



Coexistence of two sympatric hermit crab species from South Brazil: the effect of the shell adequacy index and circadian movement patterns

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Abstract Gastropod shells play an important role in the life story of hermit crabs, influencing biological characteristics directly. The adequacy of shells for hermit crabs can be evaluated through the Shell Adequacy Index, which calculates the shell's ideal size/weight compared to the actual dimensions of the occupied shells. To avoid competition for shells, animals can display a variety of strategies including alterations in their circadian rhythms. This study aimed to evaluate if two sympatric species of hermit crabs—*Pagurus brevidactylus* and *Pagurus criniticornis*—are competing for the best fitting shells and if they present differences in their circadian rhythms. Their shells were identified and measured regarding

the aperture length and width. The shell adequacy was calculated using linear models of the Shell Aperture Length and Width, and the period of activity of the animals was filmed for 24 h and later analyzed. The period between 10 am and 2 pm represented daytime, while 10 pm to 2 am represented nighttime. *Pagurus brevidactylus* occupied mainly *Cerithium atratum* and *Claremontiella nodulosa* shells, while *P. criniticornis* occupied mainly *C. atratum* shells. Our results showed that the two species are inhabiting shells with similar traits, which may indicate competition. The species do not present distinct activity periods; however, the shell occupation pattern suggests a competition at the functional level.

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Introduction

Empty gastropod shells play a vital role for most hermit crab species' life history (Kellogg 1976). As these animals lack a calcified abdomen, they require external structures for protection (Vance 1972b; Kellogg 1976; Williams and McDermott 2004). The quality of the shell can have an important influence on different aspects of the hermit crab biology such as: population structure, size, reproduction, mortality, growth, among others (Vance 1972a; Abrams 1980; Buckley and Ebersole 1994; Carlon and Ebersole 1995; Angel

2000; Gorman et al. 2015; da Silva et al. 2018; Staniski et al. 2018; Rodrigues et al. 2020).

Since empty shells are only available after the gastropods' death, they can constitute a limiting resource for hermit crabs (Vance 1972a; Bertness 1981b; Mantelatto et al. 2016). Limitation can lead to competition between hermit crabs (Reese 1969). Competition may be aggressive or opportunistic (Osorno et al. 1998). Considering all factors related to the various characteristics a shell can present, along with the possibly low availability of suitable empty gastropod shells in an environment (Bollay 1964), hermit crabs may not always find the best shells, therefore occasionally occupying poorly fitted ones (Vance 1972a). Hermit crabs do not select shells randomly, instead, they inspect the available ones looking for the most adequate (Ragagnin et al. 2016; Suárez-Rodríguez et al. 2019). Conditions often associated with the quality of shells are the presence/absence of epibionts, internal volume, size and weight. To quantify shell quality regarding how they fit hermit crabs, Vance (1972a) created the Shell Adequacy Index (SAI). This index uses a linear model of the measurements of hermit crabs and shells to calculate the shell's ideal measurements, comparing them to the observed ones [for more information on the SAI, see Vance (1972a)].

In intertidal zones, several hermit crab species often coexist (Imazu and Asakura 1994; Gherardi and Nardone 1997; Alcaraz et al. 2020; da Silva et al. 2020). Since species share the same scarce resources (da Silva et al. 2020, 2021), this coexistence is said to be often mediated by shell competition, either by exploitation or interference (Vance 1972a; Kellogg 1977; Bertness 1981a; Gherardi and Nardone 1997; da Silva et al. 2020). The competition by exploitation is related to the use of shared resources and depends on their availability in the environment, indirectly affecting competing species. Meanwhile, competition by interference has direct effects since it consists of an animal literally inhibiting others from accessing a shared resource and does not necessarily depend on resource availability (Holdridge et al. 2016).

One mechanism that animals may develop to avoid competition is adopting different circadian rhythms. The circadian rhythms are regulated by an internal clock allowing the organisms to anticipate and prepare for changes in the environmental conditions, aligning their activities to the most appropriate time periods of the day (Vitaterna et al. 2001). Different

circadian rhythms may reduce competition by interference, decreasing the encounter rates among hermit crabs (Collins 2005; Strauss and Dirksen 2010). Although crustaceans are often more active during nighttime (Drzewina 1906; Palmer 1971; Sokolowicz et al. 2007), as seen for *Clibanarius antillensis* Stimpson, 1859 (da Silva et al. 2022a, b), they can also show no activity pattern at all or be influenced by environmental features such as tides (Guerra-Castro et al. 2007; Simões et al. 2010).

The present study aims to evaluate the likelihood of competition in two sympatric species of hermit crabs: *Pagurus brevidactylus* (Stimpson, 1859) and *Pagurus criniticornis* (Dana, 1852), both abundant species inhabiting the sublittoral region on rocky and sandy shores (McLaughlin 1975; Leite et al. 1998; Mantelatto et al. 2007; Sant'Anna et al. 2012). First, the shell competition will be assessed (using the SAI) by testing if one species is occupying best fitting shells, while the other uses sub-optimal ones. Then, the circadian patterns in both species will be investigated through controlled experiments to evaluate possible differences related with shell competition.

Methods

Sampling

The specimens were sampled at Sepultura Beach (27°08'28.67"S and 48°28'41.41"W), in the municipality of Bombinhas, Santa Catarina, on the southern Brazilian coast. For the shell adequacy analysis, specimens of *Pagurus brevidactylus* and *Pagurus criniticornis* were sampled seasonally in May 2017 (autumn), August 2017 (winter), October 2017 (spring), and March 2018 (summer), with one expedition per season. To collect the hermit crabs for this study, we conducted sampling on various substrates, including rocks, algae beds, and consolidated/unconsolidated substrates during low tide. This allowed for improved visibility of the animals with the aid of snorkels. We employed free diving techniques, which are commonly used in sublittoral sampling. Two divers were deployed to the study area, and each sampled for a period of 1 h during daylight hours. For the study of shell adequacy, we separated the collected animals according to their respective species. These specimens were immediately frozen and placed in

labeled plastic bags for storage. Later, the specimens were preserved in 70% ethanol to ensure their suitability for future analyses.

For the movement activity experiment, samples were conducted in October 2016, at the same location, during daylight, at low tide for two consecutive days. The animals were stored in plastic bags filled with local water and stored in thermic boxes. All specimens were transported to the Aquatic Biology Laboratory at Universidade Estadual do Centro-Oeste (UNICENTRO), Guarapuava, Paraná State, Brazil.

Shell occupation and shell adequacy index

Six species coexisted in the sampled area: *Calcinus tibicen* (Herbst, 1791); *Clibanarius antillensis* Stimpson, 1859; *Dardanus insignis* (de Saussure, 1857); *Paguristes tortugae* Schmitt, 1933; *Pagurus brevidactylus* (Stimpson, 1859), and *Pagurus criniticornis* (Dana, 1852) (da Silva et al. 2021). Both species of the genus *Pagurus* are closely related phylogenetically, being part of the “Provenzano group” (Sultana et al. 2022) and are also the most abundant ones in the area, thus being selected as models for this study. Animals were thawed in room temperature (20–25 °C), carefully removed from their shells with the aid of fine tweezers and identified to species level with the aid of a stereomicroscope, following Melo’s (1999) taxonomic key.

The shells occupied by each hermit crab were identified according to Rios (2009), and shell occupation pattern was described based on their measurements. The length and width of the shell aperture were measured with a digital caliper (0.1 mm precision). Then, shells were weighed with an electronic precision scale (0.01 g). After measurements, all animals were deposited in the Aquatic Biology Laboratory at the Center for Educational and Technological Development of Guarapuava (CEDETEG) at UNICENTRO, Guarapuava, Parana state, Brazil.

The Shell Adequacy Index (SAI) was adapted from Vance (1972a). This index is based on the linear equation for a hermit crab and a shell’s morphometric features. In the present study, the cephalothoracic shield length (mm) (CSL) was used as the hermit crab variable and the shell aperture length (mm) (SAL) and aperture width (SAW) as the shell variables. First, data were log-transformed as recommended by Vance (1972a) to decrease residual variance. Then,

the linear equations ($\ln y = a + \ln x * b$) between shell aperture length and cephalothoracic shield length, and between shell aperture width and cephalothoracic shield length for both species were obtained separately. Afterwards, Vance’s Shell Adequacy Index was calculated for each specimen based on the obtained equation (see results for the equation).

The result obtained from the linear equation is expected to indicate the ideal shell size for a given hermit crab. The SAI was then calculated according to the formula $\frac{Occupiedshellsize}{Idealshellsize}$. If the SAI for a given hermit crab is equal to 1, it is an indicative of an ideal shell fit, while values higher or lower than 1 indicate shells larger or smaller than ideal, respectively. With this information we evaluated the shell fit of each sampled animal. The SAI values were compared between species using the Wilcoxon rank-sum test (non-parametric data). In order to investigate the resource utilization between hermit crab species we applied a permutation multivariate analysis of variance (PERMANOVA) to compare the morphological parameters of occupied shells. We selected the following shell attributes: Shell aperture height, shell aperture width and shell weight. Then, a nMDS was employed to create a visual representation of the morphological shells’ attributes occupied by the hermit crabs.

Movement activity

We studied 14 specimens of *P. brevidactylus* and 15 of *P. criniticornis*. All hermit crabs presented intact morphology, were in intermoult stage and had their cephalothoracic shield length (CSL) measured. The experiments carried out with these specimens to study the movement patterns were conducted during a 24 h period. For that, groups of co-specific individuals were acclimated for two weeks in aquarium tanks (70×35×25 cm, approximately volume of 61 L) with shell gravel and rocks as substrate. The aquariums were linked through a rearing system with a skimmer biological filter (Gregati et al. 2010). Water quality was kept close to natural conditions: 35 salinity, 24 °C (± 1 °C), and a 12-h dark/12-h light photoperiod. The hermit crabs were fed daily ad libitum with ornamental fish ration, nori algae, and pieces of fish muscles twice a day (during nighttime and daytime).

After acclimation, animals were individually placed in plastic trays filled with 1 L of water from the original aquarium tank. Each observation tray had a sandpaper-checkered bottom (2×2 cm) to facilitate hermit crabs' movement. Each specimen was filmed for 24 h with a security camera (Sony® Infrared SO, 1400 lines, 811×508 pixels) placed 30 cm above the tray. During the nighttime period, infrared light-emitting diode (LED) lamps were attached to the camera. Animals were not fed during the experiment.

For each specimen, we measured the time they moved (in seconds) and the distance traveled in the tray (in cm) between 10 am to 2 pm (daytime) and from 10 pm to 2 am (nighttime). We also calculated the mean movement time and mean distance traveled for each species. Total movement time and distance traveled were compared both between species, and between periods using a two-way ANOVA. First, we used the distance traveled as the dependent variable, and species and period as the independent variables. Then, we used the movement time as the dependent variable, and species and period as the independent variables.

We also calculated the movement rate of each animal as the ratio between the distance traveled and the time spent moving. This was used to evaluate if their speed changed between periods. To test this hypothesis, we used a two-way ANOVA with the movement rate as the dependent variable, and species and period as the independent variables.

Results

Shell Occupation

Significant differences among occupied shell morphological attributes were observed between the hermit crab species (PERMANOVA, Pseudo- F (2, 1263) = 110.63, $p < 0.001$). (Fig. 1). These differences indicate that *P. brevidactylus* is exploring and occupying more morphologically diverse shells than *P. criniticornis*. This can be seen as the number of occupied shell species by each species: *P. brevidactylus* occupied 21 different gastropod species whilst *P. criniticornis* occupied only 5 different species (Table 1).

Shell Adequacy Index

The allometric equations used to calculate the SAI for *P. brevidactylus* were $\ln\text{SAL} = \ln\text{CSL} * 0.339 + 0.123$ ($r^2 = 0.49$) for shell aperture length and $\ln\text{SAW} = \ln\text{CSL} * 0.479 + 0.129$ ($r^2 = 0.57$) for shell aperture width.

The allometric equations used to calculate the SAI for *P. criniticornis* were $\ln\text{SAL} = \ln\text{CSL} * 0.431 + 0.081$ ($r^2 = 0.56$) for shell aperture length and $\ln\text{SAW} = \ln\text{CSL} * 0.51 + 0.131$ ($r^2 = 0.62$) for shell aperture width.

The shell adequacy index based either on shell aperture length (Wilcoxon test $W = 115,017$, $p = 0.12$)

Fig. 1 nMDS plot indicating the shells' morphological attributes used by each hermit crab species. Red: *Pagurus brevidactylus*. Blue: *Pagurus criniticornis*

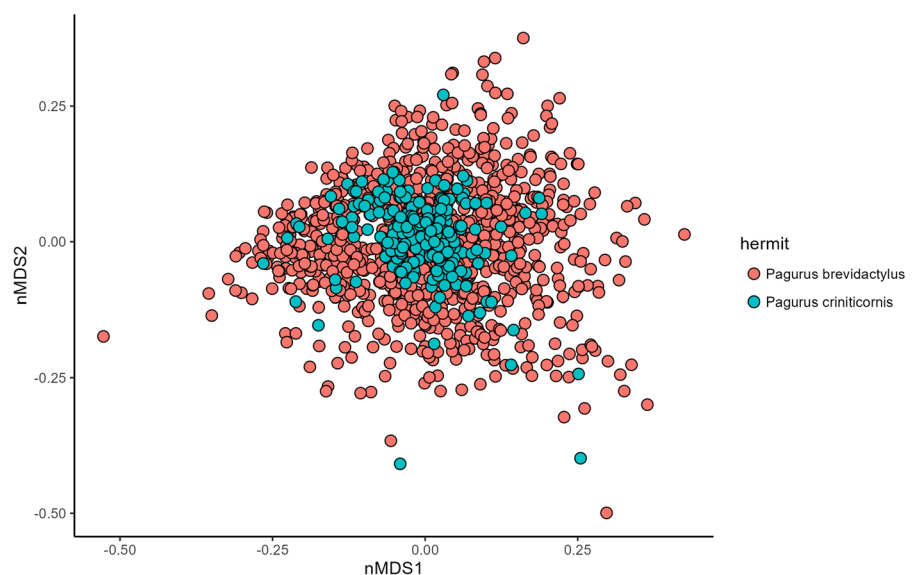


Table 1 Number of individuals per species and biomass of the gastropod species' shells occupied by *Pagurus brevidactylus* and *Pagurus criniticornis* at Sepultura Beach, Bombinhas/SC

Gastropod species' shells	<i>Pagurus brevidactylus</i>		<i>Pagurus criniticornis</i>		Total
	N (%)	Mean \pm SD	N (%)	Mean \pm SD	
<i>Cerithium atratum</i>	660	0.56 g \pm 0.35	235	0.73 g \pm 0.3	895
<i>Claremontiella nodulosa</i>	220	0.72 g \pm 0.37	2	0.75 g \pm 0.19	222
<i>Stramonita brasiliensis</i>	30	0.69 g \pm 0.79	1	–	31
<i>Stramonita haemastoma</i>	25	1.2 g \pm 0.8	4	2.1 g \pm 1.06	29
<i>Leucozonia nassa</i>	14	1.1 g \pm 0.82	–	–	14
<i>Anachis lyrata</i>	13	0.48 g \pm 0.28	–	–	13
<i>Costoanachis</i> sp.	13	0.29 g \pm 0.28	–	–	13
<i>Agathistoma viridulum</i>	11	0.76 g \pm 0.52	1	–	12
<i>Coralliophila aberrans</i>	8	0.40 g \pm 0.29	–	–	8
<i>Pisania pusio</i>	4	1.95 g \pm 1.4	–	–	4
<i>Astraliium latispina</i>	4	0.62 g \pm 0.36	–	–	4
<i>Phrontis alba</i>	4	0.21 g \pm 0.04	–	–	4
<i>Mitrella dichroa</i>	3	0.08 g \pm 0.04	–	–	3
<i>Modulus modulus</i>	2	0.27 g \pm 0.06	–	–	2
<i>Favartia cellulosa</i>	2	1.69 g \pm 0.62	–	–	2
<i>Gemophos auritulus</i>	2	4.71 g \pm 0.1	–	–	2
<i>Terebra taurina</i>	2	0.34 g \pm 0.14	–	–	2
<i>Cabestana felipponei</i>	1	–	–	–	1
<i>Epitonium novangliae</i>	1	–	–	–	1
<i>Littoraria flava</i>	1	–	–	–	1
<i>Polinices uberinus</i>	1	–	–	–	1
Total	1021		243		1264

or shell aperture width (Wilcoxon test $W = 115,864$, $p = 0.17$) did not differ between species (Fig. 2).

Movement Activity

For *P. brevidactylus*, we used animals with mean CSL of 3.1 mm (± 0.44 mm SD), ranging from 3.0 mm to 4.4 mm. They occupied shells with mean SAL of 7.2 mm (± 1.31 mm SD) ranging from 4.9 mm to 9.1 mm and mean SAW of 5.1 mm (± 0.96 mm SD) ranging from 2.7 mm to 6.7 mm. For *P. criniticornis*, we used animals with mean CSL of 2.7 mm (± 0.5 mm SD) ranging from 2 mm to 3.5 mm. These inhabited shells had mean SAL of 4.5 mm (± 1.4 mm SD) ranging from 2.6 mm to 7.1 mm and mean SAW of 3.65 mm (± 1.5 mm SD) ranging from 2.2 mm to 8.1 mm.

Non-significant differences were found regarding movement activity patterns. Neither of the species showed differences in activity time (Two-Way

ANOVA, $df = 1$, $F = 0.593$, $p > 0.05$) or between periods (Two-Way ANOVA, $df = 1$, $F = 0.899$, $p > 0.05$), with no interaction between period and species either ($df = 1$, $F = 0.001$, $p > 0.05$) (Fig. 3). Thus, both species presented no activity pattern for either day or night. Regarding distance traveled between species (Two-Way ANOVA, $df = 1$, $F = 0.008$, $p > 0.05$) or between periods (Two-Way ANOVA, $df = 1$, $F = 2.221$, $p > 0.05$), the species showed no differences. Also, no difference was found when we tested the interaction between period and species either (Two-Way ANOVA, $df = 1$, $F = 0.015$, $p > 0.05$) (Fig. 4). For movement rate, the two-way ANOVA showed no differences between species ($df = 1$, $F = 0.064$, $p > 0.05$) or between periods ($df = 1$, $F = 0.625$, $p > 0.05$), and no difference was found when we tested the interaction between period and species either ($df = 1$, $F = 0.982$, $p > 0.05$) (Fig. 5).

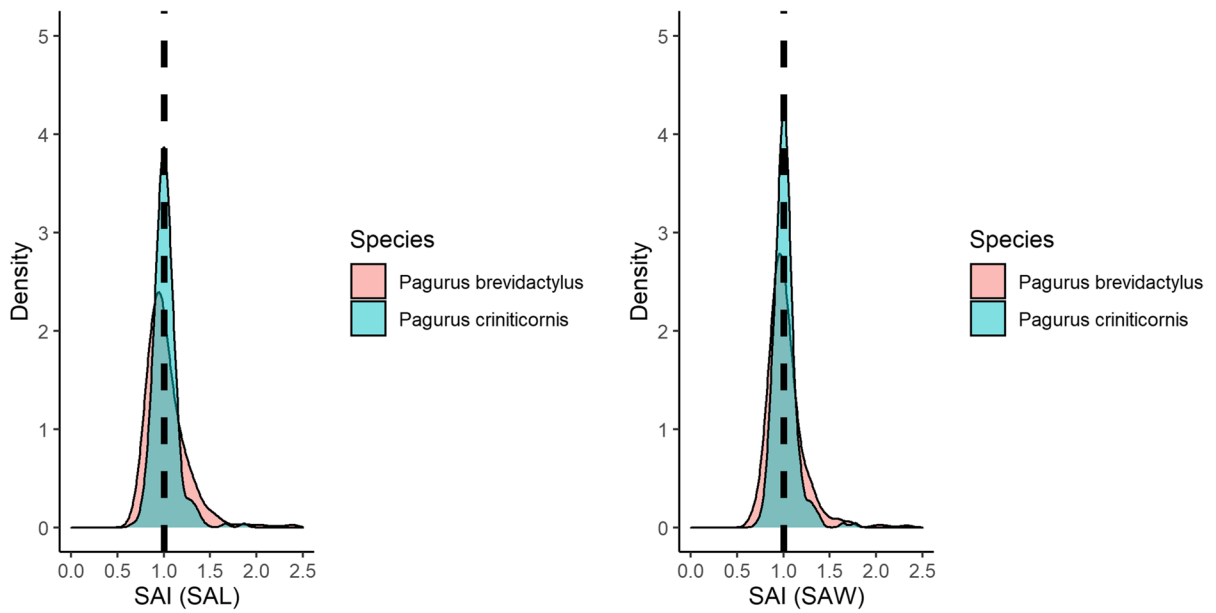


Fig. 2 Values of Shell Adequacy Index (SAI) based on carapace shield width (SAW) and length (SAL) for each hermit crab species. The dashed line indicates the optimal SAI value (SAI=1)

Fig. 3 Boxplot indicating the time spent moving (seconds) between treatments. Line inside the box indicates the median, the box indicates the first and third quartiles, and whiskers indicate minimum and maximum

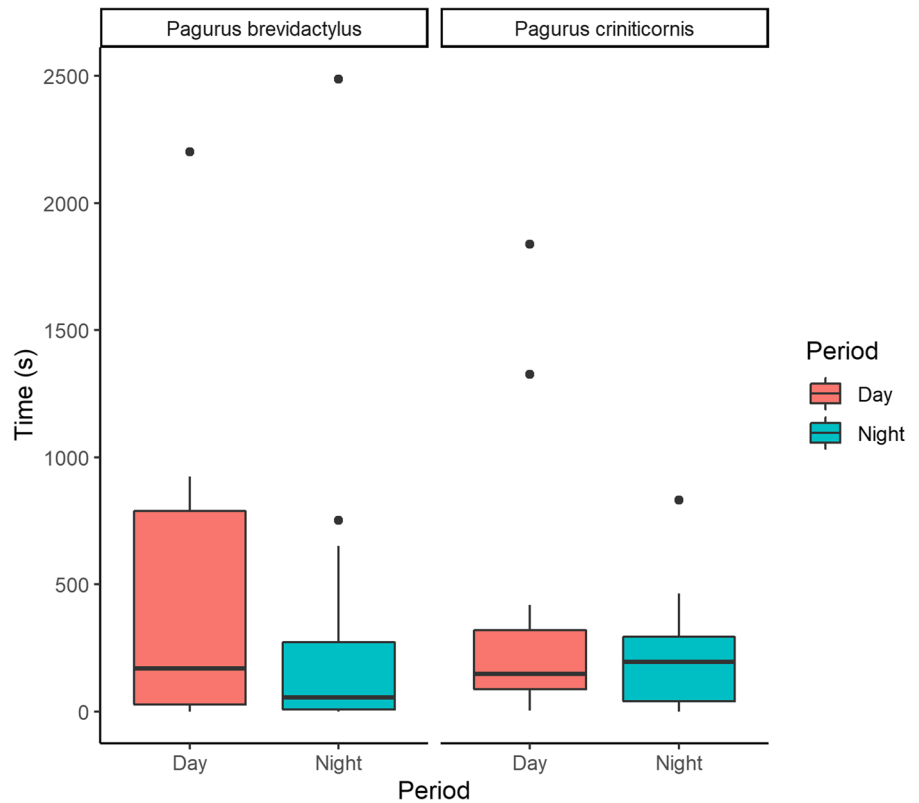


Fig. 4 Boxplot indicating the distance moved (cm) between treatments. Line inside the box indicates the median, the box indicates the first and third quartiles, and whiskers indicate minimum and maximum

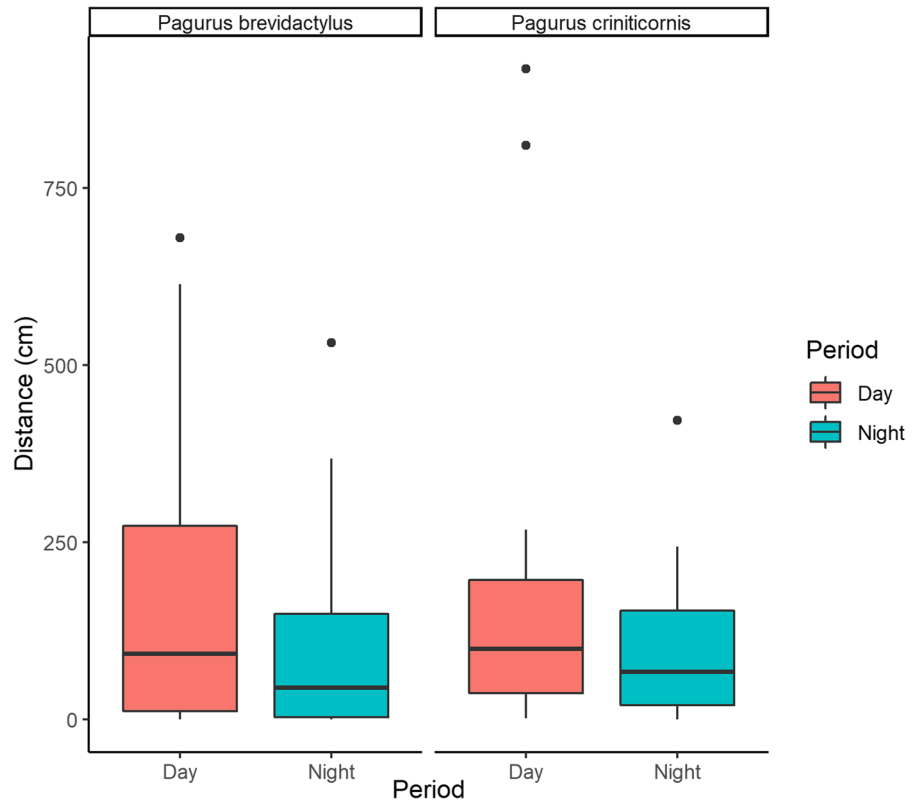
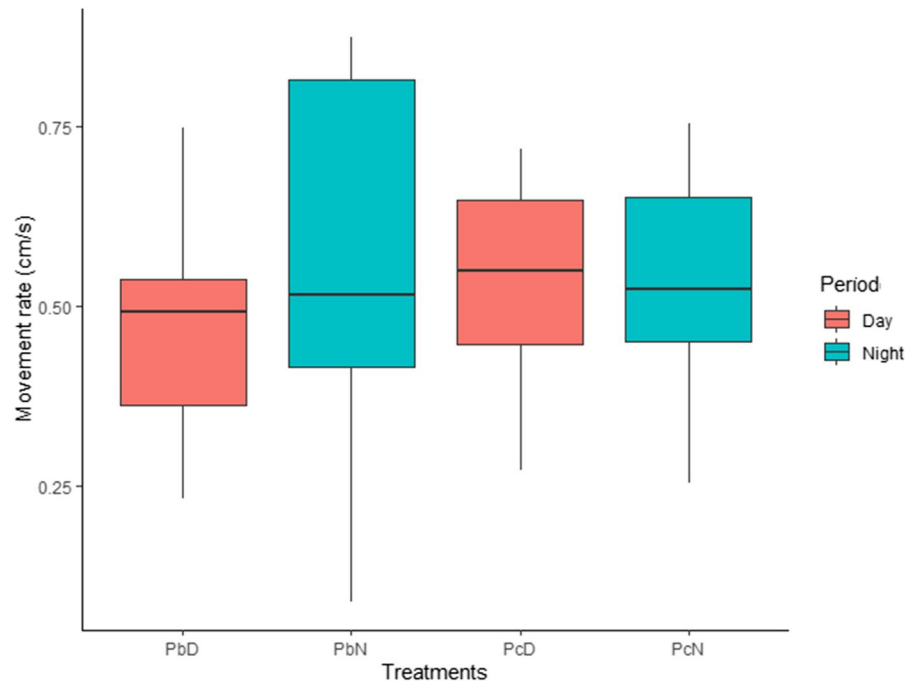


Fig. 5 Boxplot indicating the movement rate (cm/s) between treatments. PbD: *Pagurus brevidactylus* daytime. PbN: *Pagurus brevidactylus* nighttime. PcD: *Pagurus criniticornis* daytime. PcN: *Pagurus criniticornis* nighttime. Line inside the box indicates the median, the box indicates the first and third quartiles, and whiskers indicate minimum and maximum



Discussion

Our results showed that the hermit crabs present similar movement pattern during their circadian cycles and presented no significant differences regarding the adequacy of the shells they are occupying, however, the occupation pattern itself revealed that *P. brevidactylus* is exploring and occupying more morphologically diverse shells than *P. criniticornis*.

Both *Pagurus* species did not present differences in their period of activity (daytime x nighttime), movement rate, or between each other. This activity pattern in both day and night has been reported for other crustaceans (Simões et al. 2010). Even though no statistical differences were found for hermit crabs' activity pattern, both *P. brevidactylus* and *P. criniticornis* are slightly more active during the daytime, possibly to avoid competition with other hermit crabs that inhabit the local area (da Silva et al. 2022a), which present a nighttime behavior, such as *Clibanarius antillensis* (da Silva et al. 2022b).

The coexistence between these two *Pagurus* species is not mediated by differential temporal niche. This could be explained by the fact that these two sympatric species are closely related (Sultana et al. 2022), thus, their circadian rhythm could have been conserved during the evolution of these species. Further comparative studies on the natural circadian rhythm of other *Pagurus* species from the “Provenzano group” and from other groups of the genera are needed in order to understand how much the circadian rhythms have been preserved throughout evolution.

Although the scarcity of empty and suitable shells may pose a problem in some marine environments, due to their limited availability (Turra and Denadai 2004, Silva et al. 2018, foresting intra and/or inter-specific competition (Vance 1972a; Bertness 1981c; Gherardi and Nardone 1997; Turra 2003), this does not seem to be the case in the study area. The quality of the occupied shells based on shell adequacy index did not significantly differ between *P. brevidactylus* and *P. criniticornis*. According to our results, most of the hermit crabs occupied shells with an index close to 1, indicating an overall good shell fit and availability in the studied area. Sant'Anna et al. (2012) studied the same two hermit crab species and noticed that while *P. brevidactylus* dominates the rocky shores, *P. criniticornis* dominates the unconsolidated substrates. Based on this information, a spatial niche partition in

which one species is more abundant in the rocky portion and the other, at the sandy portion, only overlapping on the transition between rocky and sandy bottoms, may be the strategy behind the coexistence of these two species, for avoiding direct competition.

Even though the number of specimens of *P. brevidactylus* occupying *C. atratum* shells was higher than that of *P. criniticornis*' (which could be due to the abundance of *P. brevidactylus* in our samples), *P. brevidactylus* presented a significative percentage of use of *C. nodulosa* shells (21.57%) in addition to *C. atratum* (64.71%). A total of 96.71% of the *P. criniticornis* specimens used *C. atratum* shells only. The preference of *Pagurus criniticornis* for *C. atratum* shells has been previously reported in another location (Leite et al. 1998; Mantelatto et al. 2007; Meireles et al. 2008; Mantelatto et al. 2016).

Our results showed that even though both species mostly occupied the same shells (*C. atratum* and *C. nodulosa*) considering the taxonomy identity of the shells, *P. brevidactylus* occupied more species than *P. criniticornis* (21 × 5 species, respectively). Moreover, when taken into account the shells measurements, results have shown *P. brevidactylus* explored shells morphologically more diverse than *P. criniticornis*. The shells' morphological attributes can be interpreted as functional traits (Violle et al. 2007; Villéger et al. 2008), and for hermit crabs, the shells aperture measures and weight are related with the size the hermit crabs can reach and their energy expenditure (Osorno et al 1998; Silva et al. 2018). Thus, considering a niche can be interpreted as a multidimensional hypervolume (Hutchinson 1957), *P. brevidactylus* presents a wider amplitude regarding the shell occupation niche, since it is occupying a more functionally diverse set of shells. The present study suggests that temporal niche, taxonomy identity and quality of the shell did not explain the coexistence between the studied species. However, differences were seen regarding the functional traits of the shells used, indicating that one species presents a wider niche amplitude considering this axis.

Hermit crabs are known for their fierce competition for shells (Turra and Denadai 2004; Sant'Anna et al. 2012; da Silva et al. 2020), employing various strategies to acquire the best-fitting shells (Gherardi and Vannini 1992, Gherardi and Nardone 1997, Sant'Anna et al. 2012). Such acquisition is often achieved through direct agonistic interactions (Lane

and Briffa 2020, 2022). Hence, the superior competitor can gain an edge by winning more contests and acquiring the best-fitting shells, exploring a more morphologically diverse set of shells, and driving the inferior competitors to occupy less optimal shell subsets. These subsets may not always be taxonomically different but functionally distinct. Therefore, the coexistence here may be achieved through *P. brevidactylus* driving its competitor, *P. criniticornis*, to occupy a different functionally smaller subset of shells.

Overall, our study showed that the competition for shells in these congener species is happening at the niche dimension related to shell occupation. Therefore, the coexistence between these species is probably being mediated by the exploitation of shells with distinct sizes/morphologies. As the niche can be seen as a n-multidimensional hypervolume (Hutchinson 1957), the functional niche could be partitioned whilst the temporal niche is not. Thus, future comparative studies are needed to understand how these circadian traits are conserved in other hermit crab's species and how the competition at the functional level is occurring.

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Data availability Data can be made available upon request.

Declarations

Conflict of Interest The authors declare there is no conflict of interest.

Ethical approval The research was conducted according to Brazilian's law and scientific ethics guidelines.

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