Variability of shell occupation by intertidal and infralittoral *Calcinus tibicen* (Anomura, Diogenidae) populations.

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Abstract

The purpose of this study was to determine the shell utilization pattern of *Calcinus tibicen* (Herbst, 1791) from the infralittoral area of Anchieta Island in order to compare it with data previously obtained for an intertidal population of Grande Beach, Ubatuba, Brazil. Hermit crabs were collected monthly from January to December 1998 on the infralittoral rocky shores of Anchieta Island using SCUBA diving methods. Animals were frozen and transported to the laboratory where they were weighed and measured for cephalothoracic shield length and width, left propodus length and height. Gastropod shell species were identified, weighed and measured for shell aperture width and length and shell internal volume. A total of 124 individuals were collected on Anchieta Island (48 males, 46 non-ovigerous females and 30 ovigerous females), occupying fifteen shell species. A positive relationship ($r > 0.60$) was obtained between the size of the shells occupied and the hermit crabs. Analysis of shell weight and crab dimensions demonstrated that this shell dimension constitute mainly the determinant for *C. tibicen* shell utilization. With respect to the size of the animals and the occupied shell types, it was observed that the larger individuals of the infralittoral population were exposed to a higher gastropod shell species variability compared to those of the intertidal population that were mainly occupying *Stramonita haemastoma* (Linnaeus, 1767) shells. In this respect, we can infer for different hermit crab populations inhabiting different areas the existence of a pattern of preference for specific shell dimensions associated with shell availability. This study corroborates the intraspecific and interespecific plasticity existing in the shell occupation process in areas with biotic and abiotic disparities.

Key-Words: Anomura; hermit crab; shell occupation

Introduction

The hermit crabs constitute an important and potential group of study in terms of the interaction between environmental resources (gastropod shells) and population dynamics. The essence of this interaction is supported by two mechanisms involving shell selection and shell occupation. The final result, *i.e.* the kind of shell utilized, is affected by different factors acting on both mechanisms.

The patterns of shell utilization vary among hermit crab populations and are influenced by the type and size of shells available in the survey, the locality (intertidal or sublitoral area) and the hermit crabs' shell preference (Mantelatto and Garcia, 2000).

Although shell utilization by hermit crabs has been examined in other areas of the world since the 60's, few reports (Scully, 1979; Manjón-Cabeza and García-Raso, 1999) are available about the differences and/or similarities of such process within populations of the same species but inhabiting different regions. According to Bertness (1980), beaches supporting hermit crab populations may differ in the abundance size and type of gastropod species present, so hermit crabs in different populations may differ in the patterns of shell occupation.

Calcinus tibicen was the fourth ranked species in terms of abundance, with a moderate influence on structure and dynamics of the hermit crab community of Anchieta Island (Mantelatto and Garcia, 2001). This species has been investigated (Oliveira, 1998; Fransozo and Mantelatto, 1998; Mantelatto and Garcia, 1999 and 2000; Garcia and Mantelatto, 2001) as part of a long-term effort undertaken to identify important ecological parameters affecting shell utilization by hermit crabs.

Thus, the objective of the present study was to evaluate the gastropod shell occupation process by *Calcinus tibicen* from the infralittoral area of Anchieta Island in order to compare it with data obtained for this species living in the intertidal area of Grande Beach, Ubatuba region. This kind of study is used to test the hypothesis of the existence of an intraspecific difference provided by the environmental selective pressure.

Material and Methods

Sampling and Analysis

Hermit crabs were obtained monthly from January to December 1998 on the infralittoral rocky shores of Anchieta Island, which surface is irregular, with many huge boulders. Specimens were captured during the daytime by three persons using SCUBA diving methods during 30 min over the same area of about 850 m^2. This methodology provided large amounts of material from this area of irregular surface and thus was considered efficient for the population study (Mantelatto and Garcia, 2001).

Animals were frozen and transported to the laboratory where they were carefully removed from their shells, weighed (WW) and measured for cephalothoracic shield length (CSL = from the tip of the rostrum to the V-shaped groove at the posterior edge), and width (CSW), left chelar propodus length (LPL) and height (LPH). Shells were weighed (SWW) and measured for shell aperture width (SAW) and length (SAL) and shell internal volume (SIV). Sex was determined from the gonopore position. Measurements were made with a caliper rule (0.1 mm) or by drawing with the aid of a camera lucida. Gastropod shell species were identified according to Rios (1994) and by Dr. Osmar Domaneschi (University of São Paulo).

The relations between hermit crab size and shell variables were determined by regression analysis and by correlation coefficients using the power function equation ($Y = a.X^b$). The chi-square test (χ^2) was used to compare the rate of occupancy of the gastropod shell species.

Results

A total of 124 individuals of *C. tibicen* were collected (48 males, 46 non-ovigerous females and 30 ovigerous females). The size frequency distribution showed a prevalence of specimens measuring 4.5 to 6.0 mm in CSL. The size range was from 2.5 mm (non-ovigerous female) to 8.5 mm CSL (males) (Figure 1).

The hermit crabs were found occupying 15 species of gastropod shells in different percentages. *Pisania auritula* was occupied in significant ($p < 0.05$) numbers (34.7%), followed by *Astraea olfersii* (18.5%) and *Cerithium atratum* (13.7%) (Table 1).

There were differences in gastropod shell species occupation between sexes. *A. olfersii* shells were significantly more occupied by males than by non-ovigerous and ovigerous females. In contrast, *C. atratum* shells were occupied in higher percentages by non-ovigerous females and *P. auritula* shells by ovigerous females (χ^2 test, $p < 0.05$).

Shell species occupation as a function of hermit crab size is illustrated in Figure 2. The diversity of shells utilized increased with the increasing of individual size.

Regressions of shell weight and crab size and weight were those that best described ($r > 0.75$) the hermit crab *versus* shell association (Table 2). This pattern was also recorded for males and ovigerous and non-ovigerous females.

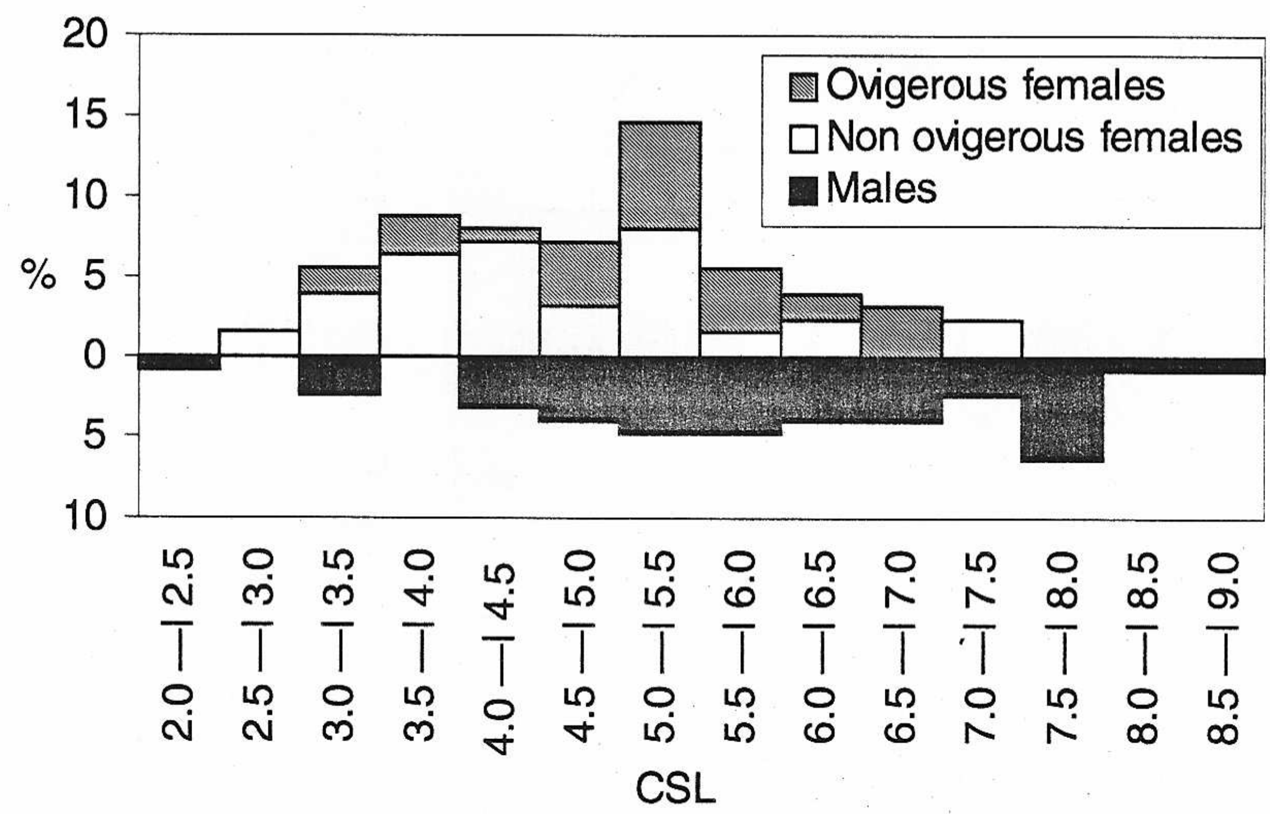

Figure 1: *C. tibicen.* Size frequency distribution (mm) for the total number of individuals collected.

Table 1: Total number of shells occupied by *Calcinus tibicen* collected on Anchieta Island.

Gastropod Shell Species	Males	Non Ovigerous Females	Ovigerous females	Total	%
Astraea sp.	01	-	-	01	0.81
Astraea latispina (Philippi, 1844)	03	01	-	04	3.23
Astraea olfersii (Philippi, 1846)	14	06	03	23	18.55
Astraea phoebia R ding, 1798	02	01	-	03	2.41
Cerithium atratum (Born, 1778)	01	12	04	17	13.71
Chicoreus tenuivaricosus (Dautzenberg, 1927)	02	-	-	02	1.61
Cymatium parthenopeum (von Salis, 1793)	02	01	-	03	2.41
Fusinus brasiliensis (Grabau, 1904)	-	01	-	01	0.81
Leucozonia nassa (Gmelin, 1791)	03	01	02	06	4.84
Modulus modulus (Linnaeus, 1758)	01	-	-	01	0.81
Pisania auritula (Link, 1807)	09	16	18	43	34.68
Pisania pusio (Linnaeus, 1758)	02	-	-	02	1.61
Stramonita haemastoma (Linnaeus, 1767)	07	02	-	09	7.26
Strombus pugilis Linnaeus, 1758	01	-	-	01	0.81
Tegula viridula (Gmelin, 1791)	-	05	03	08	6.45
Total	48	46	30	124	100

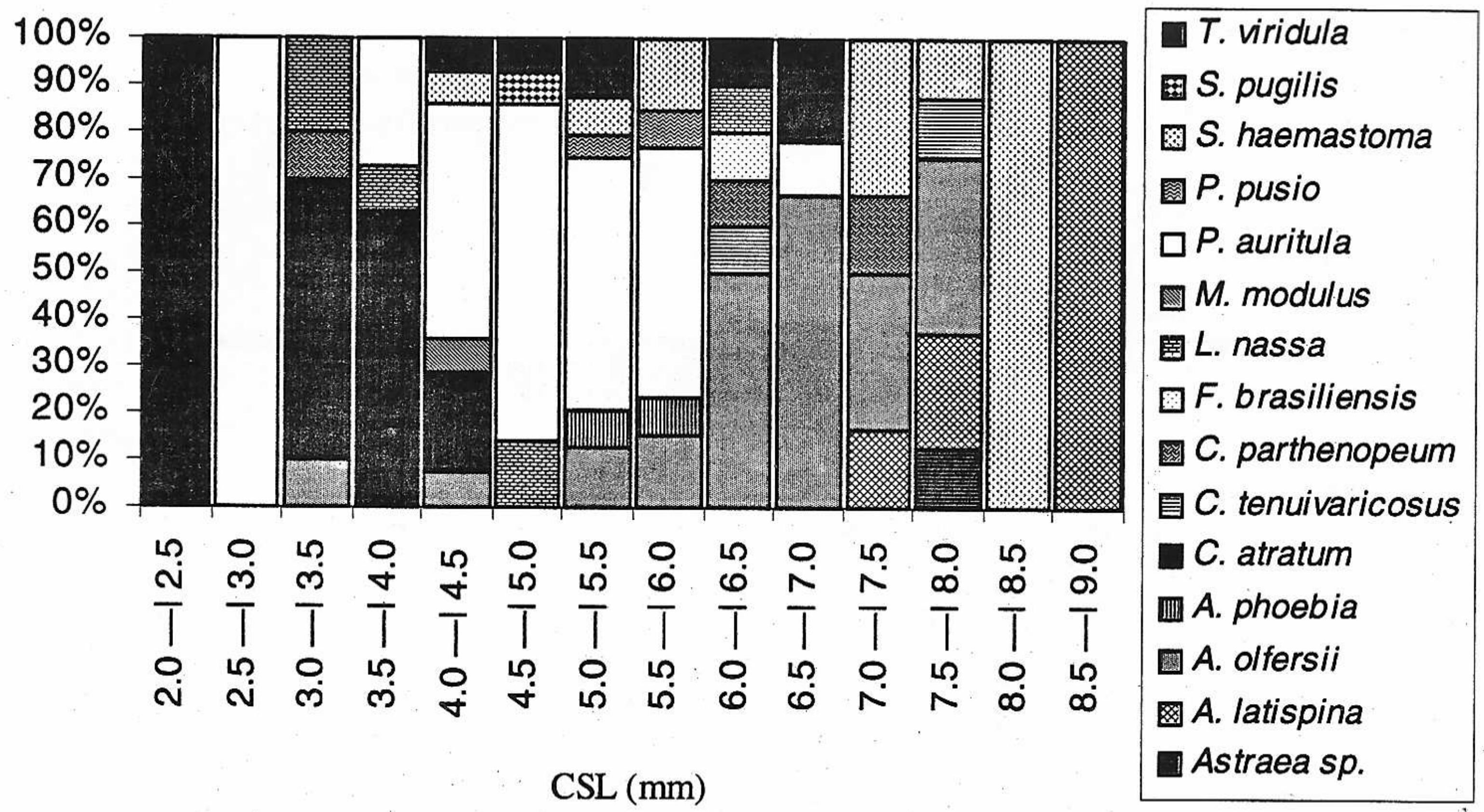

Figure 2: *C. tibicen*. Gastropod shell species occupation as a function of hermit crab size.

Table 2: Regression equations for the relations between hermit crab dimensions and occupied shells. (N = number of individuals; r = correlation coefficient; CSL = cephalothoracic shield length: CSW = cephalothoracic shield width; LPL = left propodus length; LPH = left propodus height; WW = hermit crab wet weight; SAW = shell aperture width; SAL = shell aperture length; SWW = shell wet weight; SIV = shell internal volume)

Relations	N	$Y = a. X^b$	r
SAW x CSL	124	$SAW = 1.06CSL^{1.22}$	0.75
SAW x CSW	124	$SAW = 1.51CSW^{1.16}$	0.69
SAW x LPL	120	$SAW = 6.09LPL^{0.51}$	0.49
SAW x LPH	121	$SAW = 1.55LPH^{1.14}$	0.78
SAW x WW	124	$SAW = 10.88WW^{0.43}$	0.74
SAL x CSL	124	$SAL = 5.24CSL^{0.53}$	0.47
SAL x CSW	124	$SAL = 5.68CSW^{0.56}$	0.47
SAL x LPL	120	$SAL = 5.73LPL^{0.52}$	0.48
SAL x LPH	121	$SAL = 1.45LPH^{1.11}$	0.73
SAL x WW	124	$SAL = 14.87WW^{0.22}$	0.54
SWW x CSL	124	$SWW = 0.15CSL^{2.04}$	0.82
SWW x CSW	124	$SWW = 0.25CSW^{2.02}$	0.78
SWW x LPL	120	$SWW = 0.27LPL^{1.83}$	0.79
SWW x LPH	121	$SWW = 0.32LPH^{1.83}$	0.82
SWW x WW	124	$SWW = 7.55WW^{0.74}$	0.84
SIV x CSL	49	$SIV = 0.11CSL^{1.23}$	0.51
SIV x CSW	49	$SIV = 0.14CSW^{1.27}$	0.53
SIV x LPL	49	$SIV = 0.13LPL^{1.26}$	0.60
SIV x LPH	49	$SIV = 0.13LPH^{1.29}$	0.57
SIV x WW	49	$SIV = 1.27WW^{0.53}$	0.65

Discussion

Differences in gastropod shells utilization can occur as a function of the area of occurrence of the hermit species. Specimens of *C. tibicen*, inhabitants of the infralittoral area of Anchieta Island, were found occupying a greater diversity of shells than the population studied on the intertidal rocky shore of Grande Beach (Mantelatto and Garcia, 2000). This can be attributed to the differences in abiotic characteristics of these two areas in terms of water dynamics, since a calm and protected area (Anchieta Island) allows a higher installation of species, in contrast to the intertidal area (Grande Beach) with high wave activity (Fransozo and Mantelatto, 1998).

The intertidal population of *C. tibicen* studied by Mantelatto and Garcia (2000) occupied seven gastropod shell species, being the most occupied ones *S. haemastoma* (71.26%), *L. nassa* (16.20%) and *P. auritula* (6.88%). On the other hand, the population of the present study occupied these same seven gastropod species and eight more, but in different proportions, being the most occupied *P. auritula* (34.68%), *A. olfersii* (18.55%) and *C. atratum* (13.71%).

No other hermit crab species that might live in sympatry with *C. tibicen*, causing interspecific shell competition was found on the rocky coast of Grande Beach (Mantelatto and Garcia, 2000). Conversely, *C. tibicen* directly coexists with other hermit crab species on Anchieta Island, such as *Dardanus insignis* (de Saussure, 1858), *Dardanus venosus* (H. Milne Edwards, 1848), *Paguristes calliopsis* Forest and Saint Laurent, 1967, *Paguristes erythrops* Holthuis, 1959, *Paguristes tortugae* Schmitt, 1933, *Pagurus criniticornis* (Dana, 1852), and *Pagurus brevidactylus* (Stimpson, 1879), that occupy the same shells but in different percentages (Mantelatto and Garcia, 2001). Thus, we may infer that the differences in gastropod shell occupancy rates found between the two populations were mainly due to the differences in shell species availability in the two sites and in function of the interspecific competition that may exists in the studied area.

Oliveira (1998), found *C. tibicen* coexisting with other six Diogenidae hermit crab species inhabiting the same gastropod shell species but in different proportions, characterizing resource partitioning. According to Bertness (1980), interespecific differences in shell occupation can be attributed to: 1) differences between the hermit crab species in shell preferences; 2) interespecific differences in hermit crab size, making the shells available to each species distinct; 3) differences between hermit crab species in habitat, affecting the shell types available to each species; or 4) differences in the ability to acquire preferred shells in interespecific shell exchanges. On the other hand, intraspecific differences in shell occupation can be attributed to a resource partitioning in order to avoid competitive conflicting behaviour and energy loss within individuals of the same population. In this sense, we agree with Lancaster (1988), that "hermit crabs are particularly good at solving the problems of limited resources and are efficient at both exploiting what they have and contesting what they have not".

Manjón-Cabeza and García-Raso (1999) pointed that the differences between shell occupations by *Diogenes brevirostris* Stimpson, 1858 in different localities were probably due to interespecific competition. However, these authors did not mention the similarities and/or differences in the shell availability. Scully (1979) found that the differences in shell utilization between two populations of *Pagurus longicarpus* Say, 1817 were the results of differences in the physical factors of the environment, that direct effects on the metabolic cost of the hermit crabs inhabiting that environment and indirect effects on the quality abundance of gastropod shells.

According to Mantelatto and Garcia (2000), the mechanisms underlying the pattern of shell utilization by hermit crabs have been found to be determined by such factors as competition, shell size, type, internal volume and shell availability. The population of the present study, as well as that studied by Mantelatto and Garcia (2000), showed a correlation between individuals and weight of the shells occupied, confirming the importance of this shell characteristic in the occupation process, despite the differences of the habitats (intertidal and infralittoral). In this sense, we may infer that the shell weight constitute mainly the determinant for *C. tibicen* shell utilization as they provide protection against brachyuran predators (Siu and Lee, 1992), water currents and the action of waves (Bertness, 1982; Oliveira, 1998).

The larger individuals of *C. tibicen* in the infralittoral population (present study) occupied a greater diversity of larger shells (*C. tenuivaricosus, C. parthenopeum, F. brasiliensis, S. haemastoma* and *S. pugilis*) compared to those from the intertidal region, which only occupied *S. haemastoma* shells (Mantelatto and Garcia, 2000). The specimens of initial and intermediate size classes presented a similar occupation pattern, utilizing a wider variety of gastropod species. This sharp and discrepant difference observed between the populations of the two localities in terms of the diversity of occupied shells in relation to individual crab size supports the hypothesis that shell occupation by *C. tibicen* in the Ubatuba region is associated with shell availability at this site. This fact is even clearer if we consider that the two populations consisted of individuals of similar sizes in all sexual categories considered.

Males attained larger sizes than females, reflecting sexual dimorphism. Different patterns of size distribution were found for males and females. This can be attributed to such factors as differential mortality and growth rates between sexes (Abrams, 1988), with males reaching larger sizes within a shorter time than females, but being influenced by shell limitation, a fact that may imply reduced survival (Fransozo and Mantelatto, 1998; Mantelatto and Garcia, 2000).

There were differences between sexes in shell species occupation. *Astraea olfersii* shells were significantly more occupied by males than by non-ovigerous and ovigerous females. In contrast, *C. atratum* shells were occupied in higher percentages by non-ovigerous females while *P. auritula* shells were mostly occupied by ovigerous females. This fact probably characterizes the intraspecific resource competition occurring mainly to guarantee a good adequacy of individual size to shells available in the survey. Differences in shell utilization between sexes were also observed by Imazu and Asakura (1994) to *Pagurus geminus* McLaughlin, 1976 and *Clibanarius virescens* (Krauss, 1843) and by Bertini and Fransozo (1999) to *Petrochirus diogenes*. These differences may be due to differences in body size, competitive ability or reproductive behaviour, respectively (Bertness, 1981; Blackstone, 1985; Imazu and Asakura, 1994).

Thus, we may infer for *C. tibicen* inhabiting different areas in the Ubatuba region, the existence of the same pattern of choice of a given shell parameter (shell weight), but a different shell type utilization in function of the availability of the gastropod shell species and of the interespecific competition. The process of shell occupation in areas with biotic and abiotic disparities (and differing from one another), suggest the need for greater care when comparing species originating from different areas.

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