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Is there variation in the occupation of Gastropoda shells and in the diurnal and nocturnal activities of the hermit crab *Dardanus insignis* (Saussure, 1858) ?

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Abstract: The presence of gastropod shells in the environment is crucial for the survival of hermit crabs, and the population's abundance is directly associated with shell availability. Furthermore, understanding the daily activity of the species contributes to elucidating changes in a community's structure. Therefore, the aim of this study was to evaluate the occupation of gastropod shells and the diurnal and nocturnal abundance of *Dardanus insignis* on the northern coast of the state of São Paulo, Brazil, at eight different depths. Among 527 hermit crabs, 292 were males, 187 were females (35 ovigerous), and 48 were juveniles. The crabs occupied shells belonging to 11 species, with *Olivancillaria urceus* being the most abundant, followed by *Siratus tenuivaricosus* and *Buccinanops gradatus*. The occupation of *O. urceus* by all demographic groups indicates its high availability in the region and is an important factor that reduces intraspecific competition within the population for this resource. The increased abundance of hermit crabs captured during the nighttime can be attributed to their predominantly nocturnal activity. Additionally, there was an observed concentration of the population at greater depths, where a higher diversity of shell species is available for occupation.

Key words: Anomura. Gastropod shell. Luminosity. Depth.

Existe variação na ocupação de conchas de Gastropoda e na atividade diurna e noturna do ermitão *Dardanus insignis* (Saussure, 1858)?. Resumo: As conchas de gastrópodes disponíveis no ambiente são imprescindíveis para a sobrevivência dos ermitões, e a abundância da população está diretamente ligada à sua disponibilidade. Além disso, entender a atividade diária da espécie contribui para elucidar as mudanças na estrutura de uma comunidade. Desta forma, o presente estudo teve como objetivo avaliar a ocupação de conchas de gastrópodes e a abundância diurna e noturna de *D. insignis* no litoral norte do estado de São Paulo, Brasil, em oito profundidades diferentes. Dentre um total de 527 indivíduos, 292 eram machos, 187 eram fêmeas (35 ovígeras) e 48 eram juvenis. Os ermitões ocuparam 11 espécies de conchas, sendo *Olivancillaria urceus* a mais abundante, seguida de *Siratus tenuivaricosus* e *Buccinanops gradatus*. A ocupação por todos os grupos demográficos de *O. urceus* indica a sua alta disponibilidade na região e é um fator importante que reduz a competição intraespecífica da população por este recurso. O aumento da abundância dos ermitões capturados durante a noite pode ser atribuído à sua atividade predominantemente noturna. Além disso, observou-se uma concentração da população em maiores profundidades, onde há maior diversidade de espécies de conchas para ocupação.

Palavras-chave: Anomura, Concha de gastrópode, Luminosidade, Profundidade.

Introduction

Dardanus insignis (Saussure, 1858) is considered the most abundant hermit crab in unconsolidated substrate in southeastern Brazil (Fransozo et al., 2011, 2012). This species belongs to Diogenidae family and its distribution covers most of the western Atlantic. In Brazil, it is registered from Rio de Janeiro to Rio Grande do Sul, from 1.5 to 500 meters depths (Rieger, 1997). These crabs are detritivores in marine environments (Samuelsen, 1970), and their food habits have contributed to the adaptive success of the group (Schembri, 1982). Moreover, they are found in various types of substrates, such as mud, sand, shell, and rocky bottoms (Rieger, 1997). The abundance and diversity of hermit crabs depend on the suitability of the environment and the occurrence of gastropod shell species (Hazlett, 1981), as there is a preference for certain species based on the conditions faced by the individual (Nirmal et al., 2020).

The patterns of shell used by hermit crab vary between populations and are mainly influenced by the size and shape of the shells available during inspection, the locality (intertidal or sublittoral area), and the morphology of the hermit crab itself (Bertness, 1980, Mantelatto & Garcia, 2000, Mantelatto & Dominciano, 2002, Nirmal et al., 2020). Shell occupancy influences several biological characteristics of hermit crabs, including growth, survival rates, and reproductive potential (Hazlett, 1981).

Studies on hermit crab populations generally provide information on abundance, size, growth, distribution by demographic groups, sex ratio, sexual maturity, and periods of reproduction and recruitment. However, relatively few studies evaluates the diurnal and nocturnal activities of this group. Among them, the most relevant studies for understanding Brazilian species are those by Ismail (2011), reporting the daytime activities under laboratory conditions; Turra & Denadai (2003), that evaluated diurnal activities for four species of hermit crabs from intertidal regions; and Steibl & Laforsch (2019), that focus on two species of the genus Coenobita (Latreille, 1829) and their diurnal activities at different tide times. Data on the diurnal and nocturnal activities of hermit crabs that specifically consider the luminosity factor in the behavior of sublittoral hermit crabs, as *D. insignis* can help elucidate the causes of changes in the structure of a community.

Trawl sampling of hermit crabs off the Brazilian coast reveals a depth-dependent behavioral pattern. The studies by Fransozo et al. (2008), Meireles & Mantelatto (2008), and Stanski et al. (2016) indicate an increase in the abundance of D. insignis with greater depths. Additionally, Frameschi et al. (2015) assessed the occupation of shells by D. insignis in regions with depths up to 20 meters, and observed that the selection of shells were based on its morphology and environmental conditions (temperature, substrate, pH, salinity). Therefore, we postulate that diurnal and nocturnal activities can influence the abundance of the hermit crab *D. insignis*, and this species selects shells available in the environment according to the needs of each demographic group within the population. To test this hypothesis, we evaluated the shell occupancy of individuals and their abundance during both the diurnal and nocturnal period on the northern coast of São Paulo state.

Material and Methods

Study area: The bay area of Ubatuba (23°26'S, 45°02'W) is located near the city of Ubatuba, on the northern coast of São Paulo (SP). Four small rivers – Indaiá River, Grande River, Lagoa River, and Acaraú River – intersect this bay, contributing organic matter and reducing the salinity of the bay water. Since October 8th, 2008, this region has been included in the Marine Environmental Protection Area (EPA) of the North Coast, established with the aim of prioritizing conservation and emphasizing the conscious use of marine resources in the region (Mantelatto et al., 2016). This coastal area has a very jagged geomorphology, characterized by contoured coves composed of estuarine environments, mangroves, rocky shores, pocket beaches, and bays (Braga et al., 2005). According to Mahiques (1995), this geomorphological characteristic is essential for the maintenance and establishment of many species, providing a favorable environment for the complete development of individuals that go through larval stages.

Data collection and laboratory analysis: Data collection was carried out during the four seasons of the year (summer, autumn, winter, and spring) in the Ubatuba region, in São Paulo, both during the day and at night. The animals were collected along eight transects at varying depths – 5, 10, 15, 20, 25, 30, 35, and 40 m (Fig. 1) – using a shrimp fishing boat equipped with double-rig trawl nets. Each trawl session lasted approximately 30 minutes in each transect, covering a sampling area of 18,000 m². In order to establish the coordinates, a Global Position System (GPS) was used, and an echo sounder recorded the depths of the sampled locations.

The individuals were sorted, packed in plastic bags, and frozen for further analysis. In the laboratory, the hermit crabs were removed from their shells and identified according to Melo (1999). Sex was determined based on the position of the gonopores and pleopod count. The hermit crabs without shells at the time of collection were counted solely for abundance analyses. The shells occupied by the individuals were identified according to Rios (1994).

Data analysis: The hermit crabs were categorized into demographic groups: adult males (AM), adult females (AF), ovigerous females (OF), and juveniles (J), as outlined in Fernandes-Góes et al. (2005). The analysis of shell species used by the demographic groups of *D. insignis* was conducted through a contingency table, with chi-square statistics obtained via Monte Carlo simulation. This method allows obtaining P values in case the expected frequencies are less than 5, as described by Peat & Barton (2005). Differences between observed and expected frequencies were assessed using standardized residuals, which were interpreted by Z- scores (Siegel & Castellan, 1988).

A generalized linear model (GLM) with binomial distribution and log-link function was employed to analyze the abundance of hermit crabs across different depths and diurnal and nocturnal periods. Depths were grouped considering transects within the cove (5 to 15 m) and those outside the cove (20 to 40 m). This model selection was based on the Akaike information criterion (Akaike, 1974), as it exhibited the lowest value among the tested models.

Correspondence analysis (CA) was performed to explore the relationship between the abundance of shell species and the sampled areas during the study period. In this analysis, absolute abundance was considered, treating each species as an independent group to minimize the influence of the sampling design (Leps & Smilauer, 2003). Prior to this analysis, all data were refined by excluding species with low-occurrence frequency (>10%) (Cuesta et al., 2006; Bertini et al., 2010).

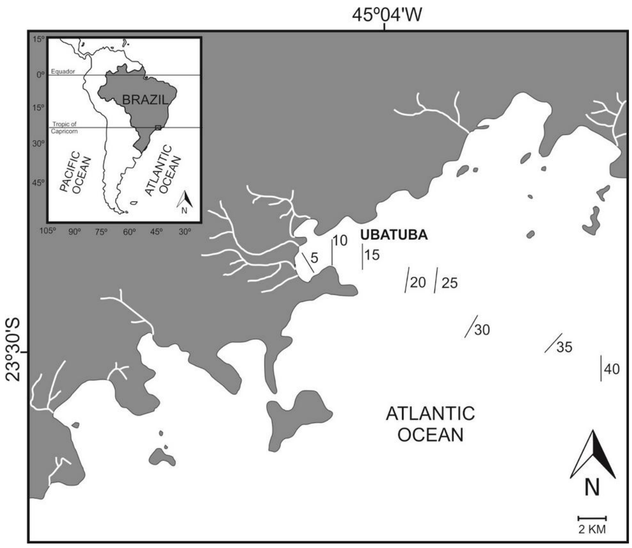

Figure 1. Map of the Ubatuba, São Paulo region where individuals of *Dardanus insignis* were collected in the year 2000, indicating the transects sampled within Ubatuba Bay and those in the outer region (20 to 40m).

Results

Overall, 527 individuals of *D. insignis* were collected, with 292 adult males (AM), 152 non-ovigerous females (AF), 35 ovigerous females (OF), and 48 juveniles (J). Among the total hermit crabs collected, 139 (26%) lacked shells and were not included in the shell occupation analyses. The hermit crabs (N = 388) utilized shells from 11 gastropod species. The most frequently occupied species among the demographic groups were *Olivancillaria urceus* (Roding, 1798) (22.9%), followed by *Siratus tenuivaricosus* (Dautzenberg, 1927) (15.2%) and *Buccinanops gradatus* (Deshayes, 1844) (13.1%) (Table I).

Significant differences were observed in shell occupation among the demographic groups (Pearson's chi-square = 47.38, p = 0.001). For males, the occupation (observed frequency) of Tonna galea (Morch, 1877) and Zidona dufresnii (Donovan, 1823) was higher than expected, whereas that of *O. urceus* and *Fusinus marmoratus* (Philippi, 1846) was lower than expected (Table 1). Among adult females, the species *S. tenuivaricosus* and *T. galea* exhibited lower observed frequency of

Table I. Contingency table of occupation of shells by demographic groups of *Dardanus insignis* collected in Ubatuba – SP. The first number corresponds to the observed frequency, and the number in parenthesis represents the expected frequency of shell occupation by the demographic groups. AM= adult males; AF= adult females; OF= ovigerous females; J= juveniles; *Means statistical differences p<0.05.

Shells	**AM**	**AF**	**OF**	**J**	**TOTAL**
Olivancillaria urceus (Roding, 1798)	43* (51.4)	30 (23.4)	12* (6.9)	4 (7.3)	89
Siratus tenuivaricosus (Dautzenberg, 1927)	38 (34.1)	9* (15.5)	5 (4.6)	7 (4.9)	59
Buccinanops gradatus (Deshayes, 1844)	31 (29.4)	10 (13.4)	7 (3.9)	3 (4.2)	51
Fusinus marmoratus (Philippi, 1846)	21* (28.3)	17 (12.9)	0 (3.8)	7 (4.0)	45
Olivancillaria vesica (Gmelin, 1791)	15 (20.2)	15* (9.2)	1 (2.7)	4 (2.9)	35
Zidona dufresnii (Donovan, 1823)	22* (16.7)	7 (7.6)	0 (2.2)	0 (2.2)	29
Stramonita haemastoma (Linnaeus, 1767)	20 (15.6)	4 (7.1)	1 (2.1)	2 (2.2)	27
Tonna galea (Morch, 1877)	16* (9.8)	1* (4.5)	0 (1.3)	0 (1.4)	17
Cymatium parthenopeum (Von Salis, 1793)	11 (9.2)	4 (4.2)	0 (1.2)	1 (1.3)	16
Conus clerii (Reeve, 1844)	2 (4.6)	2 (2.1)	4 (0.6)	4* (0.7)	12
Semicassis granulata (Born, 1778)	5 (4.6)	3 (2.1)	0 (0.6)	0 (0.7)	8
Total	224	102	30	32	388

occupation than expected, while *Olivancillaria vesica* (Gmelin, 1791) had higher occupation. Meanwhile, ovigerous females occupied *O. urceus* more than expected, and juveniles occupied *Conus clerii* (Reeve, 1844) more than expected (Table I).

The GLM results for the distribution of hermit crabs revealed significant differences between the depths of the inner region (5 to 15m) and the outer region (20 to 40m) of the cove (Wald Chi-square = 21.683; p = 0.000). Additionally, there was a significant interaction between the period (diurnal and nocturnal) and depth (Wald Chi-square = 5.989; p = 0.014), indicating a higher abundance of individuals in the outer region of the cove during the nocturnal period (Fig. 2). Furthermore, a greater diversity of shell occupation by species was observed at greater depths (Fig. 3).

The correspondence analysis indicated that axis 1 and axis 2 explained 46.2% and 28.2% of the total variation, respectively (Fig. 4). The shells of *O. vesica*, *Semicassis granulata* (Born, 1778), *B. gradatus*, and *O. urceus* exhibited high correspondence with the 30-m and 35-m transects, while the remaining species – *Z. dufresnii*, *F. marmoratus*, *Cymatium parthenopeum* (Von Salis, 1793), *S. tenuivaricosus*, *Stramonita haemastoma* (Linnaeus, 1767), and C. clerii – showed higher correspondence with the 40-m transect. Meanwhile, the species *T. gallea* exhibited higher correspondence with the 10-m transect.

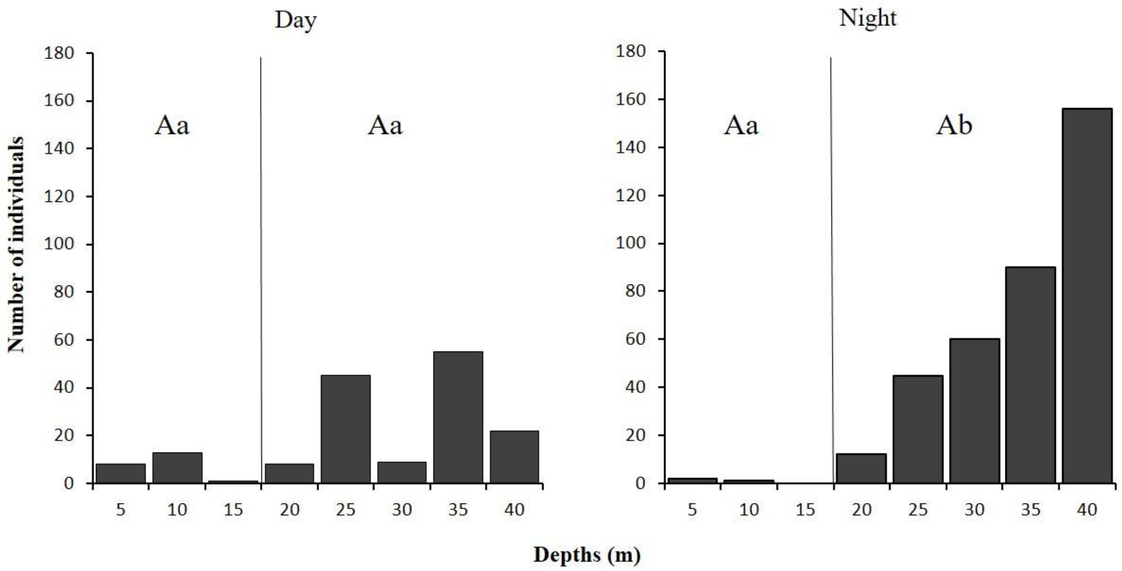

Figure 2. Abundance of individuals of hermit crab *Dardanus insignis* collected in Ubatuba – SP in different transects during the day and at night. Capital letters indicate a significant difference in the comparison of means between depths (5 to 15m and 20 to 40m) within the same period (day and night). Lowercase letters indicate significant difference when comparing mean depths (5 to 10m and 20 to 40m) between periods (day and night).

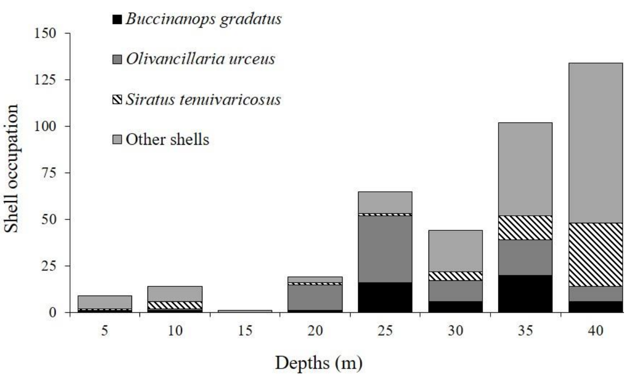

Figure 3. Distribution of the most abundant shells occupied by the hermit crab *Dardanus insignis* according to depth, collected in Ubatuba - São Paulo in the year 2000.

Discussion

In the present study, the hermit crab *D. insignis* occupied 11 species of gastropod shells. Among them, *O. urceus* was significantly more abundant compared to other species. One of the crucial factors influencing the choice of shells by hermit crabs is their greater availability in the environment (Fransozo et al., 2008). This shell species is the most readily available on non-consolidated sea bottoms in southeastern Brazil (Miranda et al., 2006; Mantelatto et al., 2007; Ayres-Peres et al., 2012) which typically inhabits sandy and muddy substrates at depths of up to 50 meters (Rios, 1994). The preference for occupying O. urceus was also noted by Frameschi et al. (2015), which suggested that this hermit crab is better adapted to this specific shell species. Additionally, the affinity for this shell by D. insignis has been consistently documented in other studies, including those by Branco et al. (2002), Fernandes-Goés et al. (2005), Mantelatto et al. (2007), Ayres-Peres et al. (2008), and Fransozo et al. (2008).

The habit of individuals from different demographic groups occupying the same shell species (in this case, *O. urceus*) reduces intraspecific competition, a fundamental factor that influences the population level of the hermit crab (Hahn, 1998). Although O. urceus was the most commonly occupied shell across all demographic groups, other shells also proved important for the species. Ayres-Peres et al. (2008) identified that *D. insignis* inhabits the coast of Rio Grande do Sul, showing variations in shell occupation. The most frequently occupied shell was that of *Buccinanops lamarckii* (Kiener, 1834), followed by B. gradatus, and only then by O. urceus. The researchers observed no variation in shell occupation among different demographic groups. Garcia et al. (2003) previously reported that this hermit crab can utilize other types of protection, not necessarily Gastropoda, such as the barnacle

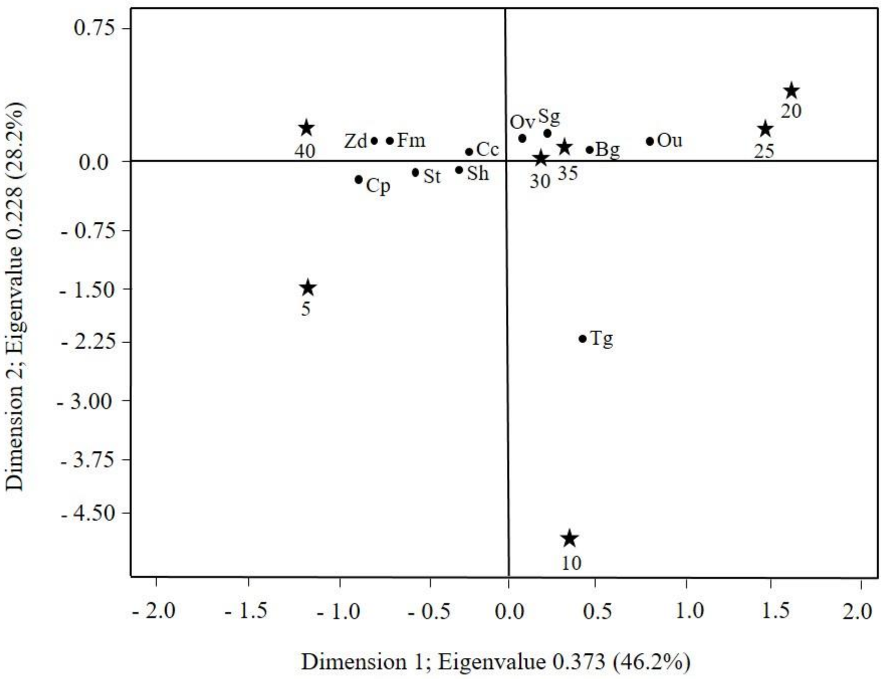

Figure 4. Correspondence analysis evaluating the abundance of shell species within the sampling areas. Circles= shell species; Stars= depths. Bg= *Buccinanops gradatus;* Cc= *Conus clerii;* Cp= *Cymatium parthenopeum;* Fm= *Fusinus marmoratus;* Ou= *Olivancillaria urceus;* Ov= *Olivancillaria vesica;* Sg= *Semicassis granulata;* Sh= *Stramonita haemastoma;* St= *Siratus tenuivaricosus;* Tg= *Tonna galea;* Zd= *Zidona dufresnii*.

shell of *Balanus venustus* (Darwin, 1854), covered with small cirriped shells of the same species.

Adult males exhibited a higher occupancy than expected for *T. galea* and *Z. dufresnii*, suggesting that shell selection is not solely influenced by species availability. Larger individuals of *D. insignis* may prefer larger shells, such as those of the aforementioned species, which feature larger shell apertures than *O. urceus*. The aperture size factor is critical in selection, as observed in other hermit crabs, including *Pagurus middendorffii* (Brandt, 1851), as described by Wada et al. (1997). Furthermore, according to Gherardi (1991), males are more susceptible to predation during competition for females and shells, with heavier shells providing additional protection for these animals.

In relation to females, a higher occupancy than expected was observed for the species O. vesica, whereas for ovigerous females, this occupancy occurred for *O. urceus*. Hazlett et al. (2005), suggested that Clibanarius vittatus (Bosc, 1802) females occupying shells larger and heavier than their ideal size tend not to be ovigerous, with ovigerous females being more frequently found using shells suitable for their size. However this observation did not align with the findings of this study. Here, all females were observed occupying larger and heavier shells, irrespective of their ovigerous condition. This outcome could be explained by the greater availability of these shells in the environment or, alternatively, due to their larger internal volume, facilitating protection for a future ovigerous condition (Miranda et al., 2006).

In the present study, juveniles occupied shells of varied sizes and shapes. Garcia & Mantelatto (2000) proposed that the diversity in the occupation of shell species during the juvenile phase likely arises from the greater availability of gastropod shell species with varying sizes in the environment. As stated by Ayres-Perez et al. (2012) the morphology and size of the shells did not appear to be determining factors for the species during the juvenile period. Regarding the individuals without shells, probably they may have become detached during the trawling activities, as these animals are rarely encountered without abdominal protection (Miranda et al., 2006).

Dardanus insignis demonstrated predominantly nocturnal activity patterns, especially at greater depths, from 30 meters onward. Additionally, the species abundance is closely linked to environmental factors, including substrate composition, as suggested by Fransozo et al. (2012). Frameschi et al. (2016) found a positive correlation between coarse, medium, and fine sand granulometric fractions and the distribution of *D. insignis* at 15 and 20 meters in depth. They stated that this hermit crab species is more abundant in transects farther from the coast due to reduced environmental fluctuations compared to coastal regions. These same environmental conditions also play a crucial role in determining the diversity and abundance not only of hermit crab species but also of associated gastropods, as highlighted by Furlan et al. (2013) and Pires (1992).

Another critical factor influencing species distribution is luminosity. According to Chiesa (2010), in their studies with crayfish, the distribution of diurnal/nocturnal activity depends on light intensity. As demonstrated in this study, there are changes in the habits of hermit crabs that vary according to the time of day and may be induced by light. This results in the development of nocturnal or diurnal behavior patterns under different light intensity cycles. Strauss & Dircksen (2010) stated that the circadian rhythms of spontaneous locomotion can reveal bimodal patterns, with increased activity both after the onset of light and after the light has been turned off, with greater activity observed with the latter, a behavior that persists under constant darkness. This observation may also explain the diurnal activities found for the *D. insignis* which were intensified at night (constant darkness). In other studies, as described by Ismail (2011), different patterns were also observed among the analyzed hermit crab species, based on variations in photoperiods. Their experiment provided evidence for circadian rhythmicity among hermit crabs. While the majority of brachyuran crabs are primarily nocturnal considering their activity, certain hermit crab species exhibit diurnal tendencies, likely because of the protective shelter provided by shell occupation (Warner, 1977). On the other hand, some species demonstrate both diurnal and nocturnal behaviors (Caine, 1980). The increased abundance of hermit crabs captured during the night may be attributed to their heightened nocturnal activity. During periods of inactivity, these animals tend to bury themselves within the substrate (Melo, 1999), making their capture more challenging.

Thus, we conclude that *D. insignis* can occupy various shell species; however, they tend to prefer the ones that are more abundant in the environment and that are better adaptable considering the needs of each group. The higher abundance at greater depths is likely influenced by factors such as luminosity and the diverse availability of shells.

Ethical statement

The present investigation did not involve regulated animals and did not require approval by an Ethical Committee

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