



PAGURIZED GASTROPOD SHELLS IN A NORTHEAST BRAZILIAN COASTAL LAGOON AT THE SEA-ESTUARY INTERFACE

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Abstract: Gastropods are known for the presence of calcareous shells, even after their death. The diversity of this resource can be reflected in the local diversity of living gastropods. These shells are used by hermit crabs as protection and against desiccation. Coastal lagoons are biodiversity hotspots and the site of recruitment of continent-sea connectivity, and their diversity is sometimes altered by connectivity events with adjacent areas. Therefore, we sought to make a list that evaluates the seasonal variation of diversity and demonstrates the pattern of shell use by hermit crab species. The samplings were standardized in six monthly repeated transects from February 2013 to January 2014, using a fishing net trawl. The shells were identified to species level and quantified. Diversity indexes were calculated, seasonally, for the assemblage of used shells. Hermit crabs used 14 species of gastropod shells, of which *Vitta virginea* and *Phrontis vibex* were the most abundant and frequent. The diversity indexes indicated a temporal variation of the shells, with April the month showing the highest difference in diversity. A reflection of the change in surface geomorphology, caused by the King Tide, its discharge and carrying of empty gastropod shells to the open sea. The usage patterns of these biogenic remains can reveal strategies of decreased intra/interspecific competition. Furthermore, we described the first record in the Brazilian Northeast of the hermit crab *C. symmetricus*, after its taxonomic resurgence.

Keywords: ecological resource; Gastropoda; *hotspots*; Paguroidea; taphonomy.

INTRODUCTION

The taxon Gastropoda Cuvier, 1797 is commonly known for its unique calcareous shell, usually helical, which shelters the entire body and, in some groups, is secondarily reduced or loses its character (Amaral & Nallin 2011). This group diversity is estimated at between 80,000 and

135,000 described species (Abbott 1989, Strong *et al.* 2008). Their shells are biogenic remains that are conspicuous in aquatic environments and serve as a resource for other taxa (Walker 1990, Fraaije 2003).

Decapod crustaceans with non-calcified abdomen, commonly known as hermit crabs (members of Superfamily Paguroidea Latreille,

1802), have a behavior of occupying empty shells of gastropods (Turra & Leite 2001) and, to a lesser extent, a variety of other shelters (bivalve shells, dead calcareous corals, sabellariid tubes, stone cavities, sponges) (Gherardi & Cassidy 1995, Imafuku & Ando 1999, Garcia *et al.* 2003, Meireles *et al.* 2003). Hermit crabs use empty gastropod shells and other shelters as protection against predation and desiccation (Hazlett 1996, Turra & Leite 2000, Barnes 2003). This resource use is a case of commensalism known as metabiosis, where an organism uses the biogenic resource of another species and depends on it for survival (Walker 1989, Wheeler 2012).

The choice and use of the gastropod shells shows preference patterns, based on the suitability (architecture and/or morphometric standard) of the body (Biagi *et al.* 2006, Terossi *et al.* 2006, Frameschi *et al.* 2013, Vale *et al.* 2017) and the resource availability in the environment (Rodrigues *et al.* 2000, Meireles *et al.* 2003, Mantelatto *et al.* 2007, Ayres-Peres *et al.* 2008, Frameschi *et al.* 2013, Vale *et al.* 2017). The suitability of an optimal shell can vary between species of hermit crabs, reflecting several selective pressures associated with the distinct habitats that act differently on each species, population and sex (Bertness 1981, Dominciano *et al.* 2009). In addition, this resource is a limiting factor to life history traits for hermit crab species, such as individual and population growth, and reproduction (Mantelatto & Garcia 1999, Mantelatto & Garcia 2000, Arguelles-Tico *et al.* 2010).

The availability of the 'shell' resource can vary according to the environment and the diversity of adjacent areas (Fotheringham 1976, Meireles *et al.* 2003). In Brazil, coastal lagoons are often found from the Parnaıba delta to southeast region (Amaral & Jablonski 2005). These are widely defined as natural lentic water bodies, located in the continental coastal region (Amaral & Jablonski 2005). It is precisely defined as superficial aquatic ecosystems, which develop at the terrestrial-marine interface, seasonally isolated or open to adjacent areas through coastal sedimentary geodynamics (Bird 1994, Kjerfve 1994, Gonenc & Wolflin 2004). It is sometimes confused with other coastal inland aquatic ecosystems, like restingas and estuaries (Esteves *et al.* 2008). Coastal lagoons

are peculiar because they accurately reflect the diversity through biogenic remains of the biota in micro-scale and macro-scale time (calcareous structure, intact and broken shells, like gastropod shells) (object of study of Taphonomy, *sensu* Efremov 1940). The species diversity, fauna surveys, and the nuances that can regulate the biota's fluctuations are scarce in this interface, as is, hypothetically, the availability of extrinsic resources (*e.g.* shells used by hermit crabs) (Kjerfve & Magill 1989, Elwany *et al.* 2003, Kibirige & Perissinotto 2003, Esteves *et al.* 2008, Moreno *et al.* 2010).

Closed coastal aquatic environments with episodes of seasonal opening undergo alterations in the biotic and abiotic composition of the environment (Kjerfve & Magill 1989, Elwany *et al.* 2003, Esteves *et al.* 2007). Therefore, this study aimed to list the shell species occupied by hermit crabs; verify the seasonal variation of the shell resource composition in a coastal lagoon system with sea-estuary interface; visualize the patterns of shell use by hermit crab species, and compare the diversity of the used resource with the literature on coastal gastropods.

MATERIAL AND METHODS

Characterization of the study area

The present study was performed in a coastal lagoon that is seasonally connected with the estuary and the sea and is located at the interface of the beach and estuary of Barra do Rio, at the mouth of the Ceara-Mirim river, state of Rio Grande do Norte (Latitude: 5° 40' 33.5" S; Longitude: 35° 3' 5" W, datum WGS84) (Figure 1a, b). The estuary is characterized as a bar-built estuary, formed by rivers of low hydrodynamism and the significant accumulation of the sediment at the river mouth (Vale & Schaeffer-Novelli 2018) (Figure 1a).

The seasonal linkage occurs when: (1) the greatest contribution of the river occurs in the rainiest months (March to July), where the increased river flows wear down the sedimentary barrier south of the lagoon; (2) occasionally, the magnitude of the syzygy tides open the connections of smaller caliber in the south and east barriers; (3) and in the King tide (Perigeon Spring tide, frequent in March in the Northeast of Brazil, *sensu* Marinha do Brasil, 2014 - <http://www.>

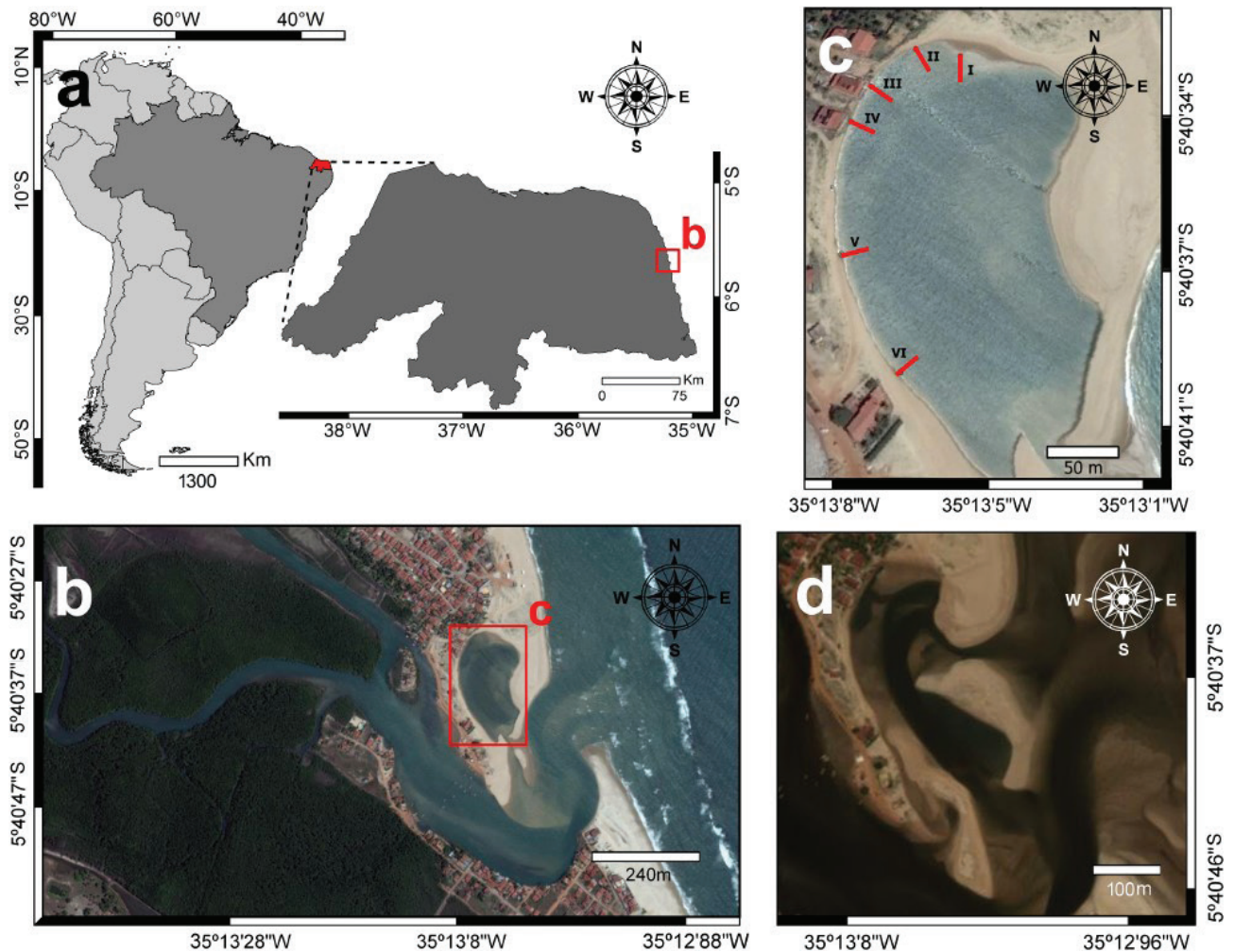


Figure 1. Map of the sampling area. (a) South America, Brazil, State of Rio Grande do Norte, emphasis on state of Rio Grande do Norte. (b) Sampling area between estuary of Ceará-Mirim river and Atlantic Ocean. (c) Coastal lagoon with sampling transect (I, II, III, IV, V and VI). (d) Event in which the magnitude of the syzygy tides, open the connections in the south and east barriers of the lagoon.

marinha.mil.br), in the largest tidal amplitudes (above the syzygy tides) overlapping with the influence of winds mainly along the sedimentary barrier to the east.

Sampling

The samplings were performed during the syzygy tide, specifically, on the second day of the tide cycle. For one year (February 2013 to January 2014), six georeferenced transects were standardized (Figure 1c). A trawl (width: 12 m; height: 2 m; mesh: 5 mm) was used as the sampling device in a 15 m line perpendicular to the lagoon margin. After trawling, the hermit crabs and the gastropod shells were packed in iceboxes and transported to the laboratory for identification and biometry procedures. All sampling was authorized by the SISBIO license #28314-1.

Identification and measurement

The shells were identified to the level of species following the descriptions proposed by Rios (2009). Afterwards, the shells were measured for total length (CSL), using a caliber (0.1 mm), and the respective hermit crabs that used the shells as shelter were identified, according to Melo (1999). The shell and hermit crab specimens were stored in the collection of the Universidade Federal do Rio Grande do Norte (Voucher GEEFAA/UFRN).

Diversity

The ecological indexes of species richness (S), abundance (n), equitability, dominance, and diversity were temporally (monthly) estimated to investigate the fluctuations of the “shell” resource. The Pielou equitability (J') considers

the distribution of species within a sample (Pielou 1966). Simpson dominance (D) considers the probability of 2 (two) individuals, randomly selected in a sample, belonging to the same species (Simpson 1949). Shannon diversity (H') considers equal quantities for abundant and rare species (Shannon 1948). In addition, Bootstrap permutations (N = 9999) were used to generate the confidence intervals for each index (95%). Finally, a Diversity t test (Poole, 1974) was performed with the diversity data (Shannon index) in peer-to-peer comparison between the months. The procedures were performed using the software Past 2.17b (Hammer *et al.* 2001).

For each shell species used, additionally, the relative abundance (*Rab*), relative occurrence in temporal scale (monthly – RO_t), and equitability (*E*) as proposed by Alves *et al.* (2012) were calculated. For this, $Rab = n/N$ (n = absolute abundance for each species, N = total of collected individuals), $RO = p/P$ (p = occurrences of each species per month, P = occurrences per month), and equitability as

$$E = \frac{Levins_j}{\ln(p_j)}$$

where, $Levins_j = -\sum_{i=1}^N Rab_{i,j} \cdot \ln(Rab_{i,j})$, p_j = number of months with occurrences of species “j”, and $Rab_{i,j}$ = relative abundance of species “j” in month “i”. “E” is the Pielou index but in this case refers to the equality of abundance of a given species in each sampled month.

Patterns of hermit crab vs. shell association

A Correspondence Analysis (CA) was performed to identify/evaluate the patterns of gastropod shell use by hermit crabs. The abundance data of each captured hermit crab species and the shell species marked were organized in a two-factor contingency table. After this, a Hellinger transformation was performed on the data to avoid potential problems of influence associations between rare hermit crab and shell species in sorting analyses (Zuur *et al.* 2007). In the CA, the observed associations of the two variables were summarized by the frequency of each cell of the table and positioned in a geometric dimensional space consistent with the associations of the table (Grenacre 1993). The CA explanatory axes resulting from the cumulative variation were greater than 70%. A Pearson Chi-square (χ^2) test with simulated

probability value was performed to validate the associations observed in CA using Monte Carlo permutations (N = 10000; Hope 1968) by the Patefield algorithm (Patefield 1981). The graphical points related to the shell species were arranged proportionally to their abundance, visualizing the association/abundance shell *vs.* hermit crab.

All statistical analyses were performed in software R (R Development Core Team 2021) using the packages: ‘ca’ to Correspondence Analysis (Nenadic & Greenacre 2007) and ‘stats’ to Pearson chi-square with Monte Carlo (R Development Core Team 2021).

RESULTS

Five species of hermit crabs were sampled in the coastal lagoon *Isocheles sawayai* Forest & de Saint Laurent, 1968, *Pagurus criniticornis* (Dana, 1852), *Clibanarius sclopetarius* (Herbst, 1796), *C. antillensis* Stimpson, 1859, and *C. symmetricus* (Randall, 1840). These crab species used 14 species of gastropod shells, among which 13 species were of subclass Vestigastropoda (1 species), Neritimorpha (2 species), Caenogastropoda (10 species) and Heterobranchia (1 species) (Table 1, Figure 2). Regarding the use, the highest occurrence and abundance in the study period were *V. virginea* (N = 178; $Rab = 0.672$; $RO_t = 1$) and *P. vibex* (N = 52; $Rab = 0.196$; $RO_t = 0.667$) (Table 1). The shell *V. virginea* was occupied by 3 species of hermit crabs (61% - *P. criniticornis*, 78.35% - *C. sclopetarius*, and 100% - *C. antillensis*) and the shell *P. vibex* by 2 species of hermit crabs (28.57% - *P. criniticornis* and 6.19% - *C. sclopetarius*) (Table 2).

In relation to the community structure, the richness varied between 1 (April) and 9 (May), total abundance between 2 (January) and 100 (May), dominance 0.250 (December) and 1 (April), diversity between 0 (April) and 1.386 (December), and equitability between 0 (April) and 1 (December and January). The months of April and August showed different ecological indexes from the other months, registering the greatest Simpson dominance indexes and lowest Shannon diversity indexes (Table 3). The peer-to-peer comparisons between the months showed statistical differences, mostly in comparisons involving the months of April and August: in

Table 1. Gastropoda species. N – total number of examples used by hermit crabs; Total length (mm); Range (minimum and maximum); \bar{x} – mean; SD – standard deviation; RAb – relative abundance; RO_t – relative occurrence at mouth. E – equitability (modified to Alves *et al.* 2009).

Gastropoda taxa	N	Total length (mm)				RAb	RO _t	E
		Range	\bar{x}	±	SD			
Subclass Vetigastropoda Salvini-Plawen, 1980								
Order Trochida Rafinesque, 1815								
Family Tegulidae Kuroda, Habe & Oyama, 1971								
1. <i>Tegula viridula</i> (Gmelin, 1791)	5	[4.7; 14.6]	9	±	4.2	0.019	0.250	0.086
Subclass Neritimorpha								
Order Cycloneritida								
Family Neritidae Rafinesque, 1815								
2. <i>Vitta virginea</i> (Linnaeus, 1758)	178	[3.6; 11.5]	7.5	±	1.4	0.672	1.000	0.747
3. <i>Vitta zebra</i> (Bruguière, 1792)	1	-	24.1			0.004	0.083	-
Subclass Caenogastropoda								
Order Littorinimorpha Golikov & Starobogatov, 1975								
Family Littorinidae Children, 1834								
4. <i>Littoraria flava</i> (P. P. King, 1832)	1	-	9.4			0.004	0.083	-
Family Cerithiidae J. Fleming, 1822								
5. <i>Cerithium atratum</i> (Born, 1778)	12	[9.1; 25.9]	15.4	±	5.6	0.045	0.583	0.162
Order Neogastropoda Wenz, 1938								
Family Muricidae Rafinesque, 1815								
6. <i>Stramonita haemastoma</i> (Linnaeus, 1767)	3	[14.0; 17.2]	20.8	±	3.3	0.011	0.167	-
Family Pisaniidae Gray, 1857								
7. <i>Pisania pusio</i> (Linnaeus, 1758)	1	-	22.9			0.004	0.083	-
8. <i>Engina turbinella</i> (Kiener, 1835)	1	-	11.3			0.004	0.083	-
Family Columbellidae Swainson, 1840								
9. <i>Costoanachis sertulariarum</i> (d'Orbigny, 1839)	4	[10.7; 14.4]	12.4	±	1.6	0.015	0.250	0.053
Family Nassariidae Iredale, 1916								
10. <i>Phrontis vibex</i> (Say, 1822)	52	[7.0; 15.3]	12.2	±	1.7	0.196	0.667	0.347
Family Olividae Latreille, 1825								
11. <i>Olivella minuta</i> (Link, 1807)	1	-	7.1			0.004	0.083	-
Family Pseudomelatomidae Morrison, 1966								
12. <i>Pilsbryspira zebroides</i> (Weinkauff & Kobelt, 1876)	1	-	8.5			0.004	0.083	-
Family Terebridae Mörch, 1852								
13. <i>Hastula cinerea</i> (Born, 1778)	1	-	15.5			0.004	0.083	-
Subclass Opisthobranchia Milne Edwards, 1848								
Subclass Heterobranchia								
Order Cephalaspidea P. Fischer, 1883								
Family Bullidae Rafinesque, 1815								
14. <i>Bulla striata</i> Bruguière, 1792	4	[20.4; 32.7]	27.4	±	5.5	0.015	0.333	0.072

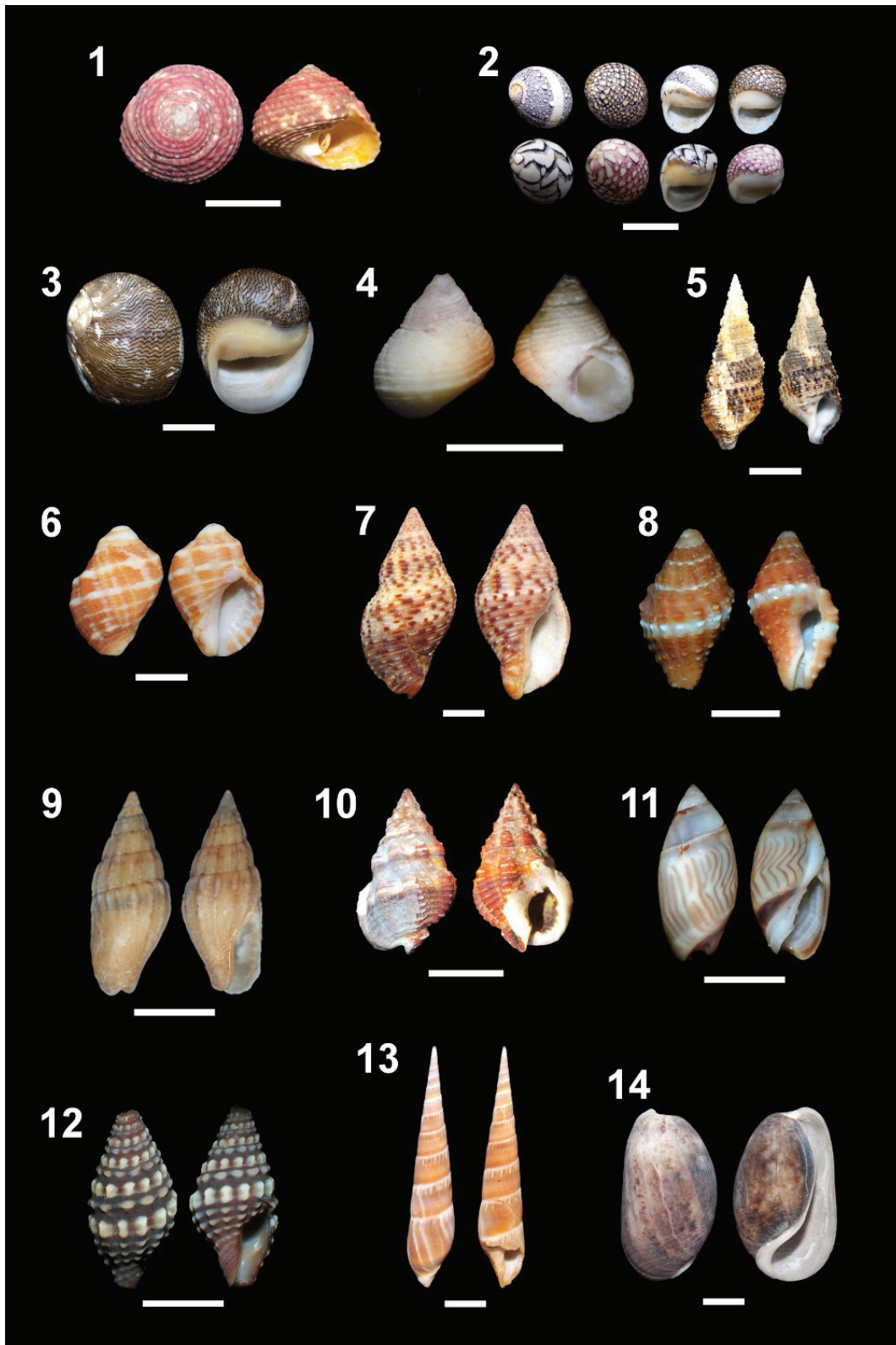


Figure 2. Gastropod species. Dorsal view (first) and ventral view (second) to each species. (1) *Tegula viridula* (Gmelin, 1799). (2) *Vitta virginea* (Linnaeus, 1758). (3) *Vitta zebra* (Bruguiere, 1792). (4) *Littoraria flava* (P. P. King, 1832). (5) *Cerithium atratum* (Born, 1778). (6) *Stramonita haemastoma* (Linnaeus, 1767). (7) *Pisania pusio* (Linnaeus, 1758). (8) *Engina turbinella* (Kiener, 1835). (9) *Costoanachis sertulariarum* (d'Orbigny, 1841). (10) *Phrontis vibex* (Say, 1822). (11) *Olivella minuta* (Link, 1807). (12) *Pilsbryspira zebroides* (Weinkauff, 1887). (13) *Hastula cinerea* (Born, 1778). (14) *Bulla striata* Bruguière, 1792. White scale bar represents 4 mm.

Table 2. Utilization of gastropod shells by hermit crabs. N – total number of shells used; % - percentage of shells used. Hermit crab species: Isa – *Isocheles sawayai*; Pcr – *Pagurus criniticornis*; Csc – *Clibanarius sclopetarius*; Can – *Clibanarius antillensis*; Csy – *Clibanarius symmetricus*. Gastropods species: SHA – *Stramonita haemastoma*; TVI – *Tegula viridula*; VVI – *Vitta virginea*; PVX – *Phrontis vibex*; CAT – *Cerithium atratum*; BST – *Bulla striata*; PZE – *Pilsbryspira zebroides*; HCI – *Hastula cinerea*; CSE – *Costoanachis sertulariarum*; OMI – *Olivella minuta*; VZE – *Vitta zebra*; ETU – *Engina turbinella*; PPU – *Pisania pusio*; LFL – *Littoraria flava*.

Species	Isa		Pcr		Csc		Can		Csy	
	N	%	N	%	N	%	N	%	N	%
SHA	2	50	-	-	1	1.03	-	-	-	-
TVI	1	25	1	0.62	3	3.09	-	-	-	-
VVI	1	25	99	61.49	76	78.35	2	100*	-	-
PVX	-	-	46	28.57	6	6.19	-	-	-	-
CAT	-	-	9	5.59	3	3.09	-	-	-	-
BST	-	-	-	-	4	4.12	-	-	-	-
PZE	-	-	1	0.62	-	-	-	-	-	-
HCI	-	-	1	0.62	-	-	-	-	-	-
CSE	-	-	2	1.24	2	2.06	-	-	-	-
OMI	-	-	1	0.62	-	-	-	-	-	-
VZE	-	-	-	-	-	-	-	-	1	100*
ETU	-	-	-	-	1	1.03	-	-	-	-
PPU	-	-	-	-	1	1.03	-	-	-	-
LFL	-	-	1	0.62	-	-	-	-	-	-

*New records of use by hermit crabs.

February-April, February-June, February-August, March- April, April-May, April-June, April-July, April-August, April-September, April-December, and, finally, May-August (Table 4).

In the correspondence analysis, we considered the significant axes that corresponded to a cumulative variation greater than 70% (Axis 1 = 53.3%; Axis 2 = 26.2%, Total = 79.5%). The CA showed an evident association between the hermit crab *I. sawayai* and the shells of *S. haemastoma* and *T. viridula*, as well as between the hermit crab *C. symmetricus* and the shells of *V. zebra*. For the hermit crabs *P. criniticornis*, *C. sclopetarius*, and *C. antillensis*, a less conspicuous relationship with the other species of gastropods was observed, and an overlapping graphical quadrant of the association between the species of gastropods and hermit crabs exists (Figure 3). The Pearson Chi-square test validated the associations observed in the CA (chi-squared = 399.75; $p = 0.0016$).

In addition, there were 2 new metabiosis records of hermit crabs and gastropods, *C. antillensis* using *V. virginea*; and *C. symmetricus*

using *V. zebra* (Table 2). Finally, the first occurrence of hermit crab *C. symmetricus* for the Northeast of Brazil was recorded.

DISCUSSION

The present study revealed the greatest diversity of shell species used by hermit crabs in a Brazilian coastal environment, accounting for 14 species of Gastropoda. Both *Vitta virginea* and *V. zebra* are frequently found in estuarine environments (Matthews-Cascon & Lotufo 2006, Blanco & Scatena 2007, Barroso *et al.* 2012). In contrast, *Tegula viridula*, *Stramonita haemastoma*, *Cerithium atratum*, *Pisania pusio*, *Engina turbinella*, *Costoanachis sertulariarum*, *Pilsbryspira zebroides*, *Hastula cinerea*, and *Olivella minuta* frequently occupy intertidal zones (Slik 1995, Amaral & Nallin 2001, Sevilla *et al.* 2003, Matthews-Cascon & Lotufo 2006, Rios 2009). The Gastropoda species *Bulla striata*, *Phrontis vibex*, and *Littoraria flava* are commonly found in both environments (Reid 1989, Amaral & Nallin 2001, Rios 2009). This discordant diversity is a

Table 3. Temporal ecological parameters of the gastropod species used by hermit crabs, in a coastal lagoon on Barra do Rio beach, Extremoz, Rio Grande do Norte. S – richness of species; n – abundance; D – dominance (Simpson, 1949); H' – diversity (Shannon, 1948); J' – equitability (Pielou, 1966); CI – 95% confidence interval. JAN – January, FEB – February, MAR – March, APR – April, MAY – May, JUN – June, JUL – July, AUG – August, SEP – September, OCT – October, NOV – November, DEC – December.

Month	Ecological parameters (temporal)				
	S (95% CI)	n	D (95% CI)	H' (95% CI)	J' (95% CI)
FEB	5 (2 - 6)	13	0.302 (0.302 - 0.858)	1.378 (0.271 - 1.411)	0.856 (0.391 - 0.908)
MAR	4 (3 - 8)	33	0.466 (0.350 - 0.703)	0.898 (0.556 - 1.353)	0.648 (0.456 - 0.746)
APR	1 (2 - 7)	22	1 (0.339 - 0.756)	0 (0.485 - 1.362)	0 (0.442 - 0.841)
MAY	9 (6 - 11)	100	0.520 (0.409 - 0.607)	1.045 (0.804 - 1.283)	0.476 (0.413 - 0.584)
JUN	5 (3 - 8)	39	0.650 (0.358 - 0.681)	0.728 (0.621 - 1.349)	0.452 (0.443 - 0.728)
JUL	4 (2 - 7)	19	0.518 (0.335 - 0.806)	0.897 (0.410 - 1.407)	0.648 (0.440 - 0.866)
AUG	2 (2 - 5)	11	0.703 (0.306 - 0.835)	0.474 (0.305 - 1.367)	0.684 (0.440 - 0.946)
SEP	3 (2 - 5)	10	0.460 (0.300 - 0.820)	0.898 (0.325 - 1.418)	0.817 (0.469 - 0.971)
OCT	3 (1 - 4)	5	0.440 (0.280 - 1)	0.950 (0 - 1.332)	0.865 (0 - 0.971)
NOV	3 (1 - 4)	6	0.500 (0.278 - 1)	0.868 (0 - 1.330)	0.790 (0 - 1)
DEC	4 (1 - 4)	4	0.250 (0.250 - 1)	1.386 (0 - 1.386)	1 (0 - 1)
JAN	2 (1 - 2)	2	0.500 (0.500 - 1)	0.693 (0 - 0.693)	1 (0 - 1)

reflection of the sampled micro-habitat, bringing together the interface of the estuarine and marine environments and faunal mixture.

Large coastal lagoons, which are connected to the sea, present low species richness as they are likely to become hypersaline by high evaporation. This condition acts as a severe biological filter to the colonization and establishment of species (Schallenberg *et al.* 2003, Sosa-López *et al.* 2007). However, small lagoons (such as the present study) with intermittent openings and, consequently, salinity fluctuations have been considered diversity hotspots (Araújo & Azevedo 2001, Naqinezhad *et al.* 2006, Kennish & Paerl 2010, Yousefi *et al.* 2012). Therefore, biogenic remains from these hotspots can be used as a resource for other species (*e.g.* empty shells of gastropods used by hermit crabs).

The diversity indexes of Gastropoda indicated a temporal variation of the 'shell' resource diversity within the lagoon, with April being a prominent period. The main reason for this temporal profile reflects the event caused by the King Tide (end of March, *sensu* Marinha do Brasil). This event has the capacity to modify the geomorphological profile of the lagoon and to provoke a greater flow in the lagoon and, thus, greater transport of species and empty shells to the region adjacent to the open sea. In fact, in April there was a

severe decrease in the diversity of shells and, consequently, of hermit crabs, using only one species of Gastropoda shell (*V. virginea*, N = 22). The King Tide event, together with the actions of wind and coastal currents, can provoke seasonal changes in geomorphology in coastal lagoons and coastal deltas (Smith 1994, Short & Klein 2016), as evidenced in the present study (Figure 1d). Such changes can influence water flow volume aspects of this environment and are well documented (Bird 1994, Nichols & Boon 1994, Grenz *et al.* 2013).

Coastal lagoons are ecotones with high environmental and biological variability (biological community), occupied by opportunistic and/or specialized species in this environment (Barnes 1988, Zaldívar *et al.* 2008). The species that dominated community composition was the Gastropoda *V. virginea* – low levels of Shannon diversity and high values of Simpson dominance – which may reflect its great dispersion and reproductive capacity. In fact, this species is abundant and opportunistic in mangroves. It stays on roots, fallen trunks, and leaves of mangrove and/or their ootheca may attach to these parts, using them as a natural raft (Matthews-Cascon *et al.* 1990, Matthews-Cascon & Martins 1999, Rios 2009, Vale *et al.* 2017), with aggregate spatial distribution (dense and extensive populations) (Matthews-Cascon *et al.* 1990, Cruz-Neta & Henry-

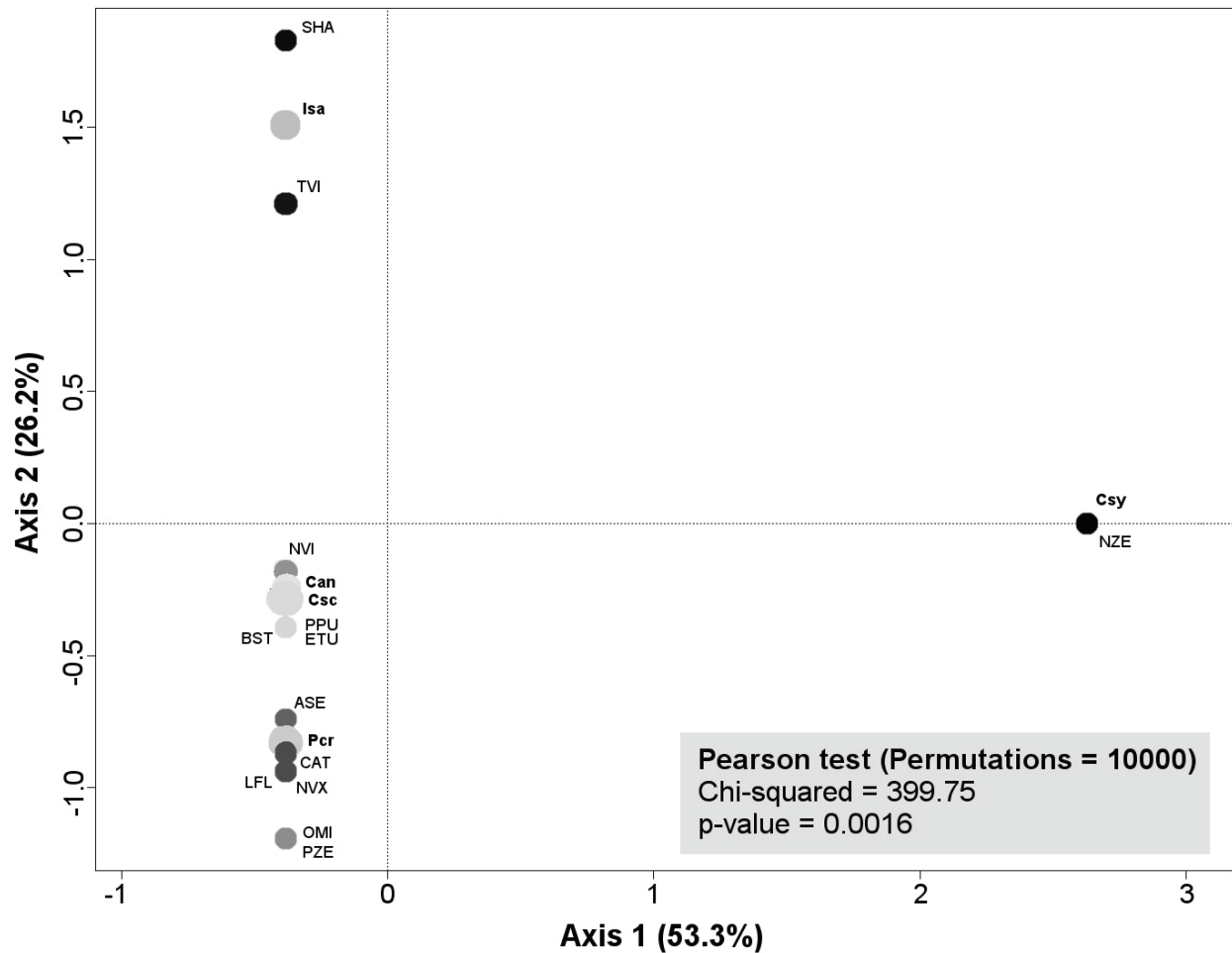


Figure 3. Correspondence analysis between hermit crabs and associated gastropod shell species. The Ellipse representation of hermit crabs did not have outstanding association with gastropod shell species. The names of species of Gastropoda were suppressed for best viewing results. Shaded box – Pearson's Chi-square test results with Monte Carlo permutations. Hermit crab species: Isa – *Isocheles sawayai*; Pcr – *Pagurus criniticornis*; Csc – *Clibanarius sclopetarius*; Can – *Clibanarius antillensis*; Csy – *Clibanarius symmetricus*. Gastropods species: SHA – *Stramonita haemastoma*; TVI – *Tegula viridula*; NVI – *Vitta virginea*; NZE – *Vitta zebra*.

Silva 2013).

The present study showed reports of living gastropod species that were already reported in the Northeastern Brazil ecoregion (*sensu* Matthews-Cascon *et al.* 1990, Matthews-Cascon & Lotufo 2003, Mereiles & Matthews-Cascon 2003, Spalding *et al.* 2007, Rios 2009). The eastern region of Rio Grande do Norte is characterized by being a division of the Equatorial South Current, from which originate the North Current of Brazil and Current of Brazil (Alves *et al.* 2012). This last current bathes all the eastern Brazilian coast and, primarily, the Northeastern Brazil ecoregion. This area favors coastal lagoon formation due to high concentration of bar-built estuaries (Vale & Schaeffer-Novelli 2018), which could make it possible that such a composition of shell species

could be found in similar habitats throughout this geological formation and ecoregion, expecting them to be sites of natural deposition of these resources (shells).

The literature confirms that the biogenic remains of gastropods reflect the composition, richness, and abundance of species in marine, estuarine, and coastal lagoon environments (Kidwell 2001, 2002, Kowalewski *et al.* 2003, Ritter & Erthal 2013). High fidelity between the composition of the living assemblage and remnants of the dead assemblage (shells and calcareous structure) has been reported. Moreover, the dead shell assemblages are subject to different means of seasonal fragmentation and accumulation in a short time, comprising a biota snapshot of an area including rare and

Table 4. Results of the diversity t-test of the monthly pairwise comparisons. Presenting the statistical significance results ($p < 0.05$) above the diagonal and the t-statistic values (difference between means in terms of standard deviations). JAN – January, FEB – February, MAR – March, APR – April, MAY – May, JUN – June, JUL – July, AUG – August, SEP – September, OCT – October, NOV – November, DEC – December. The p-values < 0.05 are highlighted in bold.

	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN
FEB		0.114	<0.001	0.377	0.052	0.177	<0.001	0.160	0.239	0.193	0.583	0.138
MAR	1.511		<0.001	0.385	0.411	0.890	0.073	0.824	0.772	0.667	0.650	0.368
APR	5.801	6.735		<0.001	<0.001	<0.001	0.042	0.003	0.069	0.067	0.029	0.337
MAY	0.902	-0.873	-8.333		0.120	0.439	0.016	0.394	0.474	0.394	0.985	0.247
JUN	2.018	0.827	-3.961	1.571		0.596	0.335	0.651	0.841	0.947	0.372	0.594
JUL	1.379	0.139	-4.001	0.784	-0.534		0.169	0.943	0.859	0.759	0.615	0.416
AUG	2.825	1.880	-2.300	2.596	0.980	1.409		0.196	0.401	0.473	0.147	0.973
SEP	1.452	0.226	-3.916	0.874	-0.457	0.072	-1.337		0.901	0.801	0.578	0.441
OCT	1.225	0.302	-2.398	0.759	-0.207	0.183	-0.883	0.128		0.913	0.566	0.544
NOV	1.381	0.446	-2.228	0.902	-0.069	0.314	-0.745	0.259	0.111		0.496	0.608
DEC	0.572	-0.480	-3.303	-0.019	-0.955	-0.523	-1.625	-0.580	-0.596	-0.707		0.281
JAN	1.897	1.089	-1.253	1.504	0.594	0.919	-0.036	0.869	0.650	0.547	1.215	

cryptic behavior species (negative phototropism, nocturnal and twilight behavior) (Peterson 1976). Also, the weather conditions that can act on the taphonomic community composition are insignificant, such as transport and dissolution after death, fragmentation and environmental changes in macro-scale (Ritter & Erthal 2013). Finally, it is important to note that hermit crabs are important taphonomic agents, and they are recognized as the influential group in the alterations of the natural stratification of shells and structural modifications (Walker 1989, Walker 1990, Martin 1999). In the present case, we suggest that, possibly, this decapod group may be “fixer agent” of a sampling of the living gastropods species in the region, independently of the opening events of the lagoon. This makes the composition of the Gastropoda shell species closer to the reality of the living community.

The new reports on the use of shells by hermit crabs showed here can confirm strategies for the reduction of intra- and interspecific competition discussed by Vale *et al.* (2017). As previously mentioned, the coastal lagoons are known as diversity hotspots (*sensu* Brazil’s Atlantic Forest - Myers *et al.* 2000, Coastal Zones - Newton & Weichselgartner 2014) and recruitment areas for marine and estuarine species (Moreno, 2000). Therefore, these areas in theory represent

significant competition for resources, generating a displacement of adaptive values of some species on the micro-scale (Schulter 2000, Grant & Grant 2006, Kingsolver & Pfennig 2007). Thus, there is evidence of increasing width of ecological niches, resource partitioning, and diversification of used resources (Roughgarden 1976). In the case of hermit crab species, this diversification of resource use may lead to the use of unusual and/or sub-optimal shells. However, the abundance of a resource can also generate displacement of characters or preferences of some species (Tilman 1982, Bloom *et al.* 1985, Abrams 1987). The use of *V. virginea* by most hermit crab species, except *C. symmetricus*, can be explained by the great availability of this resource, as evidenced by *C. sclopitarius* and *Pagurus criniticornis* by Vale *et al.* (2017). These types of evidence were also reported by the corresponding analysis, which also detected the already known metabiosis of hermit crab *I. sawayai* and Gastropoda *S. haemastoma* (Hebling & Wernick 1974, Pinheiro *et al.* 1993, Negreiros-Fransozo *et al.* 1997, Galindo *et al.* 2008). These previously mentioned studies showed that *I. sawayai* has a strong association with *S. haemastoma* shells in different micro-scales and environments of the South America coast.

The hermit crab *C. symmetricus* was recorded for the first time on the northeast coast of Brazil,

and ecological information has been added, such as its habitat of occurrence and the shell use of *V. zebra*. Recently, this species underwent a proposal of taxonomic “resurrection”. The syntypes primarily evaluated as *C. vittatus* belonged to a taxonomic entity already designated and described for South America, *C. symmetricus*. Morphological data, with emphasis on color, and molecular data from many collections in Brazil (Negri *et al.* 2014) were used for this resurrection evaluation. Therefore, with the data of the present study, the geographic distribution of the species now fills a gap between the known distributions to the north (Suriname – type locality – and state of Pará) and more to the southeast (states of Bahia, Rio de Janeiro, Paraná, and Santa Catarina), being a new record in the Northeastern Brazil ecoregion. To consolidate the distribution and resurrection of the species, we suggest that environmental suitability studies should be conducted to elucidate the *C. symmetricus* distribution, confronting the *C. vittatus* distribution.

Coastal depositional systems are contemporaneous in geological time scale, and their processes, composition (biological, geological, and abiotic), and dynamics are still little explored. Faunistic surveys and monitoring in these environments require attention since it constitutes a diversity hotspot, an environment of species recruitment (fish and macroinvertebrates). The recreational use and occupation of areas around these environments are often found on the Brazilian coast under the influence of the Atlantic Forest and Mangrove biomes. Thus, it is of utmost importance to study the biodiversity of these environments to support studies on management and conservation of these resources. In addition, these areas are relevant to the life history of species that use the shells or other resources present in the lagoons at this sea-estuary interface.

ACKNOWLEDGEMENTS

The authors of this article would like to thank Professor D’Oliveira RG, Simone LRL and Andrade LCA for their support in confirming the taxonomic identifications of the species of the gastropod shells and the members of the Laboratório de Fauna Aquática in sampling. This study was financed in part by the Coordenação de Aperfeiçoamento de

Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 (scholarship - Sávio ASN Moraes). They acknowledge the Ministério do Meio Ambiente (MMA), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and Sistema de Autorização e Informação em Biodiversidade (SISBIO) for license #28314-1. The authors declare no conflict of interest.

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Submitted: 3 May 2021

Accepted: 13 July 2022

Published online: 03 August 2022

Associate Editor: Vinicius Giglio