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Shell occupation by the hermit crab *Dardanus insignis* (Decapoda, Diogenidae) from the north Coast of São Paulo state, Brazil

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Abstract

The pattern of shell occupation by the hermit crab *Dardanus insignis* (Saussure, 1858) from the subtropical region of southeastern coast of Brazil was investigated in the present study. The percentage of shell types that were occupied and the morphometric relationships between hermit crabs and occupied shells were analyzed from monthly collections conducted during two years (from January 1998 to December 1999). Individuals were categorized according to sex and gonadal maturation, weighed and measured with respect to their cephalothoracic shield length (CSL) and wet weight (CWW). Shells were measured regarding their aperture width (SAW), dry weight (SDW) and internal volume (SIV). A total of 1086 hermit crabs was collected, occupying shells of 11 gastropod species. *Olivancillaria urceus* (Roding, 1798) was most commonly used by the hermit crab *D. insignis*, followed by *Buccinanops cochlidium* (Dillwyn, 1817), and *Stramonita haemastoma* (Linnaeus, 1767). The highest determination coefficients ($r^2 > 0.50$, $p < 0.01$) were recorded particularly in the morphometric relationships between CSL vs. CWW and SAW vs. SIV, which are important indication that in this *D. insignis* population the great majority the animals occupied adequate shells during the two years analysed. The high number of used shell species and relative plasticity in pattern of shell utilization by smaller individuals of *D. insignis* indicated that occupation is influenced by the shell availability, while larger individuals demonstrated more specialized occupation in *Tonna galea* (Linnaeus, 1758) shell.

Keywords: associated species, interspecific relationships, gastropod shells, Anomura.

Ocupação de conchas pelo ermitão *Dardanus insignis* na costa norte do estado de São Paulo, Brasil

Resumo

O padrão de ocupação de conchas pelo ermitão *D. insignis* (Saussure, 1858) na região subtropical da costa sudeste do Brasil, foi investigada no presente estudo. Foram analisadas a percentual de tipos de conchas que foram ocupados e as relações morfométricas entre os ermitões e conchas ocupadas, a partir de coletas mensais realizadas durante dois anos (de janeiro de 1998 a dezembro de 1999). Os indivíduos foram classificados de acordo com o sexo e maturação, pesados e medidos em relação ao comprimento escudo cefalotoracico (CEC) e peso úmido (CPU). As conchas foram medidas em relação à sua largura de abertura (LAC), peso seco (PSC) e volume interno (VIC). Um total de 1.086 ermitões foram coletados, ocupando conchas de 11 espécies de gastrópodos. *Olivancillaria urceus* (Roding, 1798) foi a mais utilizada pelo ermitão *D. insignis*, seguido por *Buccinanops cochlidium* (Dillwyn, 1817), e *Stramonita haemastoma* (Linnaeus, 1767). Os maiores coeficientes de determinação ($r^2 > 0,50$, $p < 0,01$) foram registrados principalmente nas relações morfométricas entre CEC e CPU contra LAC e VIC, que é uma importante indicação de que nesta população de *D. insignis* a grande maioria dos animais ocupavam conchas adequadas durante os dois anos analisados. O elevado número de espécies de conchas utilizadas e a relativa plasticidade no padrão de ocupação de conchas pelos menores indivíduos de *D. insignis* indicaram que a ocupação é influenciada pela disponibilidade de conchas, enquanto os indivíduos maiores demonstraram uma ocupação mais especializadas na concha de *Tonna galea* (Linnaeus, 1758).

Palavras-chave: espécies associadas, relações interespecíficas, conchas de gastrópodos, Anomura.

1. Introduction

Anomuran crustaceans are important members of the intertidal and sublittoral communities due to their fundamental role in marine trophic chains (Negreiros-Fransozo et al., 1997). The adaptation and association of hermit crab species to their substrates reveal a complex structure in their communities (Martínez-Iglesias and García-Raso, 1999) given that they need to occupy structures produced by other organisms, such as polychaete tubes (Gherardi and Cassidy, 1995) and gastropod shells (Hazlett, 1981). According this author, hermit grabs usually protect their soft abdomens within these shells, which are selected according to the biology and morphology of the species.

Despite the adaptations to search, encounter, and select shells (Rittschof, 1980; Mesce, 1982), the availability of these shells in the environment is limited (Childress, 1972; Bertness, 1980). Due to this fact, some authors (Spight, 1977; Wilber Junior and Herrnkind, 1984) suggest that shell availability in the environment has a positive influence on hermit crab populations, given that this resource is indispensable for the growth and protection of these organisms. In addition, the characteristics of a given shell occupied by a hermit crab can differ according to its species, reflecting fine differences in the selection of this resource that, in addition to variation in habitat, act in different ways depending on the species of hermit crab (Bertness, 1981). Although the process of shell selection has been investigated exhaustively (e.g. Hazlett, 1992; Bertini and Fransozo, 2000; Meireles and Mantelatto, 2005; Bulinski, 2007; Laidre, 2011; Arce and Alcaraz, 2011), the landscape of a given location can regulate the persistence (or lack thereof) of these anomurans, particularly due to their capacity to influence the community that provides shell resources, i.e. the abundance and diversity of gastropods (Meireles et al., 2003).

The hermit crab *Dardanus insignis* (Saussure, 1858) is distributed across the western Atlantic, ranging from eastern United States to the Gulf of Mexico, Antilles, Brazil (from Rio de Janeiro to Rio Grande do Sul) to Uruguay and Argentina, being found from shallow waters up to 500 m in depth, and in different types of substrate, including mud, sand, shell, and rocky bottoms (Rieger, 1997). Being adapted to a variety of habitats, it is the most abundant species of the family Diogenidae in the sublittoral of southeastern Brazil (Fransozo et al., 1998; 2011; Frameschi et al., 2014). Despite the scarcity of studies on its biology, a few studies have been carried out on its larval development (Hebling and Mansur, 1995), population dynamics (Branco et al., 2002; Frameschi et al., 2013b), and regarding the biological characteristics that determine the symbiotic association between *D. insignis* and the porcelanid *Porcellana sayana* (Leach, 1820) (Meireles and Mantelatto, 2008).

Populations of *D. insignis* deserve particular attention regarding their stability, given that these populations or individuals experience constant perturbation caused by trawl nets (Keunecke et al. 2007). According to Costa et al. (2005) the constant shrimp fisheries in south and southeast Brazil, as well as the anthropic effect caused by tourism, are the main causes for the decrease in local fishery resources. Due to the nonselectivity of the nets, the benthic fauna is greatly impacted, leading to injuries or even the death of the organisms that inhabit the area as they are considered as bycatch of fishing (Wassenberg and Hill, 1989).

The catches of marine shrimps off the Brazilian coast increased to a peak production in the 1980s of approximately 52,252 tons (FAO, 2012). During the 1990s and 2000s, the catches decreased by 26 and 9%, respectively, followed by a 4% increase during 2010 (FAO, 2012). This fluctuation in the shrimp catch suggests the possibility that the population features of species that are part of the bycatch, such as *D. insignis*, are being affected. When considering these impacts, it becomes relevant to investigate the use of shells by hermit crabs, given that an understanding of this relationship can be used for future comparisons in monitoring initiatives to assess the stability of the populations and communities in which they occur. Thus, the present study analyzed the occupation pattern of gastropod shells by the hermit crab *D. insignis* in a subtropical region on the Brazilian coast, considering the percentage of shell occupation and demonstrating the shell variables that best fit the hermit crabs.

2. Material and Methods

Hermit crabs were collected monthly from January, 1998 to December, 1999 in three bays, namely Ubatumirim (UBM), Ubatuba (UBA), and Mar Virado (MV), all of which in the municipality of Ubatuba (23°33'36"W - 45°11'32"S, 23°26'10"W - 45°01'36"S, and 23°23'00"W - 44°54'48"S, respectively) (Figure 1). A shrimp-fishing boat equipped with double-rig nets (mesh size 20 mm and 15 mm in the cod end) was used for trawling, covering an area of 18,000 m^2 at depths of 5 to 20 m. At each transect was trawled for 2 km over a period of 30 min.

After each trawl, hermit crabs were inspected, frozen, and transported to the laboratory. Hermit crabs were identified according to Melo (1999); the gastropod shells occupied by hermit crabs were identified according to Rios (1994). Individuals of *D. insignis* were counted, manually removed from their shells, sexed based on the position of

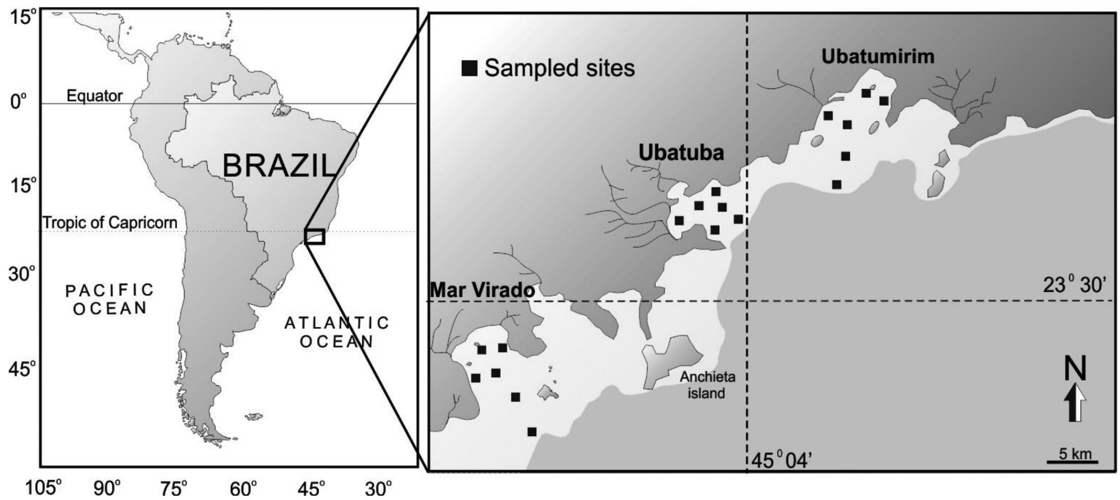

Figure 1. Map of the Ubatuba region indicates localities of collection.

the gonopores (on the coxa of either the third or the fifth pair of pereiopods in females and males, respectively), weighed (wet weight, CWW) in a precision balance (0.01 g) and had their cephalothoracic shield length (CSL) measured using a caliper (0.10 mm). After removing the hermit crab, each shell was measured with respect to its dry weight (SDW) and then kept in an oven for 24h at 60°C. Their aperture widths (SAW) and the internal volume (SIV) was measured by filling the shell with water and later transferring it to a graduated pipette (Conover, 1978). Hermit crabs were grouped into the following demographic groups: males, non-ovigerous females, and ovigerous females. The determination of the distribution of crabs into CSL size classes used the Shapiro-Wilks test for normality. Differences in the percentage of species of shells occupied in each bay by each demographic group were assessed through the chi-square ($\chi 2$) test (test of independence). Data on the measured variables of both hermit crabs and shells were log-transformed to better approximate normal distributions (Sokal and Rohlf, 1995). The size and weight of shells occupied by different demographic groups were tested using a one-way ANOVA, followed by a Tukey test (Zar, 1996). Relationships between hermit crab dimensions and occupied shells were verified by linear regression analyses and determination coefficients, namely Y = hermit crab variables (CSL and CWW), and X = shell variables (SAW, SDW, and SIV) (Sokal and Rohlf, 1995). The significance level used in all tests was $p < 0.05$ (Zar, 1996).

3. Results

A total of 1086 hermit crabs of the species *D. insignis* was collected over the course of two years, occupying shells of 11 gastropod species (Table 1). Hermit crabs were grouped into 11 size classes, with 2.0 mm intervals, starting from a minimum size of 2 mm (CSL). The distribution of individuals into size classes showed non-normal patterns, with an unimodal distribution in each of the three bays (Shapiro-Wilks, UBM, W=0.93; UBA, W=0.91; MV, W=0.98, $p<0.05$ for all locations). Out of 348 individuals collected in the UBM bay occupying shells of nine gastropod species, 215 were males (61.8%), 116 were non-ovigerous females (33.3%), and 17 were ovigerous females (4.9%), In UBA, shells of 11 gastropod species were occupied by 570 specimens, of which 365 were males (64.04%), 148 were non-ovigerous females (26.03%) and 57 were ovigerous females (10.0%). In the MV bay, a total of 168 specimens were collected inhabiting shells of only four gastropod species, of which 101 were males (60.1%), 66 were non-ovigerous females (39.3%) and a single ovigerous female (0.6%).

Shells of *Strombus pugilis* (Linnaeus, 1768), *Zidona dufresnei* (Donovan, 1823), and *Olivancillaria urceus* (Röding, 1798) were significantly heavier (Anova, $F = 70.28$; $p < 0.001$) than those of the remaining species (Table 1). With respect to aperture width ($F = 110.25$; $p < 0.001$) and shell internal volume ($F = 74.45$; $p < 0.001$), *Tonna galea* (Linnaeus, 1758) was the largest among the occupied species, whereas *O. urceus* was the smallest (Table 1). These last shell, *O. urceus*, was most commonly used by the hermit crab *D. insignis* in all three bays (UBM: $\chi^2 = 273.9$; UBA: $\chi^2 = 259.7$; MV: $\chi^2 = 83.91$; $p < 0.01$ for all bays), followed by *Buccinanops cochlidium* (Dillwyn, 1817), and *Stramonita haemastoma* (Linnaeus, 1767). In the context of shell occupation by different demographic groups, the shell of *O. urceus* was significantly more used by males and non-ovigerous females in all three bays (UBM: $\chi^2 = 82.95$, $\chi^2 = 104.7$; UBA: $\chi^2 = 140.2$; $\chi^2 = 94.96$; MV: $\chi^2 =140.2$; $\chi^2 = 94.96$; $p < 0.01$ for all groups) (Figure 2). Ovigerous females occupied mostly the shell of *O. urceus* in UBM ($\chi^2 = 7.12$; $p < 0.01$) and UBA ($\chi^2 = 0.6$; $p = 1.05$) (Figure 2a, b), yet in MV only a single ovigerous female was captured, which nevertheless was also found in a shell of *O. urceus* (Figure 2c).

Table 1. *D. insignis*. Characterization of 1086 occupied gastropod shells, and results of ANOVA followed by Tukey test, where different letters indicate significant differences among gastropods shell species ($p < 0.05$) (OP = occurrence percentage; SD = standard deviation). Bold letters indicate the abbreviation of each gastropod species.

Gastropod species	n	Weight (g) Max.	Weight (g) Min.	Weight (g) Mean ± SD	Aperture Width (mm) Max.	Aperture Width (mm) Min.	Aperture Width (mm) Mean ± SD	Internal Volume (mL) Max.	Internal Volume (mL) Min.	Internal Volume (mL) Mean ± SD	OP (%)
Olivancillaria urceus ***(Ou)*** (Röding, 1798)	583	76.61	1.81	16.8 ± 7.78**a**	14.7	3.2	7.76 ± 1.76**a**	15.7	0.3	4.15 ± 1.69**a**	54
Buccinanops cochlidium ***(Bc)*** (Dillwyn, 1817)	177	18.63	1.09	8.24 ± 3.45**b**	17.9	4.8	11.71 ± 2.46**b**	16.6	0.4	6.46 ± 2.97**b**	16
Stramonita haemastoma ***(Sh)*** (Linnaeus, 1767)	92	28.04	1.66	10.14 ± 5.37**b**	19.4	4.7	10.75 ± 2.95**c**	18.5	0.4	5.13 ± 3.35**ad**	8.4
Siratus tenuivaricosus ***(St)*** (Dautzenberg, 1927)	58	28.88	1.73	8.33 ± 4.56**b**	16	5.9	10.10 ± 2.03**c**	15	0.4	3.87 ± 2.57**a**	5.3
Cymatium parthenopeum ***(Cp)*** (Von Salis, 1793)	53	27.6	2.07	9.79 ± 5.65**b**	15.5	6.1	10.12 ± 2.16**c**	22	1	5.81 ± 4.05**bd**	4.8
Semicassis granulata ***(Sg)*** (Born, 1778)	34	39.87	3.07	12.43 ± 8.28**b**	18.6	6.4	12.52 ± 2.55**bd**	28	3.5	12.21 ± 6.80**c**	3.1
Tonna galea ***(Tg)*** (Linnaeus, 1758)	28	54	3.36	13.32 ± 10.64**b**	47.3	16.2	23.21 ± 6.77**e**	180	5	47.90 ± 45.00**e**	2.4
Fusinus marmoratus ***(Fm)*** (Philippi, 1846)	24	26.5	4.42	13.82 ± 7.00**b**	15.2	7.2	11.09 ± 2.39**bc**	22	1	8.62 ± 6.30**d**	2.1
Strombus pugilis ***(Sp)*** (Linnaeus, 1768)	24	69.8	21.75	45.08 ± 12.43**c**	11.9	6	8.75 ± 1.53**ac**	15	10	11.45 ± 1.79**c**	2.1
Zidona dufresnei ***(Zd)*** (Donovan, 1823)	12	80.99	23.07	45.44 ± 17.12**c**	27.7	8.4	15.87 ± 5.33**d**	50	10	28.00 ± 13.33**e**	1.1
Polinices lacteus ***(Pl)*** (Guilding, 1834)	1			8.45			19.4			5.6	0.9

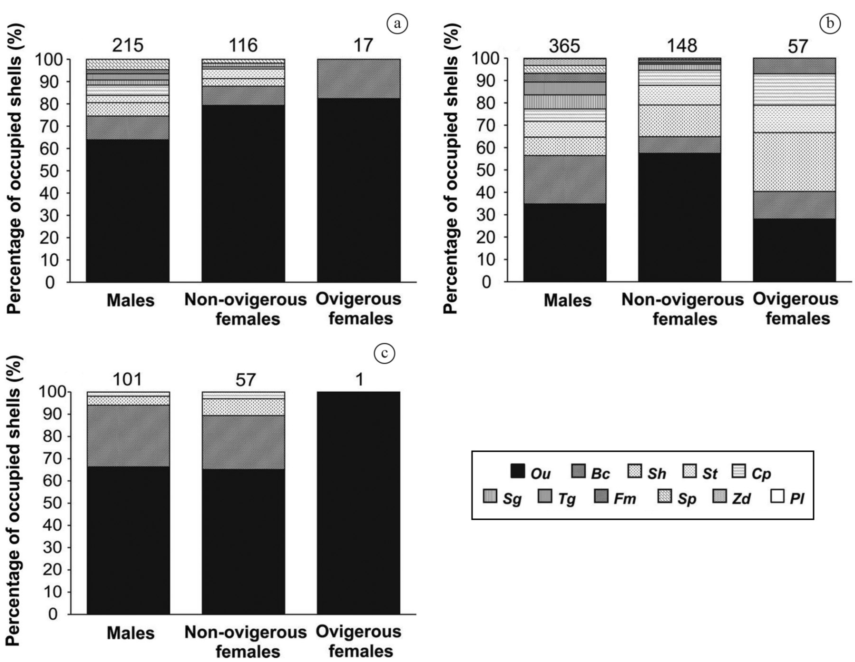

Figure 2. *D. insignis*. Percentage occupancy of different gastropod species for each demographic group in each bay, Ubatumirim (a), Ubatuba (b) and Mar Virado (c). Number above each column indicates number of hermit crabs of each demographic group. Abbreviations as in Table 1.

With respect to the occupation of shells of different size classes by *D. insignis*, shells of *O. urceus* were the most commonly used by the first three size classes (grouping by size of cephalothoracic shield length), both for males and females. There was more variety in the fourth size class (8.0|-10.0 mm) for both sexes, including shells of *O. urceus*, *B. gradatus*, *S. haemastoma*, *Siratus tenuivaricosus* (Dautzenberg, 1927), and *Cymatium parthenopeum* (Von Salis, 1793). Only males occurred in the 6th size class (12.0|-14.0 mm), usually in of shells *T. galea* (Figure 3).

The relationship between the traits of the occupied shell and the corresponding hermit crab were tested separately for each sex and showed the highest coefficients of determination in the case of males ($r^2 > 0.50$; $p < 0.01$), such that shell weight (SDW) was the only variable that did not show significant association. On the other hand, aperture width (SAW) and shell internal volume (SIV) showed the highest coefficients of determination (Table 2).

Correlating hermit crab dimensions to shell variables indicated that the cephalothoracic shield length (CSL)

Table 2. *D. insignis*. Regression equations in relation to the sex of the hermit crabs.

Relationships	Groups	N	Linear Equation Y = a X+b	r^2
CSL *vs.* SAW	Males	681	CSL = 0.094·SAW + 0.766	0.76*
	Non-ovigerous females	330	CSL = 0.201·SAW + 0.629	0.65*
	Ovigerous females	75	CSL = 0.304·SAW + 0.542	0.61*
CSL *vs.* SDW	Males	681	CSL = 0.711·SSDW + 0.121	0.07^{ns}
	Non-ovigerous females	330	CSL = 0.680·SDW + 0.085	0.05*
	Ovigerous females	75	CSL = 0.832·SDW - 0.007	0.01^{ns}
CSL *vs.* SIV	Males	681	CSL = 0.608·SIV + 0.337	0.75*
	Non-ovigerous females	330	CSL = 0.637·SIV + 0.253	0.55*
	Ovigerous females	75	CSL = 0.667·SIV + 0.265	0.45*
CWW *vs.* SAW	Males	681	CWW = –1.891·SAW + 2.393	0.77*
	Non-ovigerous females	330	CWW = –1.461·SAW + 1.867	0.62*
	Ovigerous females	75	CWW = –1.280·SAW + 1.781	0.62*
CWW *vs.* SDW	Males	681	CWW = 0.001·SDW + 0.409	0.08^{ns}
	Non-ovigerous females	330	CWW = –0.063·SDW + 0.276	0.05^{ns}
	Ovigerous females	75	CWW = 0.445·SDW - 0.013	0.02^{ns}
CWW *vs.* SIV	Males	681	CWW = –0.285·SIV + 1.053	0.76*
	Non-ovigerous females	330	CWW = –0.181·SIV + 0.771	0.55*
	Ovigerous females	75	CWW = –0.084·SIV + 0.868	0.45*

N = number of individuals; r^2 = determination coefficient; CSL = shield length; CWW = wet weight of hermit crabs; SAW = aperture width; SDW = shell weight; SIV = shell internal volume. ns = not significant. *$p < 0.01$.

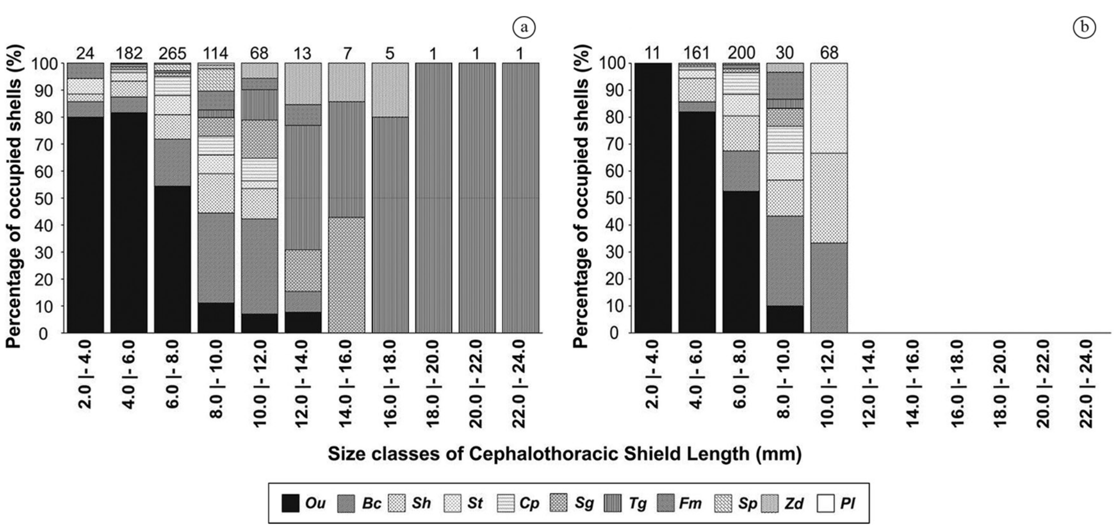

Figure 3. *D. insignis*. Percentage occupancy of different gastropod species in each size classes by males (a) and females (b). Number above each column indicates number of hermit crabs of each size classes. Abbreviations as in Table 1.

showed the highest correlation coefficients. In particular, CSL *vs.* SAW and SIV; CWW *vs.* SAW and SIV were the relationships that best described the association between hermit crabs and the occupied shells. Regression analyses of all nine shell species most commonly occupied by *D. insignis* indicated significant relationships for most of them (p < 0.01). Only one relationship (CWW *vs.* SDW) of the shell of the species *S. pugilis* showed a low determination coefficient (r^2 = 0.04) e and did not reach statistical significance (Table 3).

Table 3. *D. insignis*. Regression equations of the studied relationships.

Gastropod species	Relationships	n	Linear Equation Y = a x + b	r^2
O. urceus	CSL *vs.* SAW	583	CSL = 0.158·SAW + 0.685	0.58*
	CSL *vs.* SDW	583	CSL = 0.470·SDW + 0.243	0.33*
	CSL *vs.* SIV	583	CSL = 0.604·SIV + 0.290	0.59*
	CWW *vs.* SAW	583	CWW = –1.644·SAW + 2.087	0.58*
	CWW *vs.* SDW	583	CWW = 0.741·SDW + 0.781	0.36*
	CWW *vs.* SIV	583	CWW = 0.277·SIV + 0.868	0.56*
B. cochlidium	CSL *vs.* SAW	177	CSL = 0.051·SAW + 0.788	0.68*
	CSL *vs.* SDW	177	CSL = 0.603·SDW + 0.320	0.37*
	CSL *vs.* SIV	177	CSL = 0.627·SIV + 0.350	0.70*
	CWW *vs.* SAW	177	CWW = –1.956·SAW + 2.402	0.69*
	CWW *vs.* SDW	177	CWW = –0.327·SDW + 1.036	0.43*
	CWW *vs.* SIV	177	CWW = –0.177·SIV + 1.037	0.67*
S. haemastoma	CSL *vs.* SAW	92	CSL = 0.142·SAW + 0.695	0.73*
	CSL *vs.* SDW	92	CSL = 0.559·SDW + 0.299	0.50*
	CSL *vs.* SIV	92	CSL = 0.679·SIV + 0.270	0.63*
	CWW *vs.* SAW	92	CWW = 1.937SAW + 2.365	0.76*
	CWW *vs.* SDW	92	CWW = –0.559·SDW + 1.062	0.57*
	CWW *vs.* SIV	92	CWW = –0.127·SIV + 0.947	0.70*
S. tenuivaricosus	CSL *vs.* SAW	58	CSL = –0.014·SAW + 0.853	0.59*
	CSL *vs.* SDW	58	CSL = 0.530·SDW + 0.350	0.65*
	CSL *vs.* SIV	58	CSL = 0.707·SIV + 0.259	0.81*
	CWW *vs.* SAW	58	CWW = –2.553·SAW + 2.991	0.66*
	CWW *vs.* SDW	58	CWW = –0.625·SDW + 1.207	0.70*
	CWW *vs.* SIV	58	CWW = 0.008·SIV + 0.877	0.84*
C. parthenopeum	CSL *vs.* SAW	53	CSL = 0.222·SAW + 0.658	0.56*
	CSL *vs.* SDW	53	CSL = 0.652·SDW + 0.240	0.64*
	CSL *vs.* SIV	53	CSL = 0.681·SIV + 0.282	0.72*
	CWW *vs.* SAW	53	CWW = –1.358·SAW + 1.932	0.56*
	CWW *vs.* SDW	53	CWW = –0.098·SDW + 0.704	0.64*
	CWW *vs.* SIV	53	CWW = –0.013·SIV + 0.829	0.72*
S. granulata	CSL *vs.* SAW	34	CSL = 0.013·SAW + 0.913	0.60*
	CSL *vs.* SDW	34	CSL = 0.610·SDW + 0.359	0.58*
	CSL *vs.* SIV	34	CSL = 0.656·SIV + 0.303	0.57*
	CWW *vs.* SAW	34	CWW = 2.127·SAW + 2.793	0.62*
	CWW *vs.* SDW	34	CWW = –0.203·SDW + 1.081	0.57*
	CWW *vs.* SIV	34	CWW = –0.117·SIV + 0.959	0.63*
T. galea	CSL *vs.* SAW	28	CSL = 0.428·SAW + 0.514	0.29*
	CSL *vs.* SDW	28	CSL = 0.977·SDW + 0.139	0.10*
	CSL *vs.* SIV	28	CSL = 0.811·SIV + 0.204	0.22*
	CWW *vs.* SAW	28	CWW = -1.019·SAW + 1.699	0.37*
	CWW *vs.* SDW	28	CWW = 0.769·SDW + 0.484	0.19*
	CWW *vs.* SIV	28	CWW = 0.209·SIV + 0.00	0.30*

CSL = shield length; CWW = wet weight of hermit crabs; SAW= aperture width of shells; SDW = shell weight; SIV = shell internal volume. ns = not significant. $^*p < 0.01$.

Table 3. Continued...

Gastropod species	Relationships	n	Linear Equation Y = a x + b	r^2
F. marmoratus	CSL *vs.* SAW	24	CSL = –0.076·SAW + 0.962	0.88*
	CSL *vs.* SDW	24	CSL = 0.478·SDW + 0.405	0.88*
	CSL *vs.* SIV	24	CSL = 0.629·SIV + 0.337	0.84*
	CWW *vs.* SAW	24	CWW = –2.373·SAW + 2.982	0.93*
	CWW *vs.* SDW	24	CWW = –0.621·SDW + 1.221	0.89*
	CWW *vs.* SIV	24	CWW = –0.181·SIV + 1.044	0.89*
S. pugilis	CSL *vs.* SAW	24	CSL = 0.635·SAW + 0.267	0.32*
	CSL *vs.* SDW	24	CSL = 0.457·SDW + 0.258	0.41*
	CSL *vs.* SIV	24	CSL = 0.609·SIV + 0.287	0.33*
	CWW *vs.* SAW	24	CWW = 0.213·SAW + 0.477	0.04^{ns}
	CWW *vs.* SDW	24	CWW = 0.488·SDW + 0.611	0.29*
	CWW *vs.* SIV	24	CWW = 0.188·SIV + 0.878	0.31*

CSL = shield length; CWW = wet weight of hermit crabs; SAW= aperture width of shells; SDW = shell weight; SIV = shell internal volume. ns = not significant. *$p < 0.01$.

4. Discussion

According to Hazlett (1981) the use of shells of different gastropod species by different hermit crab species can be explained by size and environmental variation, including protection from factors to which they are exposed, such as osmotic stress, energetic expenditure, and the action of waves. Thus, individuals of different sizes and sexes seek shells that best fit their morphology, which would vary according to different crab demographic groups and to availability of shells in the environment.

The results of the present study indicate a smaller suite of shells occupied by hermit crabs than compared to those of Miranda et al. (2006), who noted the occupation by ovigerous females (and only ovigerous females) of shells of 15 gastropod species. Such differences can be justified by the shell diversity rather than by the abundance of gastropod species in the region, given that nine of the species recorded in the abovementioned study showed low occupation rates (> 3%), whereas in the present study only the species *Polinices lacteus* (Guilding, 1834), used by a single individual, and *Z. dufresnei*, used by 12 individuals, showed low occupancy.

Shells of the gastropod *O. urceus* were the most used by *D. insignis* in a region at higher latitude according to Ayres-Peres et al. (2008). When compared to the present study, which also recorded *O. urceus* as the most occupied shell in all three bays (>50%) and, given its high occupation rate, we can assume that there is both a occupation and a better adaptation of the hermit crab *D. insignis* to occupy this species. According to Abrams (1988) differential growth patterns among the sexes directly influence shell occupation, yet this was not recorded in the present study, which indicates a consistent pattern in the choice for the occupation species of shell. Hahn (1998) suggested that the occupation of the same shell species (in this case, *O. urceus*) decreases intraspecific competition, which has a positive influence at the population level. This fact might be associated with the competitive dominance of *D. insignis* in the sub-littoral region (*see* Fransozo et al., 2008, 2011; Ayres-Peres et al., 2008). Hazlett et al. (2005) suggests that male hermit crabs that use for the most part a given species of shell are considered specialists and allow for a higher effectiveness in the mating process in comparison to hermit crabs with generalist occupation patterns, occupying shells of different species according to their availability in the environment. In this study, only males were recorded among the largest size classes, and also showed specialization, given that they occupied mostly the shells with the largest aperture width (*T. galea*). In the case of hermit crabs, males are usually larger than females (Manjón-Cabeza and García-Raso, 1998; Branco et al., 2002; Martinelli et al., 2002; Litulo, 2005) to reduce competition risks, which is a consequence of the evolution of male reproductive strategies given the advantages that an asymptotically larger size can provide (Asakura, 1995).

Despite indicating a higher diversity of occupied shells, Miranda et al. (2006) also indicated that *O. urceus* was the most used shell by ovigerous females of *D. insignis*. The small number of shell species occupied by ovigerous females in the present study when compared to males and non-ovigerous females might have been due to their restriction to only two size classes. This reduced diversity of occupation by ovigerous females was similar to that reported for other diogenid species, such as *Petrochirus diogenes* (Linnaeus, 1758) and *Calcinus tibicen* (Herbst, 1791) (studied by Bertini and Fransozo, 2000 and Garcia and Mantelatto, 2000; respectively); as well as the pagurid *Pagurus exilis* (Benedict, 1892), studied by Terossi et al. (2006). This similarity implies the existence of a restriction in the choice of shells by ovigerous females. According to Hazlett et al. (2005) females of *Clibanarius vittatus* (Bosc, 1802) that occupied heavier shells - larger than their ideal size - tended not to be ovigerous, whereas ovigerous females were most commonly found in adequate shells. When analyzing egg production strategies in *Paguristes* *tortugae* (Schmitt, 1933), Mantelatto et al. (2002) reported that the occupation of some shells provided an increase in fecundity. The same was shown for *Loxopagurus loxochelis* (Moreira, 1901) by Torati and Mantelatto (2008), who also showed that this increase in fecundity takes place particularly when the shell is lighter.

The difference in shell utilization patterns between juveniles, males, and females has already been observed in several hermit crab species (Blackstone and Joslyn, 1984; Imazu and Asakura, 1994). Although the present study has not identified juveniles, Fernandes-Góes et al. (2005) investigated the population biology of *D. insignis* and considered as juveniles those individuals that would correspond in the present study as the first size class, *i.e*. 2.0-3.9 mm. Based on this assumption, the results of the present study suggest that, during juvenile growth, the morphology of the animal and the shell are not determining factors in the choice of the resource, given that hermit crabs categorized as juveniles (both males and females) are found in a shells with a variety of shapes. The variation of occupation in the smaller size classes was verified by Ayres-Peres et al. (2012) and Frameschi et al. (2013a) when they analyzed the utilization of shells by the hermit crab, *L. loxochelis* at the same site of the present study. This diverse exploration of shell species by *D. insignis* in the first four size classes is likely because of the presence of a larger availability of gastropod species with varied sizes in the environment (Mantelatto and Garcia, 2000).

The size of commonly used shells is well correlated with the cephalothoracic shield size in hermit crabs (Hazlett, 1981). In morphometric analyzes carried out for males of *D. insignis*, high correlation coefficients were found in relation to those of females (ovigerous and non-ovigerous). This fact should be due to the capacity of larger males to win agonistic encounters for the possession of empty shells, which enables them to occupy the "best" shells in nature (Asakura, 1995). According to Abrams (1980) the size of the occupied shell is usually well correlated with the size of the hermit crab and therefore is considered as "adequate". Regression analyses conducted to assess different shell species inhabited by *D. insignis*, considering CSL and CWW *vs*. SAW and SIV, showed the highest correlation coefficients. These relationships also resulted in high determination coefficients for the hermit crab *P. diogenes* (Bertini and Fransozo, 2000). On the other hand, the relationships between shell weight (SDW) and hermit size and weight (CSL and CWW) showed the smallest coefficients, probably because regressions calculated based on shell weight (SDW) do not reflect properly the fit between the hermit crab and the shell because encrusting epifauna can increase the weight of the shell considerably (e.g. Conover, 1978; Sandford, 2003).

The variation in shell use patterns demonstrates that its occupation by the specie investigated in the present study is strongly linked: (1) to the availability of this resource in nature, possibly including the presence for occupying the shell of the gastropod *O. urceus*; and (2) to the animal size. Thus, the smallest hermits occupied a greater variety of shells, taking into account that there is a greater availability of small gastropod´s shells than large gastropod´s shells, according with Bollay (1964) small individuals may not be considered so dependent on a determinate gastropod shell species as the big ones are. Consequently, the larger individuals (males) do not find many shells options, preferring to occupy the *T. galea*, due it has low weight comparing to others with similar size (*Zidona dufresnei* and *Semicassis granulata*). The specialized occupation of shells, especially by larger individuals, together with the reproductive strategies of *D. insignis* (see Miranda et al., 2006) are factors that determine the marked abundance of the species in the non-consolidated sublittoral of the subtropical region of the Brazilian coast.

Therefore, one can conclude that, on the north coast of São Paulo State, Brazil, fifteen years ago, the species *D. insignis* occupies shells that are adequate to their morphology, and the replica of the method used in our study, together with the results presented here, is useful for monitoring this species and, consequently, the environmental conditions found in the studied region.

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