.42 \pm 0.24$  mm, and from adolescents to adults was  $35.69 \pm 0.09$ , while in females it was  $26.78 \pm 0.19$  mm and  $37.70 \pm 0.16$  mm, respectively (Figure 5). The relative growth of the gonopod was positive allometric in juvenile males and negative allometric in both adolescent and adult males (Figure 6, Table I). It differed between juveniles and adolescents ( $F_{1,314} = 223$ ,  $p < 0.001$ ), but the difference between adolescents and adults was only marginally significant ( $F_{1,357} = 3.26$ ,  $p = 0.07$ ). In females, the abdomen width showed a positive allometric growth in juveniles and adolescents, but an isometric growth in adults (Figure 6, Table I). The growth of the abdomen was different between juvenile and adolescent females ( $F_{1,231} = 5.64$ ,  $p = 0.018$ ), as well as between adolescent and adult females ( $F_{1,296} = 118.29$ ,  $p < 0.001$ ; Table I).

## Discussion

Overall, our results indicate that the biological aspects of *Plagusia depressa* are similar to those of other brachyurans. For instance, we found (1) relatively unbiased sex ratios, (2) sexual size dimorphism, (3) continuous breeding season, (4) egg mass increasing with female body mass, (5) males attaining maturity at smaller sizes than females, and (6) primary and secondary sexual characters unfolding allometric changes

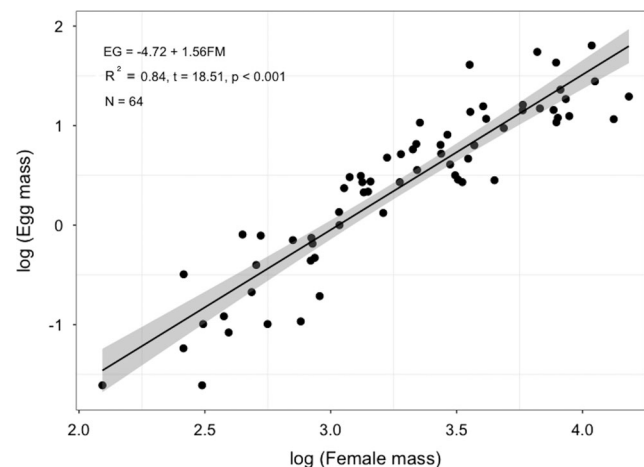


**Figure 3.** Monthly proportion of ovigerous females of *Plagusia depressa* from Coruripe, Alagoas, Brazil.

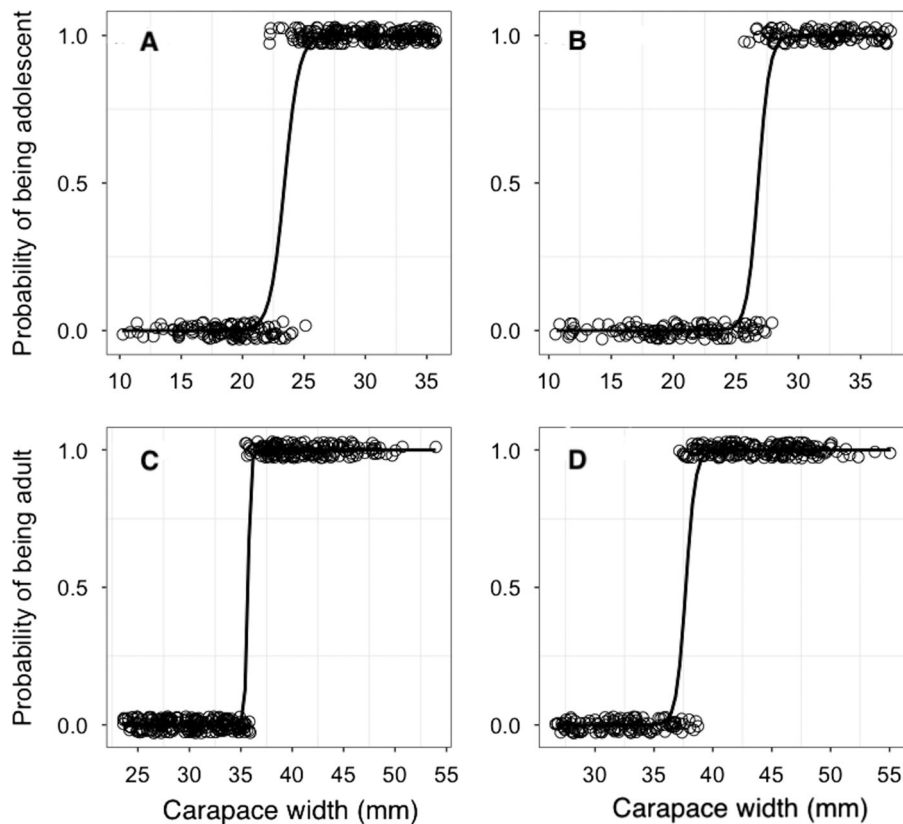
throughout ontogenetic development. We consider possible explanations and consequences for each of these aspects and also make use of a brief comparative approach with other crustaceans.

We found a consistent pattern of male-biased sex ratio in the majority of size classes, except for the three last classes of larger individuals. Although these ratios were not significant in most cases, they might suggest that males grow – at least slightly – at a higher rate and/or have higher survival rates early in life than females (Díaz and Conde 1989; Johnson 2003). Alternatively, females might grow at a lower rate than males due to continuous offspring production – what maintains the continuous breeding activity of the species – but still reach larger sizes than males because of higher continuous growth

rates or longer life span (Díaz and Conde 1989; but see Arendt 1997). This could possibly explain the female-biased sex ratio among larger individuals that we observed here. Furthermore, the maintenance of an unbiased sex ratio throughout the period of study suggests that it does not vary during the continuous breeding activity in this species, indicating that these parameters are not related in *P. depressa* (although breeding activity was continuous, a seemingly decrease was observed during the rainy season and beginning of the dry season, but sex ratio remained unbiased). Such pattern of unbiased sex ratios, both among size classes and throughout the year, is a rather common pattern among brachyuran crabs (e.g. Díaz and Conde 1989; Bas et al. 2005; Bezerra and Matthews-Cascon 2007; Branco et al. 2010), but yet not the



**Figure 4.** Relationship between egg mass and female body mass in *Plagusia depressa* from Coruripe, Alagoas, Brazil.



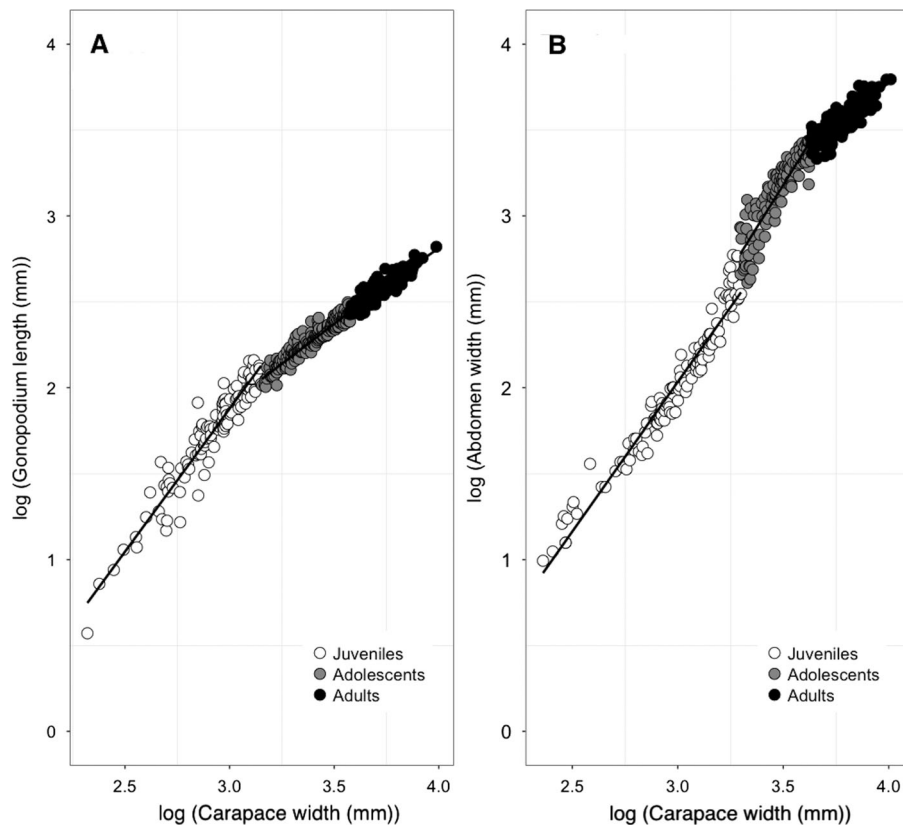
**Figure 5.** Logistic regression ( $L_{50\%}$ ) indicating the size of transition from juveniles to adolescents and from adolescents to adults, in both males (a and c) and females (b and d) of *Plagusia depressa* from Coruripe, Alagoas, Brazil.

case in other species (e.g. Spivak et al. 1991; Johnson 2003; Ribeiro et al. 2003; Sforza et al. 2010; Turner et al. 2011; Castiglioni et al. 2011a).

The breeding activity was continuous throughout the period of study, with a peak from April to July. This period corresponds to the end of the dry season and beginning of the rainy season, suggesting that *P. depressa* intensifies its breeding activity to maximize larval recruitment in the rainy season. Because rainfall leads to a higher discharge of nutrients from rivers into coastal waters, resulting in an increase in phytoplankton productivity, the larval development of *P. depressa* could be facilitated during this period of the year (Mallin et al. 1993; Christy and Morgan 1998; Litulo 2004). However, we did not find an influence of rainfall on the breeding activity. Moreover, temperature, an environmental parameter commonly found to be a major factor influencing reproductive activity in crustaceans (Sastry 1983), also did not play a role in the breeding activity. Nevertheless, temperature is unlikely to be a limiting factor in the area of our study because of its low variability and high averages throughout the year (Air temperature =  $24.17 \pm 0.95$ ; water temperature =  $24.6 \pm 0.95$ ). Such lack of association between the environmental factors and the

breeding activity of *P. depressa* is possibly a bias due to the short period of our study, such as might have been the case in Cobo (2002) and Lira et al. (2013) – yet this was not the case in other studies (Cobo and Fransozo 2003; Litulo 2004; Castiglioni et al. 2011a).

As in a variety of crustaceans – and other organisms in general – we found that larger, heavier females of *P. depressa* produces disproportionately heavier broods than smaller, lighter females. This result can be simply interpreted as a consequence of the increase in space of the egg chamber (Hines 1982; Figueiredo et al. 2008; Ferrari et al. 2011; Lira and Calado 2013), which is possible because the growth of the abdomen is also positive allometric in relation to body size before females reach sexual maturity. Although this explanation is certainly true, there are at least three alternative explanations for this result. First, females might invest disproportionately more energy into offspring when achieving a given body size or body mass. Assuming that larger crabs are usually also older, this can be translated into higher reproductive investment later in life, which would likely trade off with investment early in life (Stearns 1976); such higher reproductive investment later in life might be linked to selection favouring larger,



**Figure 6.** Relative growth of the gonopod length on male body size (a), and of the abdomen width on female body size (b) of *Plagusia depressa* from Coruripe, Alagoas, Brazil.

heavier females. Second, larger females might also have a higher food intake or feed on items that are more nutritious than the items smaller females feed on, thereby being able to invest more energy into offspring. Finally, as these two hypotheses are not mutually exclusive, they can both play a role in the production of heavier offspring. Nevertheless, these hypotheses remain untested in *P. depressa*.

We found that the onset of sexual maturity is achieved at a smaller size in males than in females, which is common among brachyuran crabs (e.g. Castiglioni et al. 2011a, 2011b; Hirose et al. 2012; Lira and Calado 2013) – yet seemingly not a predominant

pattern since other species present an opposite pattern (Sampedro et al. 1999; Fernández-Vergaz et al. 2000; Schejter and Spivak 2005; Araújo et al. 2012; Waiho et al. 2016). This suggests a stronger selection for larger sizes at maturity in females such that brood size in the first reproductive event is maximized, which is possible because fecundity commonly increases with body size – as was the case in *P. depressa*. Also, because growth typically trades off with reproduction (Stearns 1976), females that start to reproduce at smaller sizes might be constrained to produce smaller and/or fewer offspring over their lifetime than females that reproduce at larger sizes.

The three apparent growth phases in both males and females indicate that substantial morphological changes take place twice over ontogenetic development in *P. depressa*, one related to the attainment of sexual maturity (from juveniles to adolescents) and a subsequent change in the adult stage (from adolescents to adults). This pattern of growth is similar to several other crustaceans (Hartnoll 1974, 1978, 1982 and references therein). Moreover, the primary (the gonopod in males) and secondary (abdomen in females) sexual characters clearly undergo a decrease in the allometric growth, a rather common pattern among brachyurans (e.g. Hartnoll 1982; Émond et al.

**Table I.** Patterns of allometric growth of the gonopod length (mm) in males and abdomen width (mm) in females relative to body size of *Plagusia depressa* from Coruripe, Alagoas, Brazil<sup>a</sup>.

Sex	Stage	Intercept	Slope ( $\pm$ SD)	$R^2$	Allometry
Males	Juvenile	-3.11	1.66 $\pm$ 0.04	0.91	+
	Adolescent	-0.88	0.93 $\pm$ 0.02	0.90	-
	Adult	-0.65	0.86 $\pm$ 0.03	0.85	-
Females	Juvenile	-3.19	1.74 $\pm$ 0.04	0.94	+
	Adolescent	-3.73	1.97 $\pm$ 0.09	0.80	+
	Adult	-0.20	0.99 $\pm$ 0.04	0.76	=

<sup>a</sup>Results based on log-transformed data. (+) Positive allometric growth; (-) negative allometric growth; (=) isometric growth.



2010; Lira et al. 2015). In males, such reduction might be related to the attainment of an optimal gonopod length such that mating success is maximized (Eberhard et al. 1998). Specifically, selection for such optimal gonopod length is seemingly strong, as it is indicated by the strong positive allometric growth of the gonopod during the juvenile stage. However, after such optimal length is achieved, any further growth might not be adaptive because it would result in reduced mating success. The negative allometric growth of the gonopod during the adolescent and especially in the adult stage provide support to this assumption.

Similarly, taking into account the rather steep relative growth of the abdomen width in the juvenile stage, selection for larger abdomen areas in females is strong in this stage and usually attributed to the fact that the abdomen functions as a chamber to incubate the eggs (Hartnoll 1982; Hines 1982; Émond et al. 2010). Therefore, a larger incubatory chamber would harbour more eggs, would protect the egg mass more efficiently, or both. After the transition from adolescents to adults, however, such (positive) relative growth is greatly reduced, and the widening of the abdomen become negative allometric, probably because of morphological constraints so to not decrease locomotor performance (Hartnoll 1974, 1982, Alumno-Bruscia and Sainte-Marie 1998).

Here, we presented a description of several aspects of the population biology of the marine crab *P. depressa*. Overall, our findings demonstrate that this species presents similar biological patterns to that of other brachyuran crabs. We hope that this study encourages other researchers to further investigate this geographically widespread – yet poorly studied – species.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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