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ARTÍCULO ORIGINAL

SHELL USE PATTERNS OF THE HERMIT CRAB *Loxopagurus loxochelis* (DECAPODA: DIOGENIDAE) IN CERRO VERDE–LA CORONILLA (ROCHA–URUGUAY)

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ABSTRACT

In this paper we describe the shell use patterns of *Loxopagurus loxochelis* in the soft bottoms of Cerro Verde-La Coronilla, a proposed marine protected area in Uruguay. In addition, shell variables were quantified and related to hermit crab parameters in order to find those variables that best explain the association between hermit crabs and shells. The population of *L. loxochelis* at La Coronilla-Cerro Verde was found inhabiting shells of nine gastropod species, *Olivancillaria urceus*, *Buccinanops monilifer* and *Hanetia haneti* being the main items. We did not find empty shells, what suggests that shell availability may be an important limiting factor in this population. Shell weight and left propodus length best described the association between hermit crabs and their host shells. Our results showed that the shell use pattern for the most occupied shell species is similar to the observed for Argentinean populations of this species, but differs from the observed in Brazilian populations. This suggests that shell preferences are more similar between closer populations in the region, and that local shell availability may affect shell selection behaviour. Coupled with the existent data, the information here provided will be useful to fill the existent geographic gaps, giving insight on large-scale ecological trends for this species.

KEY WORDS: hermit crabs, gastropods, shell use, Cerro Verde-La Coronilla, Uruguay.

RESUMEN

Patrones de uso de caparazones del cangrejo ermitaño** Loxopagurus loxochelis **(Decapoda: Diogenidae) en Cerro Verde–La Coronilla (Rocha-Uruguay). En este trabajo se describen los patrones de uso de caparazones de *Loxopagurus loxochelis* en los fondos blandos de Cerro Verde–La Coronilla, propuesta como la primer área marina protegida del Uruguay. Además, se cuantificaron variables del caparazón y se relacionaron con parámetros de los cangrejos para encontrar las variables que permiten explicar la asociación entre los cangrejos ermitaños y los caparazones. La población de *L. loxochelis* se encontró habitando caparazones de nueve especies de gasterópodos, siendo *Olivancillaria urceus*, *Buccinanops monilifer* y *Hanetia haneti* los ítems principales. No se encontraron caparazones vacíos, una evidencia que sugiere que la disponibilidad de caparazones puede ser un factor limitante de importancia. El peso de los caparazones y el largo del propodo izquierdo fueron las variables que mejor describieron la asociación entre los ermitaños y sus caparazones. Nuestros resultados muestran que el patrón de uso de caparazones de las especies más utilizadas es similar a lo observado para poblaciones argentinas de la misma especie, pero difiere de lo observado para las poblaciones brasileñas. Esto sugiere que las preferencias en el uso de caparazones son más similares entre poblaciones más cercanas en la región, y que la disponibilidad local de caparazones puede afectar el comportamiento de selección de caparazones. Asociado a la información existente, los datos aquí provistos serán útiles para llenar los vacíos existentes, permitiendo un conocimiento mas detallado de los patrones ecológicos a gran escala geográfica para esta especie.

PALABRAS CLAVE: cangrejos ermitaños, gasterópodos, uso de caparazones, Cerro Verde-La Coronilla, Uruguay.

INTRODUCTION

Shell production by mollusks in marine habitats plays an important ecological role, introducing complexity and heterogeneity into benthic environments (Gutiérrez *et al.,* 2003). Among other functions, empty gastropods shells constitute an obligate requirement for most hermit crabs (but see García *et al.,* 2003). The presence and

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relative abundance of different gastropod species, species-specific shell host preferences, and the strength of interspecific competition for the limited supply of empty shells determine the types and sizes of shells occupied by hermit crabs, affecting the fitness and demographic structure of their populations (Bach *et al.,* 1976; Bertness, 1980; Hazlett, 1981).

Shell selection by hermit crabs is not a random process, since several hermit crab species select for shell characteristics that diminish predation risk, such as hardness (Wilber, 1990; Brown, 1992), coloration (Partridge, 1980), and shell integrity (McClintock, 1985). One other important shell feature is the aperture/shell axis ratio (Bertness, 1981). There is also some evidence that hermit crabs choice may be influenced by local environmental conditions, for instance selecting heavier shells in areas of higher water turbulence and wave action (Partridge, 1980).

Loxopagurus loxochelis (Moreira, 1901) (Anomura, Diogenidae) is endemic of the Atlantic coast of South America, occurring in Southern Brazil (north of São Paulo to Rio Grande do Sul states), Uruguay and Argentina (Melo, 1999; Mantelatto *et al.,* 2004; 2006). In addition, this species has been widely studied in Argentina and Brazil, with several studies on its ecology (Mantelatto & Martinelli, 2001; Bertini *et al.,* 2004; Mantelatto *et al.,* 2004; 2006), reproductive biology (Bertini *et al.,* 2004; Scelzo *et al.,* 2004; Torati & Mantelatto, 2008) and shell use patterns (Martinelli & Mantelatto, 1999; Biagi *et al.,* 2006). For these reasons, this species constitutes an ideal model species to analyze regional trends in hermit crab ecology.

Most experimental studies analyzed species preferences in shell hosts under an ethological point of view, since the term "preference" implies behaviour. When "preference" is used as a behavioural trait, the hermit crab is regarded as preferring shell host A over shell host B if an encounter with A is more likely to result in shell occupancy than an encounter with B. However, an ecological definition of preference should focus on the proportions of different niches occupied relative to the proportions of available items in the habitat (Singer, 2000; Chase & Leibold, 2003). In this vein, Meireles *et al.,* (2003) characterized the gastropod shell availability in the infralittoral area of Anchieta Island (Ubatuba, SP, Brazil), while Martinelli & Mantellato (1999) performed a study on shell preferences following an ecological approach. However, studies on shell preferences neither "ethological" nor "ecological" are available for Uruguayan populations of *L. loxochelis*.

In this work we aimed to a) provide basic data on *L. loxochelis* in the soft bottoms of Cerro Verde-La Coronilla, proposed as the first marine protected area in Uruguay, b) characterize species composition and relative frequency of gastropod shell hosts and c) examine the relationships between shell variables and hermit crab parameters. Coupled with the existent data, the information here provided will be a first approach to fill the existent geographic gaps, giving insight on large-scale ecological trends for this species.

MATERIAL AND METHODS

Sampling

Samplings were made onboard the artisanal fishing vessel "Dommy", during January and May 2007. The fishing gears employed consisted in: a) a bottom trawl net (BTN) with a 9 m horizontal opening, 1.2 m high and a 25 mm stretched mesh in the cod ends and b) a Piccard dredge (PB), with a horizontal aperture of 0.60 m and 10 mm mesh size. In each date some 9 stations were

Table 1.- Geographic coordinates of the sampling stations and spatial distribution of *Loxopagurus loxochelis* in Cerro Verde – La Coronilla. Number of individuals collected and percentage of total hermit crabs collected are also shown.

Station	Latitude S°	Longitude W°	N° Hermit crabs	%
S1*	33°56´376	53°30´550	9	14.52
S2*	33°57´213	53°31´293	15	24.19
S3*	33°58´282	53°31´313	19	30.65
S4*	33°55´872	53°29´825	17	27.42
S5**	33°57´256	53°29´554	1	1.61
S6**	33°58´245	53°30´371	0	0.00
S7***	33°55´942	53°27´861	0	0.00
S8***	33°56´921	53°28´183	1	1.61
S9***	33°59´028	53°29´500	0	0.00

* Outer break; ** 5-10m depth; *** 10-15m depth. Station 4 was located in waters shallower than 5 m because muddy bottoms precluded trawling in the planned zone.

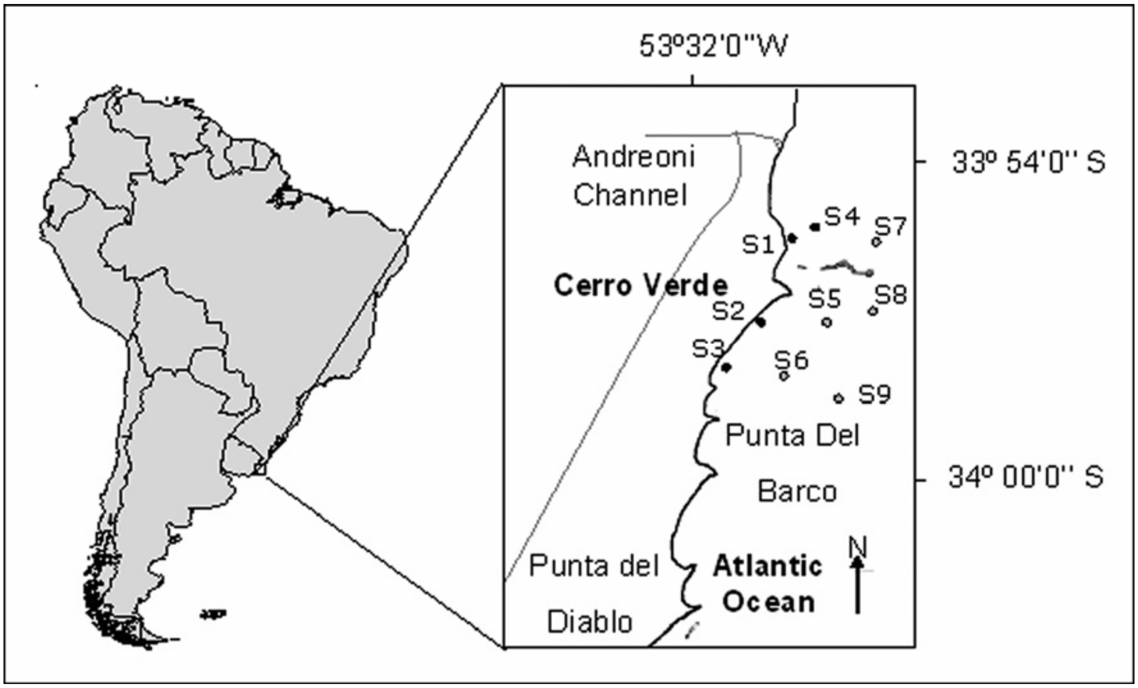

Figure 1: Distribution of the surveyed stations with presence of *Loxopagurus loxochelis* (•) and stations with less than 2 individuals (○) at Cerro Verde-La Coronilla (Uruguay). Station 4 (S4) departed from systematic design and is considered as an outer breaker station.

allocated based on a systematic stratified design, between the outer breaker and approximatelly 10-15 m (Figure 1; Table 1). In each station, 10 minutes tows were performed with the BTN, while 5 minutes tows were performed with the PB. The exact location of the stations was determined by Garmin-Etrex Global Positioning System (GPS), depth was measured usign onboard ECOSONDA. Some adittional (N= 14) specimens were obtained from previous research in the area using similar methodology.

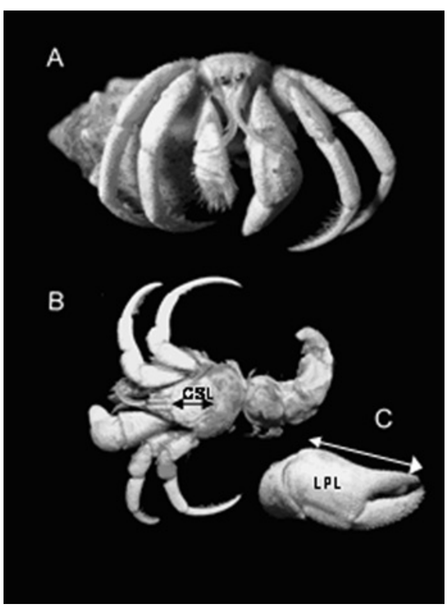

Figure 2: Frontal (A) and dorsal (B) view of *Loxopagurus loxochelis* (19.15 mm CSL) and frontal view of its left propodus (C), showing measurements taken for statistical analysis. CSL: cephalotoracic shield length, LPL: left propodus length.

Measurements taken

Once landed, all hermit crabs collected were fixed in 10% formalin and taken to laboratory, where all specimens were weighed (hermit wet weight, HWW; to the nearest 0.1 g) and its cephalothoracic shield length (CSL) and left propodus length (LPL) measured to the nearest 0.01 mm with a digital caliper (Figure 2). In addition, their shell hosts were identified to species level and measured (aperture length, AL) and weighed (shell weight, SW). Voucher material is deposited at the National Museum of Natural History, Montevideo (MNHNM).

Data analysis

With these data, we evaluated the statistical significance of the differences in occupancy rates between shell hosts by means of a Chi-Square test, with expected frequencies according to a uniform distribution (*i.e.* the occupancy rate is the same for all host shell species). Aperture Length Frequency Distributions (ALFD) of the shells occupied by hermit crabs discriminated by species were constructed, and the nature and proportion of the resource being utilized by the hermit crabs examined. The normality of the distribution was evaluated by means of the Kolmogorov-Smirnov test. An one-factor analysis of variance (ANOVA) was also peformed to analyse differences in AL between the most ocuppied shells, and when differences were found, an Unequal N HSD post-hoc test was employed to detect significant differences between pairs of species (Zar, 1999). Ordinary least squares linear regressions were performed in order to evaluate if the shell host AL and SW were correlated with hermit crab CSL, LPL and HWW.

RESULTS

Some 75 individuals of *L. loxochelis*, CSL= 6.09 ± 3.19 mm (ranging from 1.61 to 19.15 mm) were collected during the field surveys. More than 95% of the hermit crabs were collected in the outer breaker (Table 1). Notice that station S4 was located in the outer breaker in waters shallower than 5 m because muddy bottoms precluded trawling in the planned zone (Figure 1) .

We did not found gastropod empty shells. *Loxopagurus loxochelis* were found inhabiting a total of nine gastropod species (Figure 3). Shell occupancy pattern differed significantly from a uniform distribution (Chi-Square = 41.94; p <0.05). ALFD has shown a normal distribution. (Kolmogorov-Smirnov d = 0.10, p = n.s.). Examination of ALFD showed that *Hanetia haneti* (Petit de la Saussaye, 1856), *Buccinanops monilifer* (Kiener, 1834), *Buccinanops duartei* Klappenbach, 1961 and *Olivancillaria uretai* Klappenbach, 1965 were represented in the smaller AL size classes; *Olivancillaria deshayesiana* (Ducros de Saint Germain, 1857) showed intermediate values of AL and *Olivancillaria carcellesi* Klappenbach, 1965, *Olivancillaria urceus* (Röding 1798) and *Stramonita haemostoma* (Linnaeus, 1767) presented the higher values. *Buccinanops cochlidium* (Dillwyn, 1817) showed the widest range of AL (Figure 4). Significant differences were detected in AL between the four most occupied shell species (ANOVA; $F_{(3, 53)}$=22.667, p<0.01), with the highest AL mean corresponding to *O. urceus*, followed by *B. cochlidium*, *B. monilifer* and *H. haneti*. The post hoc test revealed that *O. urceus* showed higher AL values than the other species (Tukey test-Unequal N HSD; all p>0.05).

Regression analysis of shell host (AL and SW) with hermit crab measurements (LPL, CSL or HWW) explained more than 50 % of variance. According to R^2 values, LPL was the variable best correlated with both shell measures, followed by CSL and HWW. The proportion of variance explained by the AL and SW differed when considering different hermit crabs measures. Shell Weight showed the best correlation with LPL, with ca. 70 % of explained variance, while CSL was best correlated with AL (Table 2).

DISCUSSION

The population of *L. loxochelis* at La Coronilla-Cerro Verde was found inhabiting shells of nine gastropod species, all previously reported for the study area (Milstein *et al.*, 1976). This figure is higher than the reported by Martinelli & Mantelatto (1999; N= 179; six gastropod species), in despite of the lower number of individuals collected in our study (N= 76). The occupancy difference may be due to a diminished availability of shells species compared with Ubatuba, where shells of 15 gastropod species were available (Martinelli & Mantelatto, 1999). In contrast, when shell supply is a limiting factor, the opportunities for selection may be diminished, forcing the crabs to occupy virtually all suitable shells. This suggests some macroecological differences in shell preferences related to latitudinal patterns in gastropod species richness.

Concerning the relative use of shell host species, our results are in accordance with previous experimental results, pointing out the importance of *O. urceus* as an important shell resource utilized by *L. loxochelis*, especially at larger sizes (Biagi et al., 2006). However, they contrasts with respect to the occupancy pattern of *B. cochlidium* (= *B. gradatum*) shells (Biagi et al., 2006). The latter study showed that *L. loxochelis* from Argentina presented no preference for any of the two offered shell

Table 2.- Regression parameters between shell host and *Loxopagurus loxochelis* measures and associated statistics.

Explanatory variable	Response variable	d.f.	b	R2
AL	CSL	67	0.783*	0.614
SW	CSL	68	0.772*	0.595
AL	LPL	62	0.830*	0.689
SW	LPL	62	0.836*	0.699
AL	HWW	69	0.751*	0.564
SW	HWW	70	0.714*	0.510

AL: aperture length; SW: shell weigth; CSL: cephalothoracic shield length; LPL: left propodus length; HW: hermit weight; b: regression parameter; *: P< 0.5

species, (*O. urceus* and *B. cochlidium*), but the specimens from Brazil significantly preferred *B. cochlidium* shells. In our study another nassariid, *B. monilifer,* was the second item in importance.

The ALFD for gastropod shells illustrated the unequal distribution of shells of different sizes. While shells of *O. urceus* are available only above certain threshold level (13 mm in the case of *S. haemastoma*), other gastropod species only provide shells of small sizes (*e.g. H.*

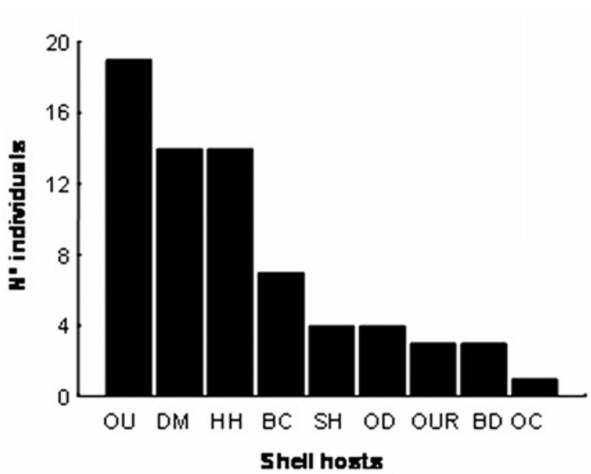

Figure 3: Frequency distribution of the shell hosts of *Loxopagurus loxochelis* at La Coronilla-Cerro Verde. OU: *Olivancillaria urceus*; DM: *Buccinanops monilifer*; HH: *Hanetia haneti*; BC: *Buccinanops cochlidium*; SH: *Stramonita haemastoma*; OD: *Olivancillaria deshayesiana*; OUR: *Olivanciliaria uretai* and BD: *Buccinanops duartei*; OC: *Olivanciliaria carcellesi*

haneti, 16 mm maximum AL). The negative effects of shell limitation has been suggested to be more common in hermit crabs that use large shells compared to small shells (Carlon & Ebersole, 1995), since the occupancy pattern is closely tied to the gastropod mortality (= shell availability) schedule, specific to each gastropod species. In the studied population empty shells were not observed, so ALFD can be regarded as a niche dimension according to modern niche theory (Chase & Leibold, 2003), since the proportion of occupied shells should be close to one. This evidence support the hypothesis that shell host availability is an important limiting factor (Provenzano, 1960; Vance 1972a; 1972b) for hermit crab populations at Cerro Verde–La Coronilla. The reduction in diversity of shell species occupied in relation to increasing hermit crab size observed by Martinelli & Mantelatto (1999) was also found in this study.

In our study, HWW was not significantly correlated with SW and AL. A significant correlation was obtained between LPL and SW, as observed in experiments of shell selection conducted on a related species, *Paguristes tortugae* Schmitt, 1933 (Mantelatto & Dominciano, 2002). In contrast, the morphometric relationships that best described the association between Brazilian and Argentinean hermit crabs and their selected shells species were those involving shell dimensions and hermit weight, independently of the shell species (Biagi *et al.,* 2006a). Experimental evidence suggests that volume is more important than weight during shell-size selection by hermit crabs (Lively, 1988). Low sample size in our study could be masking some relations, because of differences specific to shell host. In addition, CSL should be used as a more reliable indicator of hermit size, since the chelae may be lost and/or in a regenerating process, biasing the regression estimates. Also, shifts in the allometric relationship between carapace and chelae length due to differential growth of chelae at the onset of sexual maturity (Lovet & Felder, 1989) may further blur this relationship. The use of multivariate methods (*e.g.* multivariate allomety) to deal with this issue is strongly suggested.

The higher abundance of hermit crabs in the outer break, and its near absence in stations deeper than 5 m, also contrast with the findings made in Ubatuba, in which crabs occurred in large numbers in deeper areas (Martinelli *et al.,* 2002). This fact could be related to sediment composition. Outer break sediments are coarser and composed of sand, differing from deeper stations in which sediments contain high

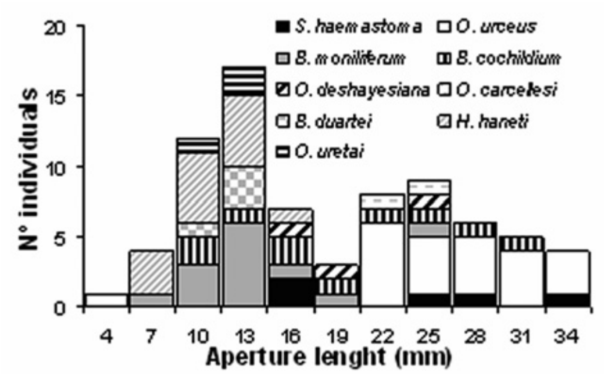

Figure 4: Summary of the aperture length frequency distribution of host shells of *Loxopagurus loxochelis* at La Coronilla-Cerro Verde. Each value represents maximum aperture length within each size class (1-4; 4-7 mm, etc.).

amounts of mud (A. Segura pers. obs.). The muddy sediments may affect their filtering structures, precluding the crabs for inhabiting this kind of bottoms. Also, the outer breaker zone may offer some protection against fish predators such as the smoothound shark *Mustelus schmitti* Springer, 1939, which preys mainly on hermit crabs. Thus, a combination of physical (different sediment composition) and biological (*i.e.* predation) factors may be affecting the spatial distribution of the hermit crabs at the studied area.

In summary, our results showed that the population of *L. loxochelis* in Cerro Verde-La Coronilla inhabits shells of nine species of gastropods, and that the shell use pattern for the most occupied shell species is similar to the observed for Argentinean crabs, but differs from the observed in Brazilian populations. This suggests that shell preferences are more similar between closer populations in the region, and that local shell availability may shape behavioural preferences during shell selection. Further studies coupling "ecological" and "ethological" approaches are needed in order to evaluate to what degree the shell host selection by hermit crabs respond to resource availability and behavioural mechanisms.

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