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## Shell occupation as a limiting factor for *Pagurus brevidactylus* (Stimpson, 1859) in the Marine State Park of Laje de Santos, Brazil

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### ABSTRACT

Hermit crabs are soft-abdomen decapods. They depend upon gastropod shells for protection, with the latter influencing growth rate, mortality and reproduction. The present work aims to provide information about the biology and reproduction of *Pagurus brevidactylus* in a conservation area in Brazilian southeastern littoral. The material was sampled through active searching by SCUBA diving and refuge traps. We analyzed population structure, fecundity, reproductive output (RO), reproductive periodicity and shell utilization for *P. brevidactylus*. In total, 54 males, 18 non-ovigerous females, 34 ovigerous females and 10 juveniles were sampled. The females had a fecundity of  $69.5 \pm 65$  eggs, which was lower than that compared to other populations from different localities. The RO ranged from 1.48% to 63.04%, with a mean of  $26.75 \pm 18.23\%$ . There was a positive relationship between egg number and female size. The animals had continuous reproduction, but they reached smaller maximum sizes when compared with other populations. The shell occupation pattern was also different from other localities, the shells of *Phrontis alba* being the most occupied; this shell has a smaller size when compared to others that *P. brevidactylus* occupies in other localities. Therefore, *P. alba* could have had limited the growth and reproduction of *P. brevidactylus*.

### ARTICLE HISTORY

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Resource; Paguroidea; rocky substrate; reproduction; shells

## Introduction

Infraorder Anomura is a monophyletic group (Bracken-Grissom et al. 2013) and is composed of seven superfamilies, with three (Galatheoidea, Hippoidea and Paguroidea) being found in São Paulo state's littoral (Brazil) (Melo 1999). The Paguridae family (hermit crabs) deserve special attention because they are adapted to use empty gastropod shells for shelter and protection (Kellogg 1976; Spight 1977; Bertness 1981; Turra and Leite 2003; Bracken-Grissom et al. 2013).

For hermit crabs, the empty shells are a limiting resource and influence their lives in many ways (Kellogg 1976); starting with larval settlement, because the metamorphosis only occurs in the presence of an adequate shell available for use (Worcester and Gaines 1997), and during reproduction for offspring success (incubated in females' pleopods) (Hazlett 1989). This relationship is a rare example found in nature where an unmodified biological structure is used as protection by different taxa: the mollusc produces its shell and,

later after its death, the shell is used for protection by the hermit crab (La Barbera and Merz 1992).

Even though shell utilization is indispensable, its occupation does not occur randomly, considering that shells in inadequate conditions can cause negative consequences for the hermit crab lives. Angel (2000), for example, concluded that hermit crabs inhabiting smaller shells had a compromised growth rate under laboratory conditions and became vulnerable to predation. Mortality in hermit crabs can decrease when they adorn shells with sea anemones (Brooks 1988) or increase when the shells become infested with epibionts. When epibionts are found internally and in higher numbers it can reduce the internal space and the aperture size, which in turn could affect choice and occupation. The presence of epibionts can also alter weight by making the shell unsuitable for small animals (Buckley and Ebersole 1994; Sant'Anna et al. 2004).

In addition, it is common to find damaged shells being used by hermit crabs. These damages can be

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cracks, broken tips and cracks in the siphonal channel. Most of the damages are concentrated in the region of the shell opening, suggesting the influence of predatory activities on the populations of hermit crabs or even on the molluscs. Physical damage to shells can make hermit crabs more likely to be predated upon because damaged shells become more fragile exposing the hermit crabs (Reese 1969; Bertness & Conningham 1981).

Thus, the availability and status (broken or infested) of shells in the environment directly affects the biology of hermit crabs; however, adequate shells are not always available for the entire population, often resulting in intraspecific and interspecific competition for this resource (Angel 2000).

That said, our aim is to study the population aspects such as population structure, fecundity and reproductive output (RO) of *Pagurus brevidactylus* (Stimpson, 1859) and their relationship with shell availability at Marine State Park of Laje de Santos (MSPLS). Species inhabiting protected areas can have differences in development due to local environmental factors (Teschima et al. 2016), and although several studies had been conducted with *P. brevidactylus* in the northern littoral of São Paulo State, Brazil (Negreiros-Fransozo et al. 1991; Mantelatto and Meireles 2004; Iossi et al. 2005; Mantelatto et al. 2005; Lima et al. 2014; among others), we are bringing the first

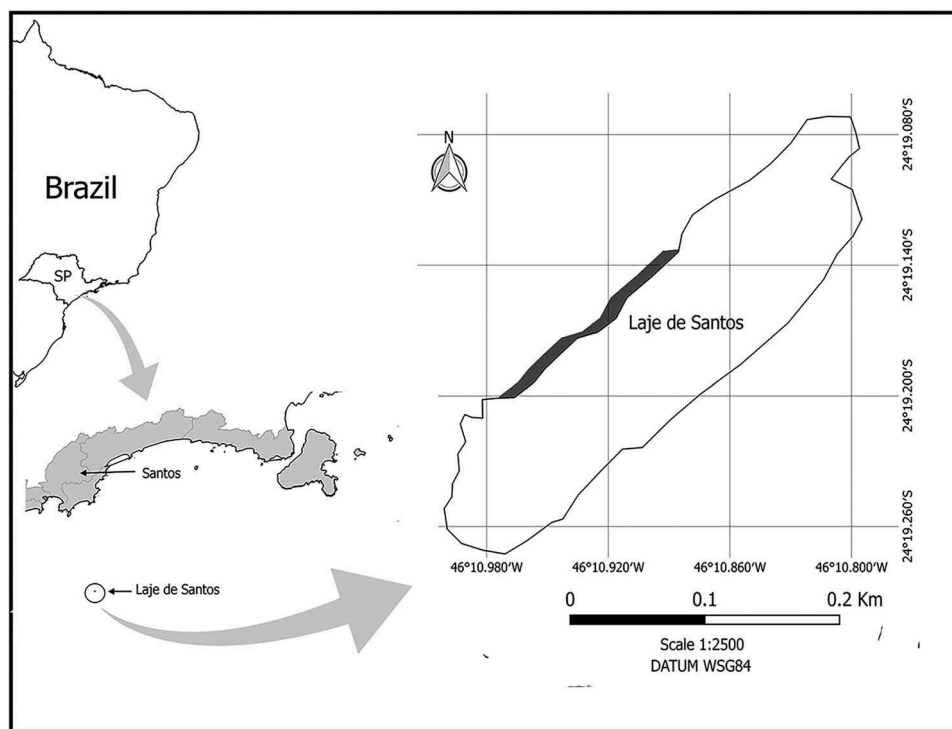
information on its biology for the MSPLS, a conservation area located in the central region of São Paulo state, and for being a conservation area, we expect to find shells of optimal sizes for full development of the hermit crab. Comparative studies are always important to understand the full biology of a determined species and its relationships with the environment, especially in protected areas to assess the management status and to help the future of the management plans.

## Material and methods

### Sampling and study area

Sampling was conducted in MSPLS (Figure 1) in the consolidated sublittoral. Laje de Santos embraces an area of 5000 ha, declared as an environmental protection area since 1993. The MSPLS has an expressive marine biodiversity due to its conservational status and well-preserved environment, which makes it an attractive spot to SCUBA divers (Instituto Laje Viva, <http://www.lajeviva.org.br/>). It is located approximately 19.4 nautical miles from the city of Santos which has the biggest harbour of Latin America, Santos Harbour.

Despite being a conservation area and important for tourism, there is little information on the fauna of MSPLS. Among the studies conducted in MSPLS, there are data for teleosts (Luiz et al. 2008), elasmobranchs



**Figure 1.** Map of the sampling area in the Marine State Park of Laje de Santos. Gray area indicates the surface sampled on the hard bottom of Laje de Santos.

(Luiz et al. 2009), turtles (Stampar et al. 2007), cnidarians (Stampar and Kodja 2007) and phoronids (Stampar et al. 2010).

The hermit crabs were sampled quarterly with SCUBA dive surveys during the daytime from June 2015 to September 2016, with two divers actively searching for the animals, with the standardized sampling effort of 1 h/diver at an average depth of 16 m. During the diving expeditions, the divers searched actively for hermit crabs on and under the rocks, and also in crevices; empty shells or those with gastropods in them were also sampled to assess the shell availability in the region. In addition, refuge traps were installed to simulate the natural reef conditions (Baine 2001). These refuge traps were in the shape of a cube with 25 cm × 25 cm × 25 cm (height × length × depth) made out of plastic nets, and inside the cube were placed 15 sets of soft plastic tubes with different diameters and six sets of small plastic nets: each tube set was composed of three tubes of the same diameter tied, and each set of nets was composed of three nets of 25 cm<sup>2</sup> tied together. In the first sampling season (15 June), four refuge traps were installed on the rocks and removed three months later during the next sampling where four new traps were installed, and this followed the entire sampling period. For the first diving session (15 June), the animals were sampled only through active searching. All the other samples were composed of active search and refuge traps. The captured animals were conditioned in plastic bags *in situ* during the withdrawal and transferred to the laboratory for the trial process.

The hermit crabs and the shells sampled were identified by specialized identification keys (McLaughlin 2003; Nucci and Melo 2007; Rios 2009), and the sexes of the crustaceans were recognized according to the gonopore position.

For further analysis, the seasons were classified as winter (June to late August 2015), spring (late September to November 2015), summer (late December 2015 to February 2016), autumn (late March to May 2016) and winter (late June to early September 2016), based on climatic factors, temperature and rainfall (Sant'Anna Neto 2005).

### Reproduction and population structure

The animals had their cephalothoracic shield length measured (SL = from the tip of the rostrum to the V-shaped groove at the posterior edge) through the image system of the stereoscopic microscope (Zeiss STEMI V6) and afterward were grouped in 0.2 mm size class intervals to evaluate population structure.

The smaller specimens (SL <0.8 mm), in which sex could not be distinguished, were classified as juveniles. The reproductive season was assessed through the presence of ovigerous females (with embryos adhered to the pleopods) in the population over the sampling seasons.

### Shell selection

Shell occupation rate was assessed through the ratio of occupied shells and total hermit crabs. The shell occupation pattern was tested with multivariate methods using PRIMER software (Plymouth Routines in Multivariate Environmental Research) (Clarke 1993; Clarke and Warwick 2001). The similarity index of Bray-Curtis was calculated for the shell occupation pattern between the demographic groups (Juveniles, Males, non-ovigerous Females and Ovigerous females), and the data were log+1 transformed a priori. The difference in shell occupation by the demographic groups (Juveniles, Males, non-ovigerous Females and Ovigerous females) was tested with a permutation-based multivariate analysis of variance (PERMANOVA) with Monte Carlo randomization and was applied a posteriori Monte Carlo pair-wise test to detect the differences among the demographic groups. Non-metric multidimensional scaling (nMDS) was used to graphically show the possible differences among the demographic groups regarding shell utilization pattern.

### Fecundity and reproductive output

For fecundity and reproductive purposes, only females with eggs in the initial developmental stages were used, the ovigerous female eggs were counted with a manual counter, and later, 20 eggs were randomly selected, photographed and measured (Terossi et al. 2010) to assess egg volume (VO), using the formula:  $VO = 1/6(a \times b^2 \times \pi)$ , in which *a* and *b* are the major and minor axes, respectively (Turner and Lawrence 1979).

Afterward, the females with their eggs were dried for 48 h at 60°C, and later, the animals and their eggs were weighed with an analytical balance (0.001 g precision) (Terossi et al. 2010) for obtaining the dry weight for both hermit crabs and egg mass. With the dry weight, it was possible to calculate the RO using the following formula (Clarke et al. 1991): (eggs dry weight/female dry weight) × 100. Those females with fewer than 30 eggs were discarded from the analysis because they could be in the process of extruding the embryos and therefore could skew the data.

## Results

### Reproduction and population structure

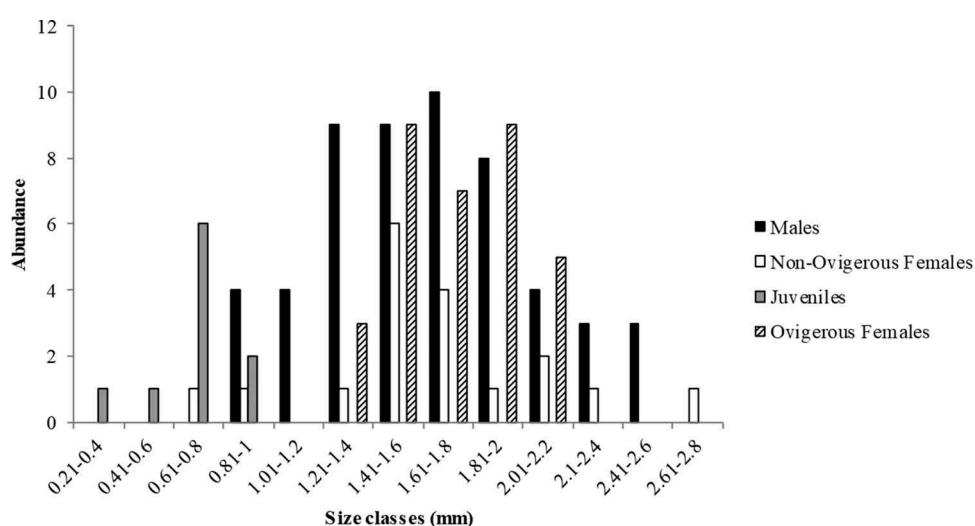
A total of 116 specimens were sampled, 104 sampled on the refuge traps and 12 through active search: 54 males (46%) ranging from 0.86 to 2.56 mm SL with a mean size of  $1.64 \pm 0.5$  mm SL, 18 non-ovigerous females ranging from 0.72 to 2.60 mm SL (16%) with mean size of  $1.62 \pm 0.51$  mm SL, 34 ovigerous females measuring from 1.33 to 2.18 mm SL (30%) with mean size of  $1.73 \pm 0.5$  mm SL, and 10 specimens classified as juveniles with sizes between 0.4 and 0.83 mm (8%) with mean size of  $0.6 \pm 0.5$  mm SL. Approximately 51% of males were between 1.21 and 1.8 mm (SL), while most

females (70%) had sizes between 1.41 and 2 mm (SL) (Figure 2). Ovigerous females were sampled throughout the entire sampling period (Figure 3).

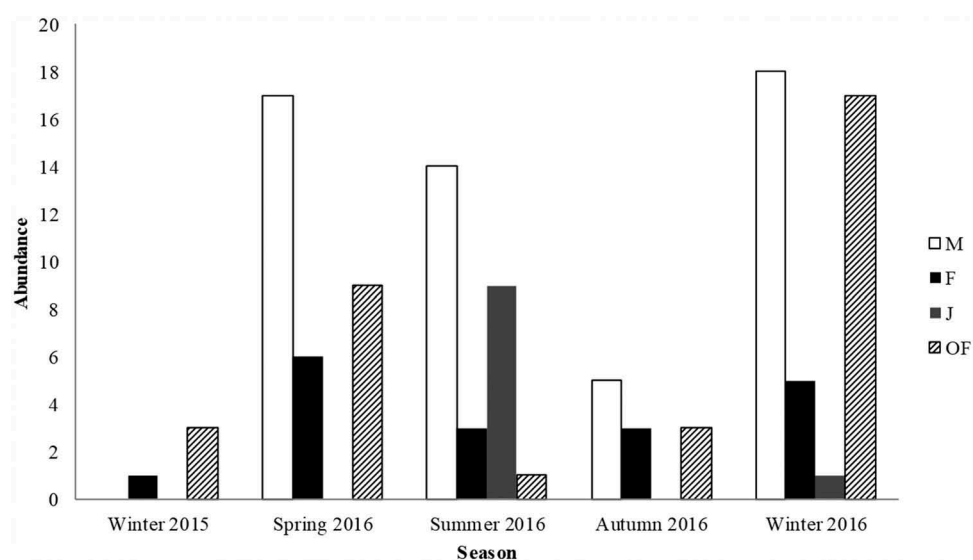
### Shell occupation

In total, 452 gastropod shells belonging to 35 species were sampled (Table 1). Of all of the gastropods species, only 24 species were occupied by *P. brevidactylus*; the shell of *Phrontis alba* (Say, 1826) was the most occupied, with an occupation rate of 41.38%.

The PERMANOVA showed a difference between the demographic groups ( $p = 0.019$ , Table 2). The Monte Carlo pair-wise tests showed differences in shell



**Figure 2.** *Pagurus brevidactylus*. Distribution of demographic groups (males, non-ovigerous females, ovigerous females, juveniles) in size classes (0.2 mm) in MSPLS.



**Figure 3.** *Pagurus brevidactylus*. Abundance of each demographic group (M: males, F: non-ovigerous females, J: juveniles, OF: ovigerous females) for each season sampled in MSPLS.

**Table 1.** Occupation pattern of gastropod shells by demographic groups (male, female, ovigerous female, juvenile) of *Pagurus brevidactylus*.

Shell	Male	Female	Ovigerous female	Juvenile	Not occupied	Occupation rate %
<i>Phrontis alba</i> (Say, 1826)	19	9	20	0	34	41.38
Unidentified	7	3	3	1	12	12.07
<i>Pisania Pusio</i> (Linnaeus, 1758)	7	1	3	0	33	9.48
<i>Anachis catenata</i> (G. B. Sowerby, 1844)	3	0	0	4	14	6.03
<i>Morula nodulosa</i> (C. B. Adams, 1845)	3	1	3	0	28	6.03
<i>Engina turbinella</i> (Kiener, 1835)	2	2	1	0	6	4.31
<i>Eudolium crosseanum</i> (Monterosato, 1869)	2	0	1	1	0	3.45
<i>Costoanachis sertulariarum</i> (d'Orbigny, 1839)	1	0	1	0	2	1.72
<i>Stramonita brasiliensis</i> Claremont & D. G. Reid, 2011	2	0	0	0	3	1.72
<i>Stramonita haemastoma</i> (Linnaeus, 1767)	1	1	0	0	3	1.72
<i>Astraea olfersii</i> (Philippi, 1846)	0	1	0	0	0	0.86
<i>Astiris lunata</i> (Say, 1826)	0	0	0	1	139	0.86
<i>Bulla striata</i> Bruguière, 1792	1	0	0	0	1	0.86
<i>Columbella mercatoria</i> (Linnaeus, 1758)	1	0	0	0	0	0.86
<i>Costoanachis sparsa</i> (Reeve, 1859)	0	0	0	1	10	0.86
<i>Engina janowskyi</i> Coltro, 2005	1	0	0	0	1	0.86
<i>Gemophos auritulus</i> (Link, 1807)	0	0	1	0	7	0.86
<i>Hesperisternia karinae</i> (Nowell-Usticke, 1959)	0	0	1	0	0	0.86
<i>Leucozonia nassa</i> (Gmelin, 1791)	0	0	0	1	1	0.86
<i>Linatella caudata</i> (Gmelin, 1791)	1	0	0	0	0	0.86
<i>Modulus modiolus</i> (Linnaeus, 1758)	1	0	0	0	0	0.86
<i>Muricopsis marcusii</i> Vokes, 1994	0	0	0	1	3	0.86
<i>Tectonatica pusilla</i> (Say, 1822)	1	0	0	0	0	0.86
<i>Urosalpinx haneti</i> (Petit de la Saussaye, 1856)	1	0	0	0	1	0.86
<i>Benthonella tenella</i> (Jeffreys, 1869)	0	0	0	0	1	0.00
<i>Boonea jadisi</i> (Olsson & McGinty, 1958)	0	0	0	0	1	0.00
<i>Calliostoma adpersum</i> (Philippi, 1851)	0	0	0	0	1	0.00
<i>Calliostoma bullisi</i> Clench & Turner, 1960	0	0	0	0	5	0.00
<i>Cerithium atratum</i> (Born, 1778)	0	0	0	0	2	0.00
<i>Guttarium muricinum</i> (Röding, 1798)	0	0	0	0	1	0.00
<i>Lithopoma tectum</i> (Lightfoot, 1786)	0	0	0	0	12	0.00
<i>Marshallora nigrocincta</i> (C. B. Adams, 1839)	0	0	0	0	2	0.00
<i>Monoplex parthenopeus</i> (Salis Marschlins, 1793)	0	0	0	0	2	0.00
<i>Seila adamsii</i> (H. C. Lea, 1845)	0	0	0	0	1	0.00
<i>Trachypollia turricula</i> (Maltzan, 1884)	0	0	0	0	1	0.00
<i>Zafra idalina</i> (Duclos, 1840)	0	0	0	0	9	0.00

Shells classified as unidentified is due to heavy incrustation or broken parts that do not allow identification.

**Table 2.** *Pagurus brevidactylus*. PERMANOVA results showing the differences in the shell usage by the demographic groups.

Source	DF	SS	MS	Pseudo-F	Perms	p(MC)
Demographic groups	3	8907.8	2969.3	2.5289	999	0.019*
Residual	16	18,786	1174.1			
Total	19	27,694				

DF: degrees of freedom, SS: sum of squares, MS: mean of squares, Perms: permutations performed, p(MC): *p*-value calculated using Monte Carlo randomization.

\* indicates significance ( $p < 0.05$ ).

occupation pattern between juveniles and males ( $t = 1.89$ ;  $p = 0.04$ ), juveniles and non-ovigerous females ( $t = 1.80$ ;  $p = 0.037$ ), and juveniles and ovigerous females ( $t = 2.41$ ;  $p = 0.004$ ). There were no differences in the shell occupation pattern between males, ovigerous females and non-ovigerous females ( $p > 0.05$ ), as shown graphically by the nMDS (Figure 4).

### Reproductive output and fecundity

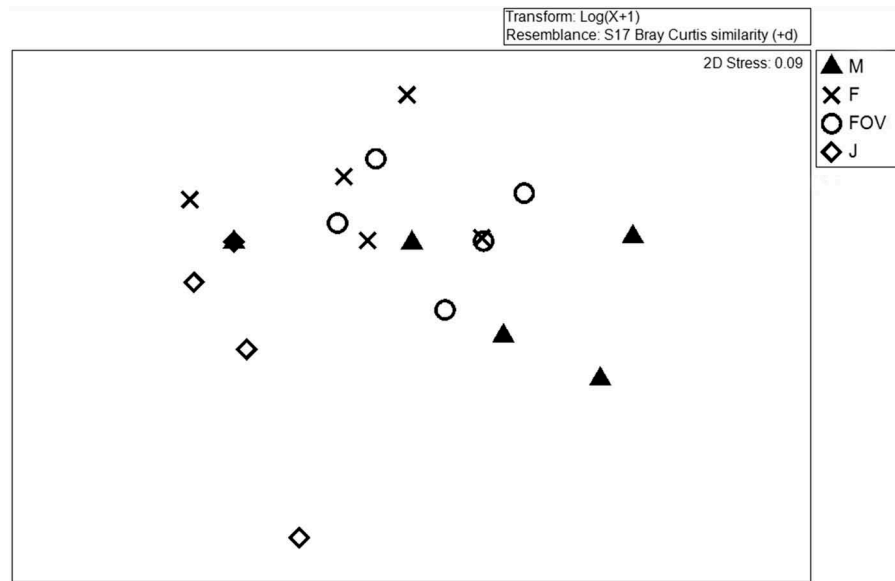
We sampled 26 females with more than 30 eggs, and the fecundity ranged from 30–304 eggs with a mean of  $84.11 \pm 66.1$  (mean  $\pm$  SD) eggs/female (Figure 5) with a mean volume of  $0.029 \pm 0.01 \text{ mm}^3$  (mean  $\pm$  SD), the RO

ranged from 5.66% to 63.04%, with a mean of  $27.7 \pm 17.6\%$  (mean  $\pm$  SD).

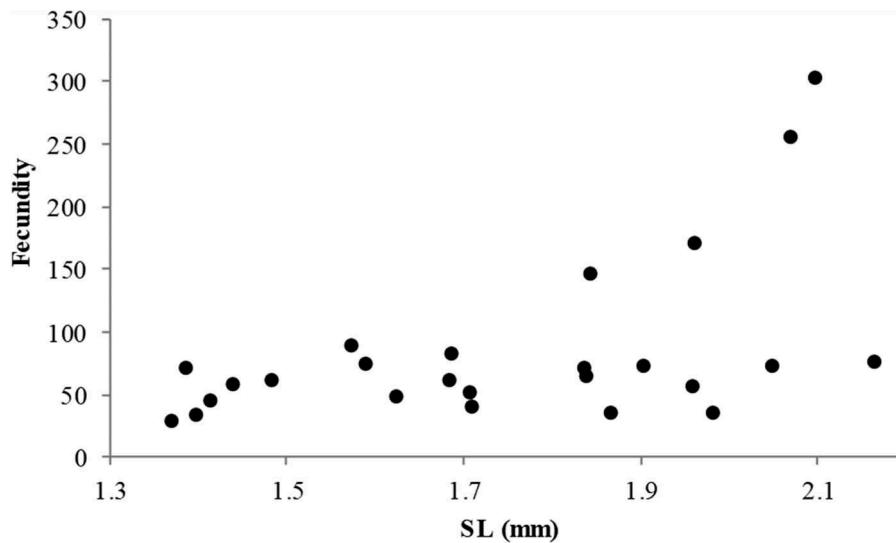
### Discussion

Our results differed concerning the reproductive aspects such as fecundity from those reported for the same species in adjacent localities (e.g. Anchieta Island  $23^\circ 83' 20'' \text{S}$  –  $45^\circ 80' 40'' \text{W}$  – São Paulo, Brazil) (Iossi et al. 2005; Mantelatto et al. 2005). Moreover, we also found some differences regarding the size classes. In the present study, the animals were smaller than those from Couves Island ( $23^\circ 25' 15'' \text{S}$  –  $44^\circ 51' 39'' \text{W}$  – São Paulo, Brazil) (Lima et al. 2014). These differences reported





**Figure 4.** *Pagurus brevidactylus*. nMDS scaling plot of similarities in shell occupation by each demographic group (M: males, F: non-ovigerous females, F OV: ovigerous females, J: juveniles) in MSPLS.



**Figure 5.** *Pagurus brevidactylus*. Dispersion graph showing the fecundity by size (SL) of the ovigerous females sampled in MSPLS.

are possibly related to the sampling method or due the shell availability in those regions, probably because the shells available at MSPLS are smaller than other localities, which could have affected population structure and animal size, the smaller shells at MSPLS prevented the animals achieving bigger sizes as in other populations studied (Negreiros-Fransozo et al. 1991; Mantelatto et al. 2005; Lima et al. 2014), which emphasizes the importance of this resource for hermit crabs. In Couves Island, the animals reach the 4 mm SL size class (Lima et al. 2014), while in Anchieta Island specimens of *P. brevidactylus* up to 3.19 mm SL were found (Mantelatto and Meireles 2004; Mantelatto et al. 2005).

Over the São Sebastião area (23°49'S – 45°24'W – São Paulo, Brazil), Negreiros-Fransozo et al. (1991) found specimens up to 3.30 mm SL, animals bigger than the largest specimen in the present study (2.60 mm SL).

Angel (2000) proposed, under laboratory conditions, that the shell characteristics directly influence hermit crab growth rate. In MSPLS, the most occupied shell (*P. alba*) is smaller than others reported in some studies. Lima et al. (2014) and Mantelatto and Meireles (2004) found most individuals of *P. brevidactylus* in shells of *Cerithium atratum* and *Morula nodulosa*, and Negreiros-Fransozo et al. (1991) found animals mainly occupying *Stramonita sp.* and *Morula sp.*, all these being gastropod species with

shells larger than *P. alba* (Rios 2009). Shell preference for hermit crabs does not always match the availability of natural conditions (Sato and Jensen 2005). In laboratory conditions, Meireles and Mantelatto (2005) showed that *P. brevidactylus* preferred shells of *C. atratum*, which is also the shell most occupied for this species in other studies (Mantelatto et al. 2005; Lima et al. 2014). Only two specimens of *C. atratum* were sampled in the MSPLS indicating a low abundance of this gastropod in the region, and since *C. atratum* was not available for the population, the hermit crabs are mainly using shells of *P. alba*, which is probably the best fitting shell available for them at MSPLS. Several authors stated that hermit crabs could have an impaired growth rate when inhabiting shells smaller than their needs (Angel 2000; Blackstone 1985), which could explain the fact that the population of *P. brevidactylus* of the MSPLS reached smaller sizes compared to populations from other sites. The occurrence of ovigerous females over the seasons suggests a continuous breeding pattern, as found in other populations of *P. brevidactylus* studied in the northern region of São Paulo state (Mantelatto et al. 2005; Lima et al. 2014). This pattern is also similar for another species in adjacent regions (Mantelatto and Garcia 1999; Mantelatto et al. 2007; Lima et al. 2014). This pattern of reproduction is commonly reported for tropical and sub-tropical species and is in accordance with the latitudinal pattern proposed for marine invertebrates (Thorson 1950; Sastry 1983).

For *P. brevidactylus*, continuous reproduction is reported with continuous recruitment (Mantelatto et al. 2005), and this recruitment usually has a peak during the summer (Negreiros-Fransozo et al. 1991; Lima et al. 2014) as seen here in the present study in which more juveniles were sampled during the summer. This pattern is seen in many crustaceans, because during the summer on the southeastern Brazilian coast, there is high primary productivity supported by the South Atlantic Central Water. This water mass brings organic matter in the water column which in turn offers food for the larvae (Negreiros-Fransozo and Fransozo 1992; Schettini et al. 1998; Lima et al. 2014).

Hermit crab males and females usually use different shell types according to their needs, and this pattern is well documented (Kellogg 1977; Abrams 1988; Imazu and Asakura 1994; among others); this differential use is primarily due to the animals' growth, as males tend to reach larger sizes than females; therefore, they need bigger shells (Imazu and Asakura 1994; Asakura 1995; Lima et al. 2014). Lima et al. (2014) and Mantelatto and Meireles (2004) reported the differential demographic use of shells by *P. brevidactylus*. However, in the present study, the same pattern was not found, as males and females occupied the same shell species (except for

juveniles); this could be explained by the low abundance of the preferred shell species used by males and females in other regions.

Ovigerous females of *P. brevidactylus* had a lower mean fecundity ( $69.5 \pm 65$  eggs) when compared to records of lossi et al. (2005) ( $158 \pm 119$  eggs) for the same species in another region with different shell resources. lossi et al. (2005) found the ovigerous females of *P. brevidactylus* mainly occupying shells of *C. atratum* and *M. nodulosa* while at MSPLS the ovigerous females occupied mainly *P. alba*. According to Rios (2009), *C. atratum* has an elongated shell with mean measurements of 34 mm  $\times$  13 mm (shell total length  $\times$  shell aperture length) and *M. nodulosa* also has an oval-elongated shell with mean measurements of 18 mm  $\times$  19 mm, although *P. alba* also has an oval-elongated shell and its mean dimensions are 15 mm  $\times$  9 mm. Since in crustaceans, the fecundity pattern is a function of the female size and weight (Hines 1982; Erdman and Blake 1988), as the shells occupied by *P. brevidactylus* are smaller, they will not reach bigger sizes consequently reducing fecundity. The high standard deviation in both studies could be related to primiparous females; these females in their first reproductive cycle often have lower fecundity than older and bigger females (Sommerton and Meyers 1983; lossi et al. 2005; Mantelatto et al. 2005), other possible cause of the high standard deviation could be related to the shell occupation by the ovigerous females. Lossi et al. (2005) showed that differences in fecundity related to shell type is significant. In the study by lossi et al. (2005), the females occupying *M. nodulosa* shells had significantly higher fecundity than those occupying *C. atratum* shells; in our study most of the ovigerous females occupied shells of *P. alba* which as mentioned before has a small shell therefore the fecundity was limited and those females that occupied other types of shells with bigger sizes produced more eggs skewing the standard deviation.

Besides shell availability in the area, there are a few aspects that should be mentioned, although they were not measured, that could also be influencing the *P. brevidactylus* population: (1) competition could be occurring for both food and shell resource availability in the MSPLS, since there are other species of hermit crabs with a similar size (*Paguristes tortugae* Schmitt, 1933) that also inhabit the sublittoral consolidated (author's unpublished data). When hermit crabs inhabit the same environment they can acquire gastropod shells by two means: exploration, when an individual is more efficient at finding and acquiring any given resource, or interference, when the individual directly interferes through agonistic behaviour



and obtains the resource from the subordinated one (Bertness 1981; Sant'Anna et al. 2012), therefore, when these shells are shared and scarce, aggressive interspecific and intraspecific interactions often occur (Hazlett et al. 1996). (2) Predation pressure is another factor, the presence of predators can influence the biology and behaviour of hermit crabs (Kulhman 1992; Gilchrist 2003) and, as pointed out by Luiz et al. (2008), the MSPSL has an ichthyofauna composed mainly of carnivores and mobile invertebrate feeding fishes that are potential predators of the hermit crabs. (3) Wave energy also should be mentioned because wave energy and flow can affect the size of benthic invertebrates (Lunt et al. 2017). Rochedo of Laje de Santos (where the study took place) is an exposed area to the hydrodynamism that could have affected the settlement of larger gastropods; thus, this could be limiting the gastropod fauna to smaller species consequently affecting the hermit crabs in the region.

The energy invested towards reproduction (RO) is similar to that found for other hermit crabs, with values higher than 20% (Carlon and Ebersole 1995; Terossi et al. 2010). In comparison to other anomurans (Lardies and Wehrtmann 1996; Hernáez and Palma 2003; Hernáez and Wehrtmann 2011), these values found for hermit crabs are high, probably because the use of shells provides shelter for the hermit crab and also provides protection for the egg mass; therefore, if the shell is large enough, the hermit crab can produce more eggs.

Therefore, we conclude that the shell availability at MSPLS could play a major role in the population of *P. brevidactylus* limiting its growth and reproduction. As the MSPLS is a protected area, this makes the fulfillment and monitoring of environmental laws even more necessary, so that this species can continue to inhabit the Marine State Park of Laje de Santos.

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