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Comparative study of shell choice by the southern endemic hermit crab *Loxopagurus loxochelis* from Brazil and Argentina

Estudio comparativo sobre elección de conchas en el cangrejo ermitaño endémico del
Atlántico sudoccidental *Loxopagurus loxochelis* de Brasil y Argentina

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ABSTRACT

This study aimed to determine the shell choice pattern of the southern Atlantic endemic hermit crab *Loxopagurus loxochelis* from two different biogeographic provinces in Brazil and Argentina. Size and shell species preferences were determined for the two most occupied shell types (i.e., *Olivancillaria urceus* and *Buccinanops gradatum*) in Caraguatatuba region (Brazil) and in Mar del Plata (Argentina). Shell occupation was analyzed considering the biometric characteristics of shells, the occurrence of shell types, and the preference of the hermit crabs for the most frequently occupied shell species. Samples were taken using otter trawl in the infralittoral area of both regions and the animals captured were measured and weighed. Shells were identified, weighed, measured and their internal volume calculated. Experiments were accomplished in aquaria where the hermit crabs were allocated together with a sufficient number of adequate sized shells. In laboratory, *L. loxochelis* from Argentina presented no preference for any of the two offered shell species, while the specimens from Brazil significantly preferred *B. gradatum* shells. It was observed that the relation between shell dimensions and shell weight were the variables that best explained the association between hermit crabs and shells. Considering that Argentinean specimens are larger than the Brazilian ones we may infer that body size is a relevant factor to explain the observed differences found in relation to shell type preference.

Key words: shell preference, Anomura, *Loxopagurus loxochelis*.

RESUMEN

Este estudio tuvo por objetivo determinar la forma de elección de conchas de caracoles por el cangrejo ermitaño endémico del Atlántico sudoccidental *Loxopagurus loxochelis* proveniente de dos provincias biogeográficas de Brasil y Argentina. Se determinaron las tallas y las preferencias de conchas entre los dos tipos de caracoles más ocupados (*Olivancillaria urceus* y *Buccinanops gradatum*) en la región de Caraguatatuba (Brasil) y en Mar del Plata (Argentina). La composición de las conchas fue analizada por las características biométricas y ocurrencia de los tipos de conchas y la selección por la preferencia del cangrejo ermitaño en relación a la especie de concha más ocupada. Las muestras fueron tomadas usando redes de arrastre en las áreas infralitorales de ambas regiones y los animales capturados fueron medidos y pesados. Las conchas de caracoles fueron identificadas, pesadas, medidas y calculado el volumen interno. Las experiencias fueron realizadas en acuarios donde los cangrejos ermitaños fueron ubicados con un número suficiente y adecuado de conchas de caracoles. En el laboratorio, *L. loxochelis* de Argentina no presentaron diferencias entre las dos especies de conchas ofrecidas, mientras los especímenes de Brasil prefirieron conchas de *B. gradatum* en forma significativa. Se observó que las relaciones de las dimensiones y los pesos de las conchas fueron aquellas que mejor reflejaron la asociación con los cangrejos ermitaños. Teniendo en consideración que los especímenes de Argentina fueron más grandes, se puede inferir que ello puede ser uno de los factores influenciando en las diferencias por las preferencias de los tipos de conchas halladas.

Palabras clave: preferencia de conchas, Anomura, *Loxopagurus loxochelis*.

INTRODUCTION

The behavior patterns of hermit crabs related to shell selection showed that this process is not by chance, but based on adequacy and availability of resources to the hermit crabs (Reese 1962, Conover 1978). Nevertheless, the specific parameters by which a shell is chosen are uncertain. Besides shell availability, almost all physical parameters have been considered in this assessment. In this manner, each shell variable has been shown to be important to different species of hermit crabs (Reese 1962, Conover 1978, Blackstone 1985, Wilber 1990, Rodrigues et al. 2000). Moreover, the fitness of a particular shell may differ between hermit crabs species, reflecting several selection pressures, which associated with different habitats, act in different ways on each crab species (Bertness 1981), in different areas (Garcia & Mantelatto 2000). Although the shell selection process has been well investigated (Vance 1972, Elwood et al. 1979, Bertness 1980, Wilber 1990, Hazlett 1992, 1996, Siu & Lee 1992, Ohmori et al. 1995, Wada et al. 1997, Garcia & Mantelatto 2001), there is a scarcity of studies comparing populations from different locations. *Loxopagurus* Forest, 1964 is a monotypic hermit crab genus represented by *Loxopagurus loxochelis* (Moreira, 1901), endemic to the southwestern Atlantic coast, and occurring in Brazil (Bahia to Rio Grande do Sul States), Uruguay, and Argentina (Melo 1999). The life cycle of *L. loxochelis* is reasonably well known in the Ubatuba region (see Martinelli et al. 2002 for a review), as well as some aspects of sperm morphology (Scelzo et al. 2004) and taxonomic status (Mantelatto et al. 2006), but the biology of this species from other areas as Argentina is poorly known except for some information on planktonic larvae (Scelzo 1976). Recent investigations on sequences of the 16S ribosomal gene made by one of us (FL Mantelatto) have showed that no marked genetic variability occurs among populations of *L. loxochelis* from Brazil and Argentina. Despite of this characteristic, some preliminary results have detected ecological differences on distribution, and size of the animals among the above mentioned populations (Mantelatto & Scelzo unpublished results). Therefore, we decided to evaluate the shell size and shell species preference by

Loxopagurus loxochelis from two populations located in different biogeographical provinces, in order to compare the mechanisms of shell selection as part of a long term comparative project to study the ecology and systematics of hermit crab fauna from both Argentinean and Brazilian provinces.

MATERIAL AND METHODS

Hermit crabs were collected in Caraguatatuba (23°S) (São Paulo, Brazil) during 2002 and in Mar del Plata (38°S) (Buenos Aires Province, Argentina) during 2003 by a fishery boat equipped with otter-trawl nets. The both localities of study are approximately distant around 5,000 km from each other. After collection the animals were transported to the respective laboratories where experiments were conducted using glass aquaria with flowing sea water. Each animal was utilized only once to avoid any acquired behavior. The animals that died during the experiments were not included in the analysis. To determine correlations between characteristics of hermit crabs and their preferred shells, regression analyses were computed. The chi-square test (χ^2) was used to compare occupancy of shell species, and morphometric relationships were established by regression analysis and correlation coefficients (r). Shell size preference data were analyzed using the simple linear regression: $\ln Y = a + b \ln X$ (where Y = shell measurements: SAW = shell aperture width; SDW = shell dry weight; SIV = shell internal volume, and X = hermit crab measurements: SL = shield length, and W = hermit weight). All shell-species experiments were conducted for the two most occupied shell species found at the field (*Buccinanops gradatum* and *Olivancillaria urceus*) in Brazilian waters (Martinelli & Mantelatto 1999) and in Argentinean waters (Scelzo unpublished results).

Shell-species preference

All experiments were conducted in a pair-wise fashion. In these tests, 15 naked hermit crabs were placed in the aquaria with 150 empty shells (75 of each species) of two different species and various and adequate sizes (*O. urceus* shells ranging from 4.3 to 11.2mm SAW

and *B. gradatum* shells ranging from 5.7 to 22.5mm). After 36 h, the hermit crabs were removed from the preferred shell, and both were measured as described above for the shell-size experiments. Each test was performed in triplicate for each hermit crab origin (Argentina and Brazil).

Shell-size preference

The experiments were conducted for each of the two shell species separately (*Buccinanops gradatum* and *Olivancillaria urceus*). In each test, 15 naked hermit crabs were placed in aquaria with a minimum of 150 empty shells (10 shells per hermit crab) of various and adequate sizes. After 36h in this free-choice situation, hermit crabs were removed from their chosen shell by submerging the apex of the shell in hot water (Garcia & Mantelatto 2001), weighed (W) and measured for SL. Shell species were identified and the SDW, SAW, and SIV determined. Measurements were made directly on the specimens with a caliper (0.1 mm) or on drawings made with the aid of a camera lucida. Tests were replicated three times.

RESULTS

Shell-species preference

A total of 75 animals were utilized (animals SL ranging from 4.7 to 9.1 mm in Argentina and from 4.3 to 7.5 mm in Brazil). No significant preference for any of the two shell species by the Argentinean specimens ($P > 0.05$) was observed. Nevertheless, there were differences in shell species selection by the hermit crabs from Brazil, being shells of *B. gradatum*

significantly ($P < 0.05$) preferred (Table 1). In general, the morphometric relationships that best described the association between Brazilian hermit crabs and their selected shells species were those involving shell dimensions and hermit weight, independently of the shell species (Table 2).

Shell-size preference

During shell-size experiments, a total of 146 animals were utilized (animals SL ranging from 4.7 to 11 mm in Argentina and from 3.1 to 7.3 mm in Brazil). Independently of the shell species and region, all the morphometric relations demonstrated the suitable association between hermit crabs and their selected shells (Table 3).

DISCUSSION

Shell-size preference

Shell preferences, as shown by laboratory choice experiments, are important determinants of shell utilization under natural conditions (Garcia & Mantelatto 2001). In shell selection experiments, the size of the selected shells was strongly correlated with the size of the hermit crabs. Lively (1988) experimentally manipulated the shell mass, and suggested that volume is more important than weight during the shell-size selection by hermit crabs. Mantelatto & Dominciano (2002) conducted experiments of shell selection with *Paguristes tortugae* and found the best correlation coefficients between SDW and the dimensions of the hermit crabs. Thus, after observing the great variation in patterns of shell occupation

TABLE 1

Preference by *Loxopagurus loxochelis* for shells of two species of gastropods offered experimentally (* = significant correlation, $P < 0.05$; ns = non significant correlation)

Preferencia de *Loxopagurus loxochelis* por conchillas de dos especies de caracoles ofrecidas experimentalmente (* = correlación estadística significativa, $P < 0,05$; ns = correlación estadística no significativa)

Site studied	Species 1 versus species 2		n	Choice 1 : 2
Brazil	<i>B. gradatum</i>	<i>O. urceus</i>	43	43 : 0*
Argentina	<i>B. gradatum</i>	<i>O. urceus</i>	32	15 : 17 ^{ns}

among different hermit crab populations (Conover 1978, Blackstone 1985, Wilber 1990, Rodrigues et al. 2000, Garcia & Mantelatto 2001, Mantelatto & Dominciano 2002, Mantelatto & Meireles 2004), we may infer about the existence of shell selection in hermit crabs varying according to shell dimensions, but also depending on hermit crab species, the origin of the population as well as the availability of resources in the area of occurrence. The correlation coefficients obtained from shell-size selection were similar for both shell species: *O. urceus* and *B. gradatum*. Such pattern of shell selection might be considered beneficial to the hermit crab's population because it provides more than one option favorable to occupancy, since the two most occupied shell species provided both good correlation coefficients.

Shell-species preference

The absence of shell species preference under laboratory conditions was found by Orians & King (1964) for *Pagurus samuelis* and *Pagurus granosimanus*, by Siu & Lee (1992) for *Clibanarius bimaculatus* and Garcia & Mantelatto (2001) for *Calcinus tibicen*. However, in other studies the hermit crabs chose, in laboratory, the shell species most occupied in the field (Abrams 1978, Elwood et al. 1979, Siu & Lee 1992, Ohmori et al. 1995, Hahn 1998). In the present study the populations of the same species presented different shell choice patterns. While specimens from Brazil chose *B. gradatum* shells in spite of *O. urceus*, specimens from Argentina presented no significant shell type preference.

TABLE 2

Regression equations for Brazilian and Argentinean chosen shell species (r = correlation coefficient; SL = shield length; W = hermit crab weight; SAW = shell aperture width; SAL = shell aperture length; SIV = shell internal volume; SDW = shell dry weight; * = significant correlation, P < 0.05)

Ecuaciones de regresión para las especies de caracoles de Brasil y Argentina seleccionadas (r = coeficiente de correlación; SL = largo del escudo; W = peso del cangrejo ermitaño; SAW = ancho de la abertura de la concha; SAL = largo de la abertura de la concha; SIV = volumen interno de la concha; SDW = peso seco de la concha; * = correlación estadística significativa, P < 0,05)

Site studied	n	Relation	Exponential equation $Y = aX^b$	Linearized equation $\ln Y = \ln a + b \ln X$	r-value
Brazil	42	SAW x SL	$SAW = 1.12 SL^{1.22}$	$\ln SAW = 0.11 + 0.20 \ln SL$	0.85*
	42	SAL x SL	$SAL = 3.03 SL^{1.07}$	$\ln SAL = 6.23 + 0.68 \ln SL$	0.85*
	42	SDW x SL	$SDW = 0.02 SL^{2.85}$	$\ln SDW = -3.91 + 1.05 \ln SL$	0.76*
	41	SIV x SL	$SIV = 0.006 SL^{3.56}$	$\ln SIV = -5.11 + 1.27 \ln SL$	0.80*
	42	SAW x W	$SAW = 8.58 W^{0.35}$	$\ln SAW = 2.15 - 1.05 \ln W$	0.90*
	42	SAL x W	$SAL = 18.16 W^{0.31}$	$\ln SAL = 2.90 - 1.17 \ln W$	0.89*
	42	SDW x W	$SDW = 3.19 W^{0.82}$	$\ln SDW = 1.16 - 1.20 \ln W$	0.81*
	41	SIV x W	$SIV = 2.13 W^{1.04}$	$\ln SIV = 0.76 + 0.04 \ln W$	0.86*
Argentina	32	SAW x SL	$SAW = 3.54 SL^{1.13}$	$\ln SAW = 1.26 + 0.12 \ln SL$	0.76*
	32	SAL x SL	$SAL = 3.64 SL^{0.60}$	$\ln SAL = 1.29 - 0.51 \ln SL$	0.54*
	32	SDW x SL	$SDW = 0.03 SL^{3.09}$	$\ln SDW = -3.50 + 1.13 \ln SL$	0.76*
	32	SIV x SL	$SIV = 0.06 SL^{2.30}$	$\ln SIV = -2.81 + 0.83 \ln SL$	0.75*
	32	SAW x W	$SAW = 25.43 W^{0.12}$	$\ln SAW = 3.24 - 2.12 \ln W$	0.36*
	32	SAL x W	$SAL = 10.51 W^{0.05}$	$\ln SAL = 2.35 - 2.12 \ln W$	0.19
	32	SDW x W	$SDW = 5.87 W^{0.31}$	$\ln SDW = 1.77 - 1.17 \ln W$	0.34*
	32	SIV x W	$SIV = 3.84 W^{0.16}$	$\ln SIV = 1.34 - 1.83 \ln W$	0.23

TABLE 3

Regression equations for each chosen shell size (r = correlation coefficient; SL = shield length; W = hermit crab weight; SAW = shell aperture width; SAL = shell aperture length; SDW = shell dry weight; SIV = shell internal volume; * = significant correlation, $P < 0.05$)

Ecuaciones de regresión para cada una de las tallas de las conchas seleccionadas (r = coeficiente de correlación; SL = largo del escudo; W = peso del cangrejo ermitaño; SAW = ancho de la abertura de la concha; SAL = largo de la abertura de la concha; SIV = volumen interno de la concha; SDW = peso seco de la concha; * = correlación estadística significativa, $P < 0,05$)

Site studied	Species	n	Relation	Transformed equation $\ln Y = \ln a + b \ln X$	r-value		
Brazil	<i>B. gradatum</i>	44	SAW x SL	$\ln \text{SAW} = 0.50 - 0.01 \ln \text{SL}$	0.69*		
		44	SAL x SL	$\ln \text{SAL} = 1.27 - 0.01 \ln \text{SL}$	0.75*		
		44	SDW x SL	$\ln \text{SDW} = -1.97 + 0.66 \ln \text{SL}$	0.60*		
		43	SIV x SL	$\ln \text{SIV} = -5.30 + 1.27 \ln \text{SL}$	0.59*		
		44	SAW x W	$\ln \text{SAW} = 2.12 - 1.10 \ln \text{W}$	0.90*		
		44	SAL x W	$\ln \text{SAL} = 2.88 - 1.17 \ln \text{W}$	0.94*		
		44	SDW x W	$\ln \text{SDW} = 1.15 - 0.40 \ln \text{W}$	0.82*		
		43	SIV x W	$\ln \text{SIV} = -0.27 - 0.03 \ln \text{W}$	0.64*		
		39	SAW x SL	$\ln \text{SAW} = 0.38 - 0.04 \ln \text{SL}$	0.84*		
	<i>O. urceus</i>	39	SAL x SL	$\ln \text{SAL} = 1.79 - 0.22 \ln \text{SL}$	0.82*		
		39	SDW x SL	$\ln \text{SDW} = -1.71 + 0.75 \ln \text{SL}$	0.77*		
		39	SIV x SL	$\ln \text{SIV} = -3.91 + 0.99 \ln \text{SL}$	0.84*		
		39	SAW x W	$\ln \text{SAW} = 1.98 - 1.27 \ln \text{W}$	0.92*		
		39	SAL x W	$\ln \text{SAL} = 3.12 - 1.43 \ln \text{W}$	0.91*		
		39	SDW x W	$\ln \text{SDW} = 1.77 - 0.46 \ln \text{W}$	0.86*		
		39	SIV x W	$\ln \text{SIV} = 0.69 - 0.25 \ln \text{W}$	0.94*		
		Argentina	<i>B. gradatum</i>	33	SAW x SL	$\ln \text{SAW} = 1.48 - 0.04 \ln \text{SL}$	0.70*
				33	SAL x SL	$\ln \text{SAL} = 0.70 - 0.02 \ln \text{SL}$	0.70*
				33	SDW x SL	$\ln \text{SDW} = -1.11 + 0.47 \ln \text{SL}$	0.52*
30	SIV x SL			$\ln \text{SIV} = -4.60 + 1.16 \ln \text{SL}$	0.81*		
32	SAW x W			$\ln \text{SAW} = 1.40 - 0.33 \ln \text{W}$	0.73*		
32	SAL x W			$\ln \text{SAL} = 1.06 - 0.31 \ln \text{W}$	0.72*		
32	SDW x W			$\ln \text{SDW} = 0.14 - 0.19 \ln \text{W}$	0.54*		
29	SIV x W			$\ln \text{SIV} = -4.71 - 3.50 \ln \text{W}$	0.85*		
30	SAW x SL			$\ln \text{SAW} = 2.57 - 0.61 \ln \text{SL}$	0.67*		
<i>O. urceus</i>	30		SAL x SL	$\ln \text{SAL} = 1.17 - 0.45 \ln \text{SL}$	0.58*		
	30		SDW x SL	$\ln \text{SDW} = -0.63 + 0.55 \ln \text{SL}$	0.70*		
	30		SIV x SL	$\ln \text{SIV} = -2.04 + 0.65 \ln \text{SL}$	0.75*		
	30		SAW x W	$\ln \text{SAW} = 3.41 - 1.77 \ln \text{W}$	0.69*		
	30		SAL x W	$\ln \text{SAL} = 2.17 - 1.61 \ln \text{W}$	0.58*		
	30		SDW x W	$\ln \text{SDW} = 0.57 - 0.62 \ln \text{W}$	0.72*		
30	SIV x W	$\ln \text{SIV} = 0.99 - 0.56 \ln \text{W}$	0.73*				

Some particular differences in shell preferences by different species may be attributed both to the size of hermit crabs and to environmental conditions, with the animals looking for protection against the factors to which they are exposed (predation, energy expenditure, osmotic stress and wave action). Furthermore according to Hahn (1998), the experience of inhabiting a specific species of shell predisposes a hermit crab to choose the same species of shell then intraspecific competition could be reduced. On the other hand, when in a free choice situation (laboratory experiments) the shells chosen are those that best fit, as demonstrated in the shell size selection experiments.

The *L. loxochelis* populations from Brazil and Argentina present differences in the mean size of the specimens, with Argentinean hermit crabs reaching larger sizes (7.11 ± 1.29 mm SL) than the Brazilian ones (5.77 ± 0.82 mm SL). This pattern agrees with the one proposed by Abele (1982), who postulated that the size of crustaceans decrease with decreasing latitude. Furthermore, according to Ohmori et al. (1995), shell utilization patterns would change for different crab sizes even within the same species.

This might explain the differences found in the patterns of shell species preference between both hermit crabs populations. Further studies, comparing in details other aspects of both populations, are needed and will undoubtedly contribute to further resolution of the biological variability in near-shore hermit crabs.

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