CLUSTERING BEHAVIOR OF HERMIT CRABS (DECAPODA, ANOMURA) IN AN INTERTIDAL ROCKY SHORE AT SÃO SEBASTIÃO, SOUTHEASTERN BRAZIL

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(With 2 figures)

ABSTRACT

The clustering behavior and cluster composition of hermit crabs as well as the patterns of shell utilization of clustered and scattered individuals were studied. This study was conducted in the intertidal region of Grande Beach, São Sebastião, southeastern Brazil. Samples were taken both in randomized transects and 1 m^2 quadrats during low tide periods. Crabs were counted, measured (shield length), and sexed. Shells were identified and had their adequacy and condition (physical damage and incrustation) recorded. Clusters ocurred mainly in air exposed areas and were dominated or composed only by *Clibanarius antillensis*. Other species like *Paguristes tortugae*, *Pagurus criniticornis*, and *Calcinus tibicen* were also present in these clusters, but in small numbers. Only one monospecific aggregation composed by individuals of *P. criniticornis* was recorded in tide pools. Almost all crabs were inactive, despite some that were submerged in tide pools. Most of the individuals of *C. antillensis* were clustered (70.88%). Scattered individuals were larger than clustered ones and occupied mainly shells of *Tegula viridula*, which seemed to be the most adequate shell to the crabs. Clustered individuals used less incrusted shells than isolated ones. In general, clustering in Grande Beach presented the same patterns of size and sex distribution, and shell utilization than others already studied, with the exception of the smaller cluster size registered in this area.

Key words: Hermit crabs, clustering behavior, *Clibanarius antillensis*, shell utilization.

RESUMO

Agrupamentos de ermitões (Decapoda, Anomura) na região entremarés de um costão rochoso em São Sebastião, sudeste brasileiro

Neste trabalho são avaliados o comportamento de agrupamento de caranguejos ermitões bem como os padrões de utilização de conchas por indivíduos agrupados e isolados. O estudo foi desenvolvido na região entremarés da Praia Grande, São Sebastião, sudeste brasileiro. As amostras foram feitas tanto com transectos quanto com quadrados de 1 m^2 aleatorizados durante períodos de maré baixa. Os ermitões foram contados, medidos (comprimento do escudo cefalotorácico) e sexados. As conchas foram identificadas e avaliadas quanto sua adequação e condição (danos físicos e incrustrações). Os agrupamentos ocorreram principalmente em áreas expostas ao ar e foram dominados ou compostos unicamente por indivíduos de *Clibanarius antillensis*. *Paguristes tortugae, Pagurus criniticornis* e *Calcinus tibicen* também ocorreram nos agrupamentos, mas em menor abundância. Um único agrupamento monoespecífico de *P. criniticornis* foi registrado em poças de marés. A grande maioria dos ermitões estavam inativos, com exceção de alguns indivíduos que estavam submersos em poças de marés. A maioria dos indivíduos *C. antillensis* estava agrupada (70,88%). Indivíduos isolados foram maiores que os agrupados e utilizaram principalmente conchas de *Tegula viridula*, as quais mostraram-se mais adequadas para os ermitões dessa população. Indivíduos agrupados usaram conchas menos incrustadas que os isolados. No geral, o comportamento de agrupamento de ermitões na Praia Grande apresentou os mesmos padrões de distribuição de tamanho e sexo e de utilização de conchas que os já descritos na literatura, embora o tamanho dos agrupamentos nessa área tenha se apresentado menor.

Palavras-chave: caranguejos ermitões, comportamento de agrupamento, *Clibanarius antillensis*, utilização de concha.

INTRODUCTION

Hermit crabs display clustering behavior and daily movements (Hazlett, 1966; Snyder-Conn, 1980; Gherardi & Vannini, 1989, 1992 and 1993) which are closely related to the tidal rhythm (Snyder-Conn, 1980). Clusters are tipically formed during low tides when the hermit crabs stay in physical contact with each other, presenting low activity and preference for shady substrates (Snyder-Conn, 1980). At flood tide the hermit crabs disperse to foraging areas and present social activities (Gherardi & Vannini, 1993), while at high tide they remain generaly inactive under boulders and in crevices (Snyder-Conn, 1980). Low and high tides are considered adverse periods due to the risks of desiccation and predation, respectively (Snyder-Conn, 1980), thus also leading the hermit crabs to look for refuges.

The clustering behavior is probably controlled by interactions between exogenous and endogenous factors related to the tidal cycle. In this way, environmental stimuli (air exposure, hydrostatic pressure, light, food availability and small scale water movements) seem to play an important role in determining the activity of the hermit crabs (Snyder-Conn, 1980; Gherardi & Vannini, 1989). The adaptative meaning of the clustering behavior was largely investigated by Gherardi & Vannini (1992, 1993). It is supposed that clusters serve as "shell exchange markets" or places were males and females can locate themselves easily. However, clustering may be a response to environmental factors, such as desiccation (Reese, 1969; Gherardi & Vannini, 1993), and habitat heterogeneity (Snyder-Conn, 1981; Turra *et al.* in press).

The aim of this study was to describe the clustering behavior of hermit crabs in the Brazilian coast, focusing cluster size (number of individuals per cluster), species composition, and shell utilization pattern. Comparisons of populational parameters and shell adequacy and condition between clustered and scattered individuals were used as evidences to discuss theories on the factors that regulate the clustering behavior in the area of study.

MATERIAL AND METHODS

This study was conducted from September to December 1994 at the Grande Beach (45°24'W; 23°49'S), São Sebastião, northern coast of São Paulo State, Brazil. The area of study is an intertidal habitat of 160 m^2 composed by cobbles and boulders irregularly arranged forming natural refuges, holes and crevices. The tides are semidiurnal with maximal variation of 2 meters.

Twenty two quadrats of 1 m^2 were sorted in the area of study in order to evaluate the dispersion pattern and the activity of the hermit crabs during low tide. A dispersion index was calculated to access the pattern of distribution of hermit crabs (Elliott, 1977). Active individuals were those that were feeding or walking. Each quadrat was characterized in relation to air exposure (total or partial) or submersion (presence of tide pools). Hermit crabs and their shells were identified and the number and size of clusters (number of individuals present in each cluster) were registered. Shell adequacy and condition were also evaluated.

The shell adequacy to the hermit crabs was evaluated using a visual index modified from Abrams (1978): 1. Hermit crab not visible; 2. Pereopods visible but chelipeds not; 3. Angle of 90° between chelipeds and the plan of the shell aperture; 4. Obtuse angle between chelipeds and the plan of the shell aperture; 5. Chelipeds closing the aperture; 6. Shield exposed. The shell condition was recorded using a modification of the condition index proposed by McClintock (1985). This index evaluates the degree of incrustation (1. shell not incrusted; 2. until 50% incrusted; 3. 50% to 100% incrusted) and of physical damage in the shells used by the hermit crabs (A. perfect; B. perforations and/or less than 4 mm of the aperture damaged; C. more than 4 mm of the aperture damaged and/or apex broken).

In order to compare the size distribution between clustered and scattered individuals, three 0.50 m wide transects were sampled during the low tide. The crabs were classified as clustered

(5 or more individuals) or scattered, removed from their shells, and sized (shield length) with a milimetric ocular under stereomicroscope. Cluster size was also recorded. The two-way ANOVA and the log-likelihood G test were both performed with a 0.05 significance level (Zar, 1984).

RESULTS

Four hermit crab species were collected in the intertidal region of Grande Beach: *Clibanarius antillensis* (Stimpson, 1862), *Paguristes tortugae* (Schmitt, 1933), *Pagurus criniticornis* (Dana, 1852), and *Calcinus tibicen* (Herbst, 1791), with *C. antillensis* being the most abundant (226 individuals in 261).

The dispersion pattern of the crabs was contiguous (I = 621.130, d = 28.84, df = 21, $p < 0.001$), and greatly influenced by the distribution of *C. antillensis*. Most of the hermit crabs were present in clusters (70.88%, $G_{[1]} = 46.96$, $p < 0.001$), that were more frequently found in air exposed areas (14 clusters out of 15). Most of the aggregates (11) were monospecific, composed only by individuals of *C. antillensis* (10) or of *P. criniticornis* (1 cluster composed by 6 individuals in a tide pool). Polyspecific clusters were dominated by *C. antillensis* but also presented individuals of *P. tortugae*, *P. criniticornis* and/or *C. tibicen*. The clusters composed or dominated by *C. antillensis* presented 5 to 42 individuals (n = 14, 12.78 ± 10.29 individuals).

The activity pattern of the hermit crabs was studied only during low tide. Scattered and clustered individuals exposed to the air were inactive, differently from some isolated and submerged ones (3 individuals) in tide pools. Some isolated hermit crabs, exposed to the air and out of refuges, presented their shells with the aperture turned upward.

In the transects 31 males and 27 females (14 ovigerous, 44.44%) of *C. antillensis* were collected (Table 1). Both males and females were more frequently found in clusters than isolated (females: $G_{[1]} = 14.85$, $p < 0.001$; males: $G_{[1]} = 3.98$, $p < 0.05$). Size showed to be more dependent on the behavioral situation of the crabs (clustered or scattered) than on their sex, although males were sligthly larger than females (Table 1).

Shell utilization differed between clustered and scattered individuals of *C. antillensis* ($G_{[5]} = 262.14$, $p < 0.001$) (Fig. 1). Shells of *Tegula viridula* (Gmelin, 1791) were more frequently occupied by scattered individuals, while shells of *Stramonita* (= *Thais*) *haemastoma* (Linnaeus, 1797), *Morula nodulosa* (C. B. Adams, 1845), *Leucozonia nassa* (Gmelin, 1791), and *Cerithium atratum* (Born, 1778) were used mainly by the scattered ones.

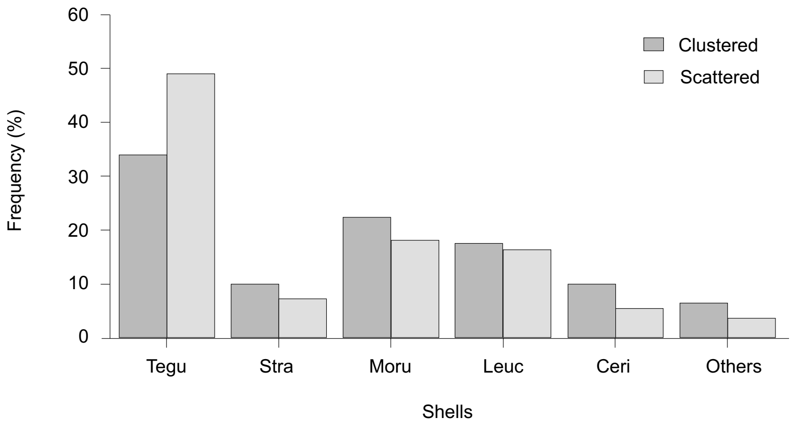

Fig. 1 — Shell utilization by clustered and scattered individuals of *C. antillensis* in the intertidal region of Grande Beach, São Sebastião, Southeastern Brazil. (Shells: Tegu, *Tegula viridula*; Stra, *Stramonita* (= *Thais*) *haemastoma*; Moru, *Morula nodulosa*; Leuc, *Leucozonia nassa*, Ceri, *Cerithium atratum*)

TABLE 1

Two-way ANOVA of the shield lenght (mm) of clustered and scattered males and females of *C. antillensis* collected in the intertidal region of Grande Beach, São Sebastião, Southeastern Brazil. ($\bar{x}$, mean; SD, standard deviation; df, degrees of freedom; MS, mean square, F, F statistic; p, probability).

	Sex					
	Females		**Males**		**Total**	
Situation	n	$\bar{x}$ ± SD	n	$\bar{x}$ ± SD	n	$\bar{x}$ ± SD
Clustered	23	2.02 ± 0.49	21	2.02 ± 0.73	44	2.02 ± 0.61
Scattered	4	3.25 ± 1.21	10	3.61 ± 1.72	14	3.51 ± 1.56
Total	27	2.60 ± 0.77	31	2.82 ± 1.35		

Two way ANOVA (sex x situation)

Source	**df**	**MS**	**F**	**p**
Situation	1	18.060	20.757	< 0.001
Sex	1	0.291	0.334	0.565
Situation*Sex	1	0.283	0.325	0.571

Shell adequacy and incrustation also differed between clustered and scattered individuals (Table 2). Shells were more adequate and incrusted for isolated than clustered crabs.

Physical damage did not show any relationship with the behavioral situation (clustered or scattered) of the crabs (Table 2). Shell adequacy also seemed to be dependent on the shell type ($G_{[16]}$ = 33.65, p = 0.006), with shells of *T. viridula* and *C. atratum* presenting better adequacy than shells of *S. haemastoma*, *L. nassa*, and *M. nodulosa* (Fig. 2).

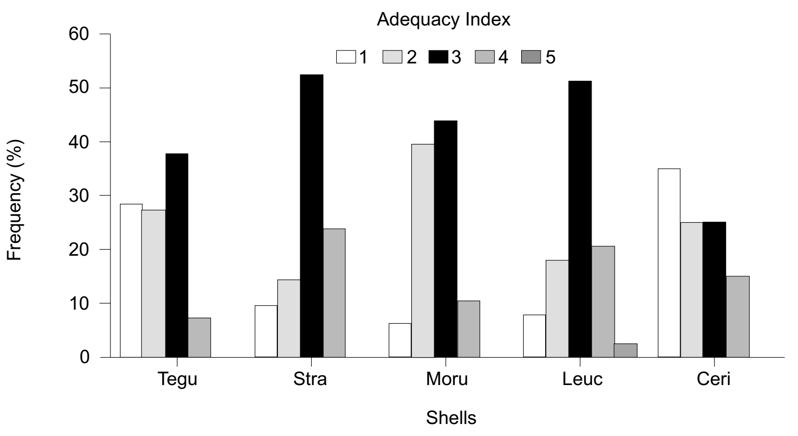

Fig. 2 — Visual adequacy of the shells most used by both clustered and scattered individuals of *C. antillensis* in the intertidal region of Grande Beach, São Sebastião, Southeastern Brazil. (Adequacy index: 1. Hermit crab not visible; 2. Pereopods visible but chelipeds not; 3. Angle of 90° between chelipeds and the plan of the shell aperture; 4. Obtuse angle between chelipeds and the plan of the shell aperture; 5. Chelipeds closing the aperture) (Shells: Tegu, *Tegula viridula*; Stra, *Stramonita* (=*Thais*) *haemastoma*; Moru, *Morula nodulosa*; Leuc, *Leucozonia nassa*, Ceri, *Cerithium atratum*)

TABLE 2

Shell adequacy and condition of clustered and scattered individuals of *C. antillensis* in the intertidal region of Grande Beach, São Sebastião, Southeastern Brazil.

Adequacy index: 1. Hermit crab not visible; 2. Pereopods visible but chelipeds not; 3. Angle of 90° between chelipeds and the plan of the shell aperture; 4. Obtuse angle between chelipeds and the plan of the shell aperture; 5. Chelipeds closing the aperture. Condition index: Incrustation: (1. shell not incrusted; 2. until 50% incrusted; 3. 50% to 100% incrusted); Physical damage: A. perfect; B. perforations and/or less than 4 mm of the aperture damaged; C. more than 4 mm of the aperture damaged and/or apex broken.

	Clustered	Scattered	G	df	p
• **Adequacy**					
Visual adequacy index			10.46	4	0.033
1	32	13			
2	38	22			
3	79	14			
4	21	6			
5	1	0			
• **Condition**					
Physical damage			0.53	2	0.768
a	92	29			
b	61	19			
c	13	6			
• **Incrustation**			**7.02**	**2**	**0.030**
1	27	14			
2	79	15			
3	63	26			

DISCUSSION

The clumped dispersion pattern registered for hermit crabs in this area is highly associated with the clustering behavior of *Clibanarius antillensis*. However, the aggregations found in Grande Beach presented less individuals than clusters of another species in other areas, such as mangroove swamps (Gherardi & Vannini, 1993). The small size of the clusters found in these rocky shore portion of Grande Beach may be related to the highly complex structure of this environment. A complex environmental structure may difficult the visual communication between conspecifics, thus reducing the ability of hermit crabs for orientation (Gherardi *et al.,* 1989). In addition, the size and arrangement of the cobbles and boulders lead to a high number of small refuges (Gherardi & Vannini, 1993) to protected the crabs against the risks of desiccation.

As expected, all hermit crabs that were exposed to the air were inactive, even those that were clustered and in refuges. At low tide the hermit crabs store water inside their shells and occupy moist microhabitats to avoid the lack of oxygen and the risks of desiccation (Gherardi *et al.,* 1989). Inactive and scattered individuals of *C. antillensis* presented the aperture of their shells turned upward. This behavior results in a higher retention of water inside the shell as suggested by Reese (1969), thus enhancing their resistence to long time exposure periods. Active individuals were registered only in tide pools. In this way, the activity pattern can be related to the easier locomotion in water due to the lightening of the shells (Gherardi *et al.,* 1989), and to the physical stress imposed by the air exposure situation.

Scattered individuals of *C. antillensis* were larger than clustered ones, as also showed in other studies with other species (Hazlett, 1966; Gherardi & Vannini, 1989; Gherardi, 1991). Small individuals have a greater surface/volume ratio and are more susceptible to desiccation than the large ones

(Gherardi & Vannini, 1992, 1993). Thus, clustering might also serve to reduce the risk of desiccation as also suggested by Reese (1969) and Snyder-Conn (1981).

Both males and females of this *C. antillensis* population occurred mainly in clusters, and 44,44% of the females were ovigerous. These results support the hypothesis that clusters may serve as places where males can easily find females (Gherardi & Vannini, 1992, 1993). In addition, clustering may also protect ovigerous females and their eggs from desiccation.

The pattern of shell utilization of hermit crabs is frequently associated with shell availability as can be seen in this area (Leite *et al.,* 1998), with *C. antillensis* occupying mainly shells of *Tegula viridula*. However, scattered individuals of *C. antillensis* used shells of *T. viridula* in higher frequencies than do clustered ones, probably because these shells presented higher adequacy than the others, as also recorded in other studies (Gherardi, 1991; Gherardi & Vannini, 1993). In addition, shells used by the scattered individuals of *C. antillensis* presented better adequacy, and higher incrustation and adequacy than that used by the clustered supporting the hypothesis that clusters may serve as "shells exchange markets" (Gherardi & Vannini, 1993).

The small size of clusters in this area also seemed to be associated with the high availability of empty gastropod shells in this area (Leite *et al*., 1998). In this way, a high shell availability may indicate a good shell adequacy to this population, thus not forcing the crabs to look for new ones in dense aggregations.

The meaning of the clustering behavior is still controversal and doubtfull. It is more parsimonious and reasonable to think that many selective forces, such as shell limitation (behavioral factor) and environmental stress (physical factor) are influencing together the clustering behavior in hermit crabs. To evaluate the role of each factor in the cluster formation it is needed a fully experimental study, isolating all possible factors to test one each time.

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