Journal of Natural History

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

Spatial distribution of the ghost crab Ocypode quadrata in low-energy tide-dominated sandy beaches

A. Turra [a] , M. A. O. Gonçalves [a] & M. R. Denadai [a]

[a] Departamento de Zoologia , Campinas, Brazil

[b] Programa de Pós-Graduação em Ecologia , Campinas, Brazil

[c] Laboratório de Biologia Aquática, Curso de Ciências Biológicas , Fundação de Ensino Octávio Bastos , Campus II, São João da Boa Vista, SP, 13.870-159, Brazil E-mail:

Published online: 21 Feb 2007.

To cite this article: A. Turra , M. A. O. Gonçalves & M. R. Denadai (2005) Spatial distribution of the ghost crab Ocypode quadrata in low-energy tide-dominated sandy beaches, Journal of Natural History, 39:23, 2163-2177, DOI: 10.1080/00222930500060165

To link to this article: http://dx.doi.org/10.1080/00222930500060165

Journal of Natural History, 2005; 39(23): 2163–2177

Spatial distribution of the ghost crab *Ocypode quadrata* in low-energy tide-dominated sandy beaches

A. TURRA[1,2], M. A. O. GONÇALVES[1], & M. R. DENADAI[1]

[1]*Departamento de Zoologia, Campinas, Brazil, and* [2]*Programa de Pós-Graduação em Ecologia, Campinas, Brazil*

(Accepted 10 January 2005)

Abstract

The spatial distribution of the ghost crab *Ocypode quadrata* (Crustacea, Brachyura) was described in five low-energy tide-dominated sandy beaches in São Sebastião Channel (Grande, Zimbro, Pitangueiras, Cabelo Gordo, and Segredo). On each beach, the zonation study was performed on five random 1 m wide transects sampled from the water line to the vegetation. In general, individuals occurred above 1 m in height in relation to mean low water (MLW) and peaked between 1.5 and 2.0 m. The sandy beaches were then divided into three 1 m wide strips (tidal levels) parallel to the water line and equivalent to medium intertidal, upper intertidal, and subterrestrial fringe to test the effect of beach and tidal level on the abundance and size of *O. quadrata*. These strips were sampled as a whole using adjacent 1 m^2 squares. A previous evaluation showed a positive significant relationship between carapace length and burrow diameter, thus supporting crab size estimates from burrow openings. The smallest individuals occurred mainly in the medium intertidal, but were also recorded in the subterrestrial fringe, which was occupied mainly by large-sized individuals. In general, the individuals were randomly dispersed within the strips and concentrated in the upper intertidal zone on all the sandy beaches. The density of *O. quadrata* varied among beaches, with a tendency to lower values on areas with very fine and poorly or moderately sorted sediments and on that most used for recreational activities (Grande). Burrow size also varied among beaches, with a tendency of smaller burrows in areas with coarser sand grains and higher tourism. These results indicate that the effect of human impact on density and size of *O. quadrata* may be confounded by the high environmental heterogeneity of the studied system, which may make it difficult to utilize this species as an indicator of the conservation status of low-energy tide-dominated sandy beaches.

Keywords: *Anthropic impact, Brazil,* Ocypode quadrata*, sandy beach, urbanization, zonation*

Introduction

The ghost crab *Ocypode quadrata* (Fabricius, 1787) (Crustacea, Brachyura, Ocypodidae) is commonly known in south-eastern Brazil as "vasa-maré", "guaruçá", "guriçá", "maria-farinha", or "siripadoca" and has a wide geographic distribution in the tropics, occurring in Bermuda, Gulf of Mexico, Central America, Antilles, Guyanas, and on the entire Brazilian coast (Melo 1996). *Ocypode quadrata* builds semi-permanent burrows mainly in the upper

Correspondence: A. Turra, Laboratório de Biologia Aquática, Curso de Ciências Biológicas, Fundação de Ensino Octávio Bastos, Campus II, São João da Boa Vista, SP, 13.870-159, Brazil. Email: turra@feob.br

Published 12 May 2005

ISSN 0022-2933 print/ISSN 1464-5262 online
DOI: 10.1080/00222930500060165

intertidal and subterrestrial zones of sandy beaches (Souza and Gianuca 1995) as do other congeneric species [*O. cordimana* Desmarest, 1825 (Barros 2001); *O. ceratophthalmus* (Pallas, 1772) (Barrass 1963); *O. cursor* (Linnaeus, 1758) (Shuchman and Warburg 1978; Ewa-Oboho 1993); and *O. gaudichaudii* H. Milne Edwards and Lucas, 1843 (Schober and Christy 1993; Trott 1998)]. *Ocypode quadrata* may be inactive during adverse conditions, such as low temperatures, intense winds and sea storms (Haley 1972; Leber 1982; Alberto and Fontoura 1999), when they shelter in their burrows and close the apertures with sand. Despite the numerical and ecological importance of species of this genus, the high mobility and burrow depths of *O. quadrata* frequently lead to underestimates of this species in benthic macrofauna studies of sandy beaches (Amaral et al. 1993, 2003; Nucci et al. 2001).

Some studies investigated the influence of anthropogenic activities, such as tourism, urbanization and flow of vehicles, on the density of *O. quadrata* (Steiner and Leatherman 1981) and its congener *O. cordimana* (Barros 2001). However, studies on the effects of these influences on other variables of the population, such as individual size (but see Fisher and Tevesz 1979) and zonation are still lacking. Species of the genus *Ocypode* are frequently used as bioindicators of urbanization in high-energy oceanic sandy beaches (Fisher and Tevesz 1979; Steiner and Leatherman 1981; Barros 2001). However, in sheltered tide-dominated areas, the low structural similarity among sandy beaches (Denadai et al. forthcoming) may prevent the identification of impacts using spatial controls alone.

The sandy beaches of the São Sebastião Channel are short and embayed, surrounded by hills and narrow coastal plains with tropical Atlantic forest. These characteristics reflect the general aspect of the northern coast of São Paulo State, south-eastern Brazil; crystalline formations directly reach the sea, and dunes are thus absent. The geological history of this area, the dominance of tides in relation to waves in beach hydrodynamism, and a complex water circulation system are cause for a marked environmental heterogeneity in the slope, sediment constitution, and faunistic composition of the intertidal sandy beaches of this channel (Nucci et al. 2001; Amaral et al. 2003; Denadai et al. forthcoming). In addition, the São Sebastião Channel has undergone a strong but irregular urbanization in the last four decades when resort houses were built on most of its beaches (Lamparelli and Moura 1999).

The aim of this study was to address the variation in density and size of *Ocypode quadrata* in five environmentally heterogeneous beaches of the São Sebastião Channel at three fixed tidal levels (medium intertidal, upper intertidal and subterrestrial fringe). These zones had equivalent heights on different beaches (in relation to mean low water, MLW) and were used to test the null hypothesis that the mean density and mean size of *O. quadrata* did not differ among zones and beaches. The environmental variables (beach slope and sediment grain size and sorting coefficient) were also compared among zones and beaches and were related to crab abundance and size.

Materials and methods

The five low-energy tide-dominated sandy beaches selected for this study, due to variation in slope, sediment composition, and human impact, are located at the southern mainland part of the São Sebastião Channel: Segredo, Cabelo Gordo, Pitangueiras, Zimbro, and Grande (Figure 1). The slope of the areas was measured using three replicate random samples on each beach. The sediment composition was evaluated, following Suguio (1973) for methodology and the Wentworth (1922) grain size scale, for five replicate random samples at each tidal level (see below) of the studied beaches. The level of tourism was

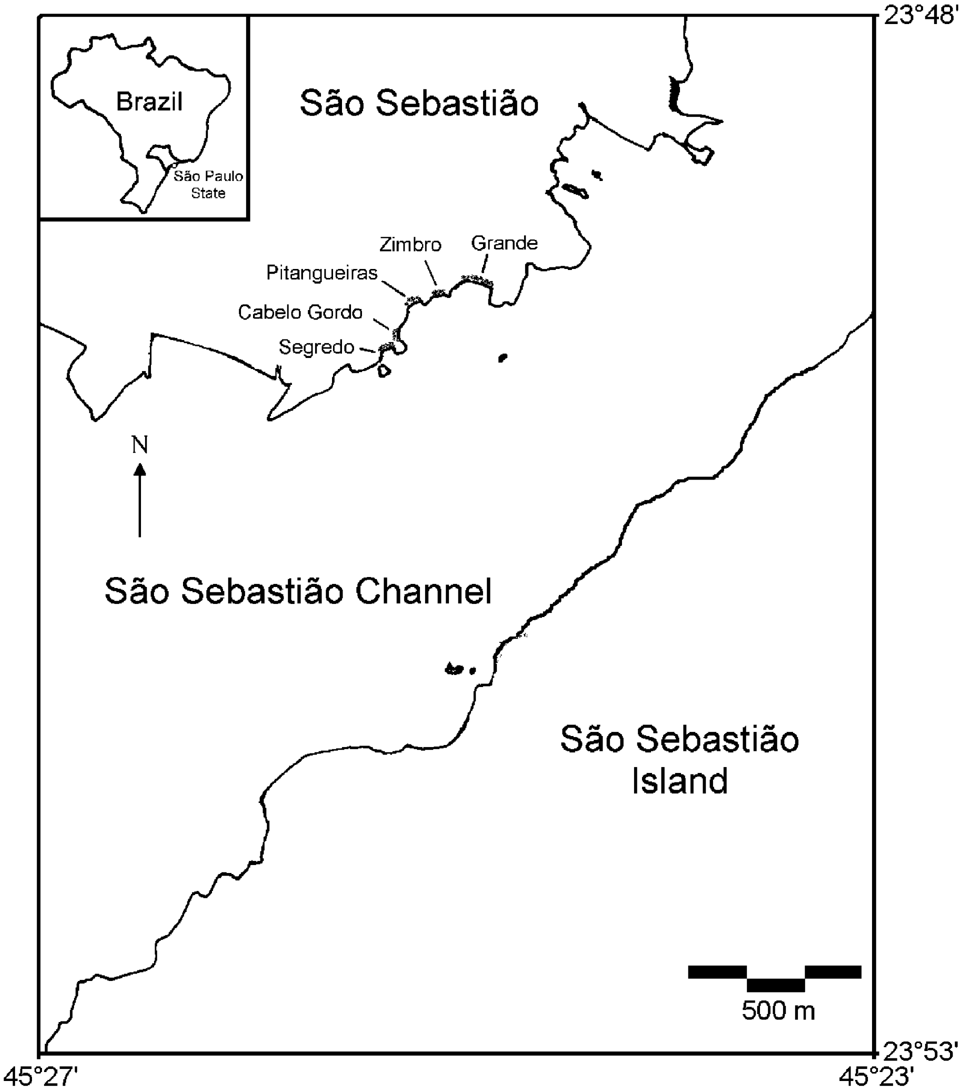

Figure 1. Map of the São Sebastião Channel, south-eastern Brazil, illustrating the five study beaches.

visually estimated by counting people on each beach on vacation and non-vacation dates. A one-way ANOVA was used to compare beach slopes. A two-way ANOVA was used to compare the differences in mean grain size and sorting coefficients among zones and beaches. The post hoc Scheffé's test was employed for pairwise comparisons.

Zonation was addressed by sampling five vertical transects randomly located on each beach. The transects were 1 m wide and their lengths were equivalent to the distance from water line (MLW, 0.0 m in relation to datum) to the end of the sand (vegetation or buildings). All transects sampled in each area had the same slopes and lengths. After this evaluation, the beaches were divided into 1 m wide strips comprising three levels in relation to the water line (MLW) with middle heights of 1.2, 1.4, and 1.9 m, which were located at medium intertidal, upper intertidal, and subterrestrial fringe, respectively. The tides in this region are semi-diurnal with a maximum range of 2 m (Furtado and Mahiques 1990). These strips were sampled along the whole beach using contiguous 1 m^2 quadrats and the number and size of burrows of *Ocypode quadrata* were recorded. The samples were concentrated in neap low tides in a single lunar period and only active and unplugged burrows were considered. Plugged burrows were considered as equivalent between areas and, as this work was conducted in periods of high temperatures (summer) and good sea conditions, the closed apertures were considered as abandoned by the crabs (see Haley 1972; Leber 1982; Alberto and Fontoura 1999). We counted the number of burrows as an estimate of crab density, as suggested by Warren (1990). A two-way ANOVA was used to test for differences in the number of burrows among beaches and zones. The dispersion pattern of *O. quadrata* was estimated using a dispersion index (I), equivalent to the ratio between the variance (S^2) and the mean of the number of individuals per quadrat (Elliott 1977). The mean burrow diameter was compared among zones and then among beaches for each zone separately by a Kruskal–Wallis test (Mann–Whitney U test was used to compare the two tidal levels of the Grande site because data were not homocedastic). The density of burrows was calculated for each level at each site. The outcomes of the ANOVAs and Kruskal–Wallis tests cited above for the comparison of the mean density and mean diameter of *O. quadrata* burrows among beaches and zones were followed by the Scheffé's test and the non-parametric Tukey-type test, respectively, for post hoc pairwise comparisons.

The relationship between the size of *Ocypode quadrata* and the diameter of its burrows was estimated through a non-destructive method. We observed that *O. quadrata* are attracted to small objects (such as seeds and small gravel) that are placed on the sand surface in the vicinity of the burrows. In addition, Wellins et al. (1989) showed that *O. quadrata* locate fruits (banana) and pieces of dead fish and mole crabs. In this way, we used small baits of dead fish meat to attract the crabs. The baits were fixed on a nylon line that was pulled in the vicinity of the burrows when the crabs were in the entrance. When the crabs "attacked" the baits they were trapped with a net. Length and width of the cephalothorax of the crabs, as well as the diameter of the burrows from which they were removed, were measured. The crabs were then released in the vicinity of their original burrows.

The environmental variables described above were related to both abundance and size of burrows of *Ocypode quadrata* through a stepwise forward multiple linear regression using beaches as replicates ($n=5$).

Results

Environmental characterization

Grande is a bathing place with a complete infrastructure for tourism and does not have physical barriers separating the shore from the urbanized back-shore. Pitangueiras has many houses that are generally separated from the beach by rocky walls. In contrast, access to Cabelo Gordo, Segredo, and Zimbro is more limited. At Cabelo Gordo there are neither physical barriers nor resort buildings, and vegetation is present in the back-shore zone, while at Segredo and Zimbro buildings are found amongst the sparse vegetation. On the Saturday before Easter (30 March 2002, 14:30 h), the number of tourists was recorded at the five studied sites as: Grande—more than 1000; Pitangueiras—about 100; Segredo—3; Zimbro—7; Cabelo Gordo—2. On a normal Saturday (23 March 2002, 15:00 h) the number of tourists totalled, respectively, more than 100; about 40; 3; 8; and 3. Thus an ordinal qualitative classification showed a descending order of urbanization and tourism for these beaches: Grande>Pitangueiras>Zimbro>Segredo=Cabelo Gordo.

The overall beach slope varied markedly among the study sites (ANOVA; F=31.791, df=4, P<0.001), with Grande being the flattest area and Pitangueiras and Zimbro the steepest (Figure 2). Segredo and Cabelo Gordo had intermediate values of slope. Berms occurred only on Pitangueiras and Zimbro. The sediment constitution differed markedly among the beaches and zones (Table I; Figure 3). The finest grains were recorded on Grande Beach, while the coarsest were recorded at Zimbro. In general, the mean grain size (phi units) showed a tendency to increase with beach height, as clearly evidenced at Segredo and Grande (Figure 3). The non-significant interaction term in the two-way

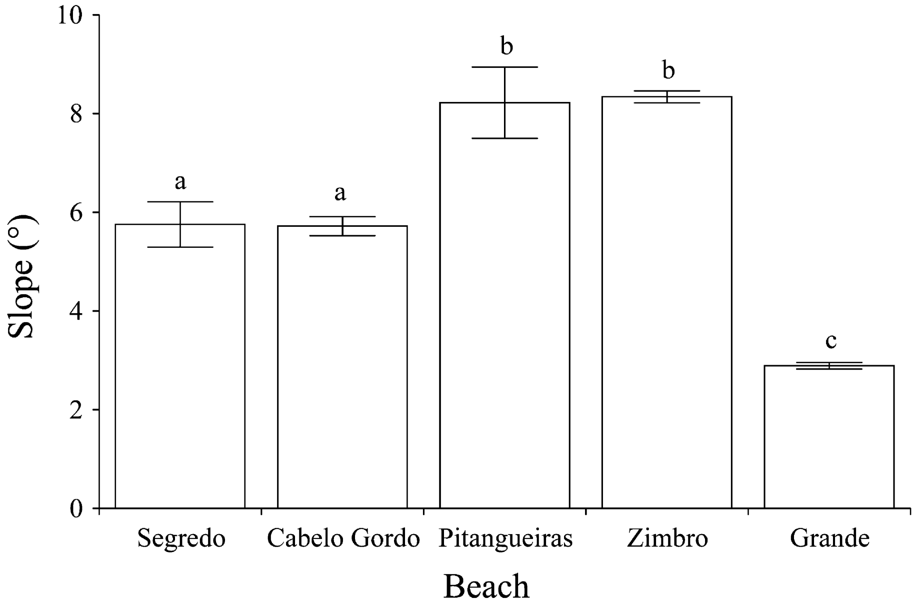

Figure 2. Mean slope (°, ±SE) of the five studied beaches calculated using three replicate random samples in each site. Identical letters indicate non-significant differences in the post hoc Scheffé's test for multiple pair-wise comparisons.

Table I. Two-way ANOVA for the mean grain size (phi) and for the mean sorting coefficient (phi) among beaches (fixed factor) and zones (fixed factor).

Source of variation	df	Mean square	F	P
Mean grain size				
Beach	4	11.838	37.325	<0.001
Zone	2	4.186	13.197	<0.001
Beach × zone	8	0.592	1.868	0.082
Residual	60	0.317		
Mean sorting coefficient				
Beach	4	0.552	20.573	<0.001
Zone	2	0.002	0.097	0.907
Beach × zone	8	0.147	5.774	<0.001
Residual	60	0.025		

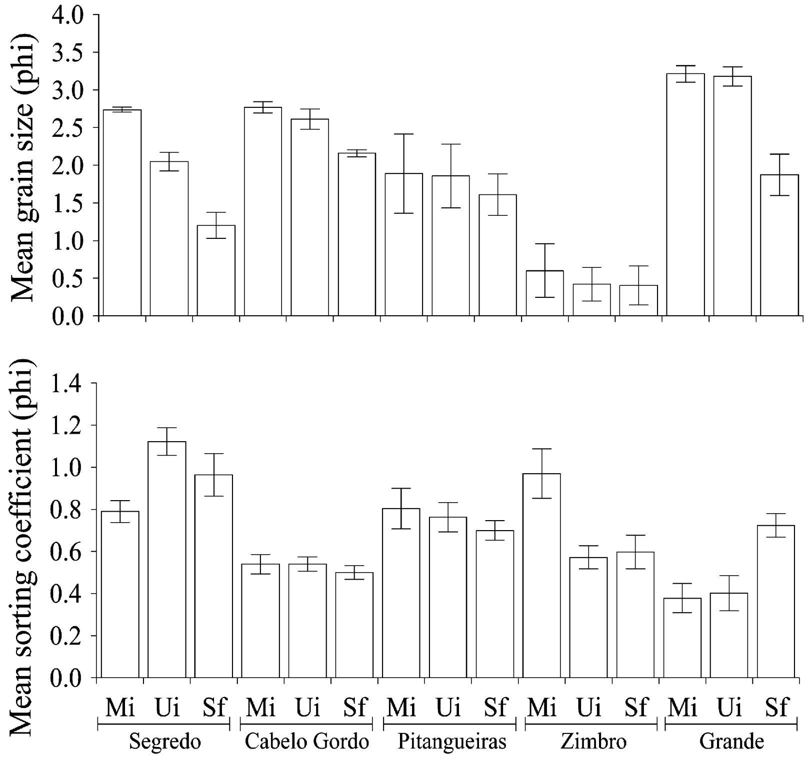

Figure 3. Mean sand grain size (phi, ±SE) and mean sorting coefficient (phi, ±SE) for each zone and beach calculated using five replicate measures in each zone. Mi, medium intertidal; Ui, upper intertidal; Sf, subterrestrial fringe.

ANOVA showed that this tendency applies to all sites. The sorting coefficient showed a marked variation among beaches but not among zones (Table I; Figure 3).

Zonation

Ocypode quadrata showed a clear zonation at all sites (Figure 4; results of all transects were pooled), with individuals occurring only above the medium intertidal zone (more than 1 m in height above MLW). The peak of density occurred in the upper intertidal, between 1.5 and 2.0 m height above the water line, while fewer individuals were recorded in the subterrestrial fringe (about 2 m above the water line). Only at Zimbro and Grande did crabs occur up to 3 m above the water line; at Segredo and Cabelo Gordo the beach did not reach this height. The peak of abundance at Pitangueiras and Zimbro was equivalent to the area subjacent to the berm. *Ocypode quadrata* showed a wider distribution on Grande. Based on these patterns of zonation, three zones were identified for testing spatial distribution within (among zones) and among beaches: medium intertidal, upper intertidal, and subterrestrial fringe.

Distribution among and within beaches

In general, crabs (burrows) were randomly dispersed but a clustered dispersion pattern was recorded in some zones (Table II). It was shown that crab density was dependent on both

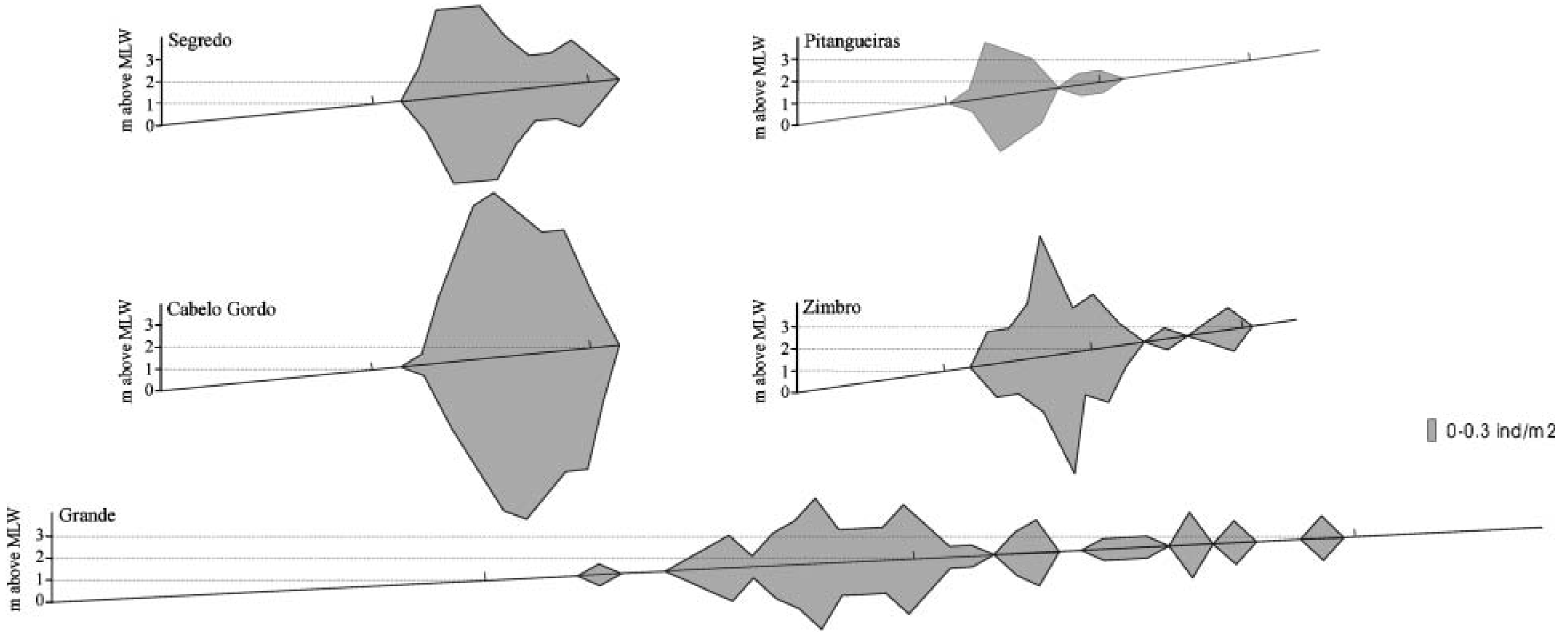

Figure 4. Schemes of zonation of *Ocypode quadrata* in the study areas. Horizontal dotted lines indicate heights of 1, 2 and 3 m above MLW (0 m). The data represent the mean number of individuals per m^2 for each 1 m interval estimated using five randomized replicated samples. This procedure was possible because different transects on the same site were equivalent in length (*x*-axis): Segredo, 21 m; Cabelo Gordo, 21 m; Pitangueiras, 24 m; Zimbro, 21 m; Grande, 56 m.

Table II. Dispersion pattern of *Ocypode quadrata* in relation to beach and tidal level based on the relationship between the variance and the mean of the number of individuals per sample (1 m^2).

Beach/level	Mean	Variance	*n*	*I*	*d*	Dispersion
Segredo						
Medium intertidal	0.025	0.025	79	78.00	0.04	Random
Upper intertidal	1.396	1.324	134	126.14	−0.40	Random
Subterrestrial fringe	0.467	0.493	92	96.07	0.41	Random
Cabelo Gordo						
Medium intertidal	0.147	0.127	68	57.88	−0.77	Random
Upper intertidal	2.855	4.547	110	173.60	3.90*	Clustered
Subterrestrial fringe	0.857	0.773	35	30.67	−0.35	Random
Pitangueiras						
Medium intertidal	0.116	0.136	242	282.55	1.84	Random
Upper intertidal	0.648	0.618	253	240.33	−0.50	Random
Subterrestrial fringe	0.253	0.559	245	539.11	10.77*	Clustered
Zimbro						
Medium intertidal	0.041	0.053	146	187.44	2.36*	Clustered
Upper intertidal	0.673	0.904	171	228.35	2.96*	Clustered
Subterrestrial fringe	0.641	0.709	131	143.79	0.86	Random
Grande						
Medium intertidal	0	0	327			
Upper intertidal	0.227	0.253	339	376.71	1.47	Random
Subterrestrial fringe	0.053	0.056	359	378.26	0.77	Random

See text for details on the calculation of the dispersion index. *n*, number of samples; *I*, dispersion index; *d*, statistic associated with the dispersion index. *$P<0.05$ with $d_{critical}=1.96$.

Table III. Two-way ANOVA for the mean number of burrows per m^2 [square root (x+1) transformation] of *Ocypode quadrata* among beaches (fixed factor) and zones (fixed factor).

Source of variation	df	Mean square	*F*	*P*
Beach	4	4.688	107.963	<0.001
Zone	2	15.089	347.528	<0.001
Beach × zone	8	2.016	46.431	<0.001
Residual	2456	0.043		

zone and beach, but the interaction term evidenced that the pattern of variation among zones was not the same for all beaches (Table III). In general, low densities were recorded in the middle intertidal, followed by a peak of density in the upper intertidal (Figure 5). Density then decreased again but the values for the subterrestrial fringe were always higher than for the middle intertidal (except at Pitangueiras). The density in the upper intertidal and subterrestrial fringe varied among beaches, but no variation was recorded for the middle intertidal zone. In the upper intertidal, the mean number of burrows was higher at Cabelo Gordo; Segredo showed smaller values than Cabelo Gordo but higher than both Pitangueiras and Zimbro, which had similar densities of burrows. The lowest density was recorded at Grande. This distinction among beaches was less evident for the subterrestrial fringe: Segredo, Cabelo Gordo, and Zimbro showed similar densities, but higher than Pitangueiras and Grande.

The burrow diameter was demonstrated to be a good estimator of crab size in the present study (cephalothorax length: $y=1.21+0.27x$, $n=38$, $r^2=0.884$, $P<0.001$; width: $y=1.02-0.43x$, $n=38$, $r^2=0.873$, $P<0.001$). The mean burrow diameter also varied

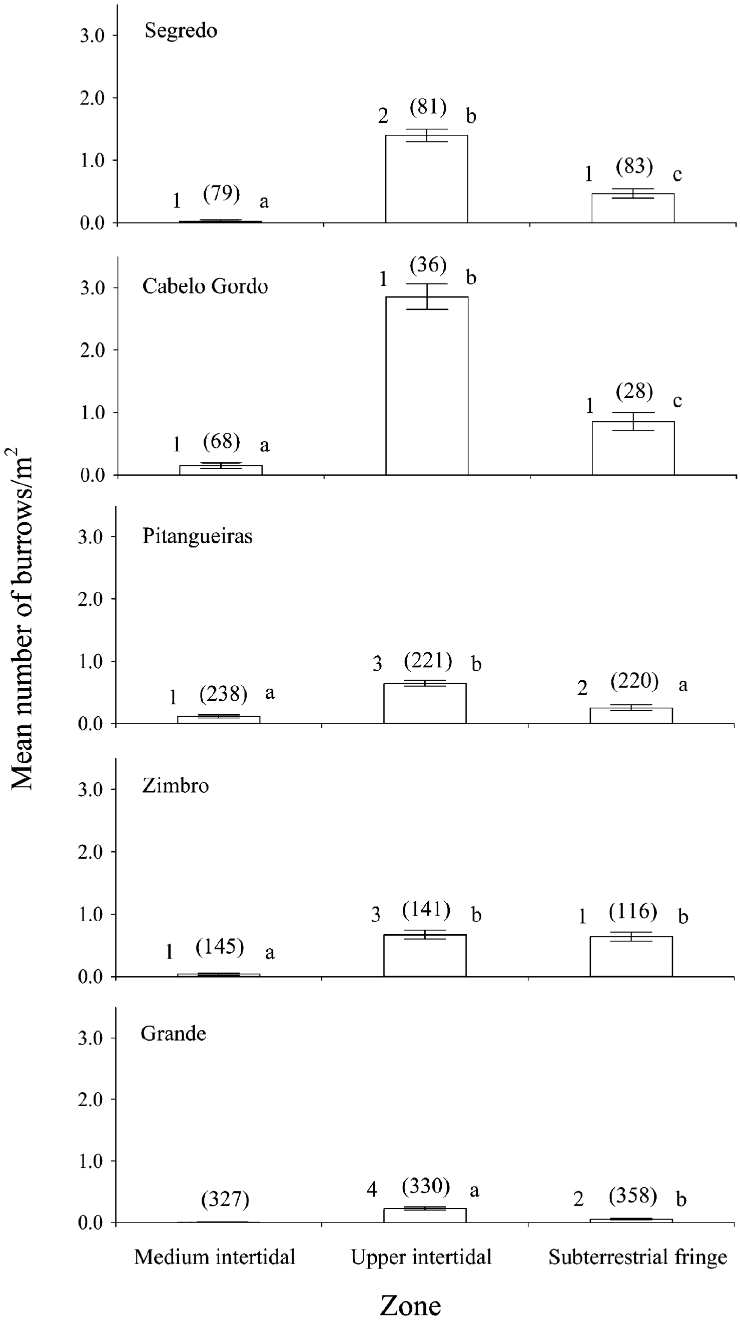

Figure 5. Comparison of the mean number of burrows per m^2 ($\pm$SE) of *Ocypode quadrata* among beaches and zones. Numbers in brackets represent the numbers of squares sampled. Numbers at the left side of the bars indicate the results of Scheffé's test for multiple comparisons of zones among beaches. Letters at the right side of the bars indicate the results of Scheffé's test for multiple comparisons of zones within beaches. Identical labels (numbers or letters) indicate non-significant differences in the post hoc Scheffé's test. See Table III for the results of the ANOVA.

Table IV. Comparison of the mean burrow diameter among beaches and zones through the Kruskal–Wallis test (*H*).

Comparison	*n*	*H*	df	*P*
Among zones				
Segredo	140	9.458	2	0.009
Cabelo Gordo	136	7.663	2	0.022
Pitangueiras	184	18.779	2	<0.001
Zimbro	141	5.338	2	0.069
Grande[a]	84	807.000	1	0.020
Among beaches				
Medium intertidal	41	14.920	3	0.002
Upper intertidal	472	65.147	4	<0.001
Subterrestrial fringe	172	47.058	4	<0.001

[a]Result of the Mann–Whitney *U* test.

among beaches and zones (Table IV; Figure 6). In general, size of the crabs increased with distance from the water line (except at Zimbro). More accurate comparisons could be made between the upper intertidal and subterrestrial fringe because of the low number of burrows in the middle intertidal. Considering only the upper intertidal and subterrestrial fringe, the largest individuals occurred at Segredo, Cabelo Gordo, and Pitangueiras, and the smallest at Zimbro and Grande.

Table V shows crab abundance and burrow size in relation to measured environmental variables. The best multiple linear regression models fitted to these data were not significant (Table VI) but indicated that abundance of *O. quadrata* has a tendency to lower values on areas with steep slopes, poorly or moderately selected sediments and on that most used for recreational activities (Grande). Burrow size showed a tendency of smaller burrows in areas with coarser sand grains and higher tourism. In both models, tourism, although with marginal or not significant results, is suggested to be the most important variable related to abundance and size of burrows of *O. quadrata* (Table VI).

Discussion

Spatial distribution

The individuals of *Ocypode quadrata* were concentrated mainly in the upper intertidal zone on the sandy beaches studied. This pattern was different from that shown by Dahl (1953) in his classic sandy beach zonation scheme. Dahl classified the subterrestrial fringe as "Talitrid–Ocypodid belt", the first group being dominant in cold-temperate regions and the ocypodids dominant in tropical and warm-temperate areas. However, Barrass (1963) considered this generality inadequate when considering specific levels. Alberto and Fontoura (1999) found higher densities of *O. quadrata* burrows at lower levels (1.0–1.4 m above MLW) than in the present study (1.5–2.0 m above MLW), with distribution limited to 2.0 m above MLW. In contrast, Leber (1982) observed that *O. quadrata* occupied the spray zone, but fed in the swash zone at night. Moreover, in São Sebastião Channel, the burrows of *O. quadrata* were not restricted to the beach, being commonly found in the terrestrial substratum, around the buildings. Barros (2001) sampled burrows of *O. cordimana* between 0 and 4 m from sand dunes or concrete walls, but found burrows up to 50 m beyond the dunes in some urban areas. These data show that the cross-shore distribution of *O. quadrata* is highly variable among beaches. This variation should be taken

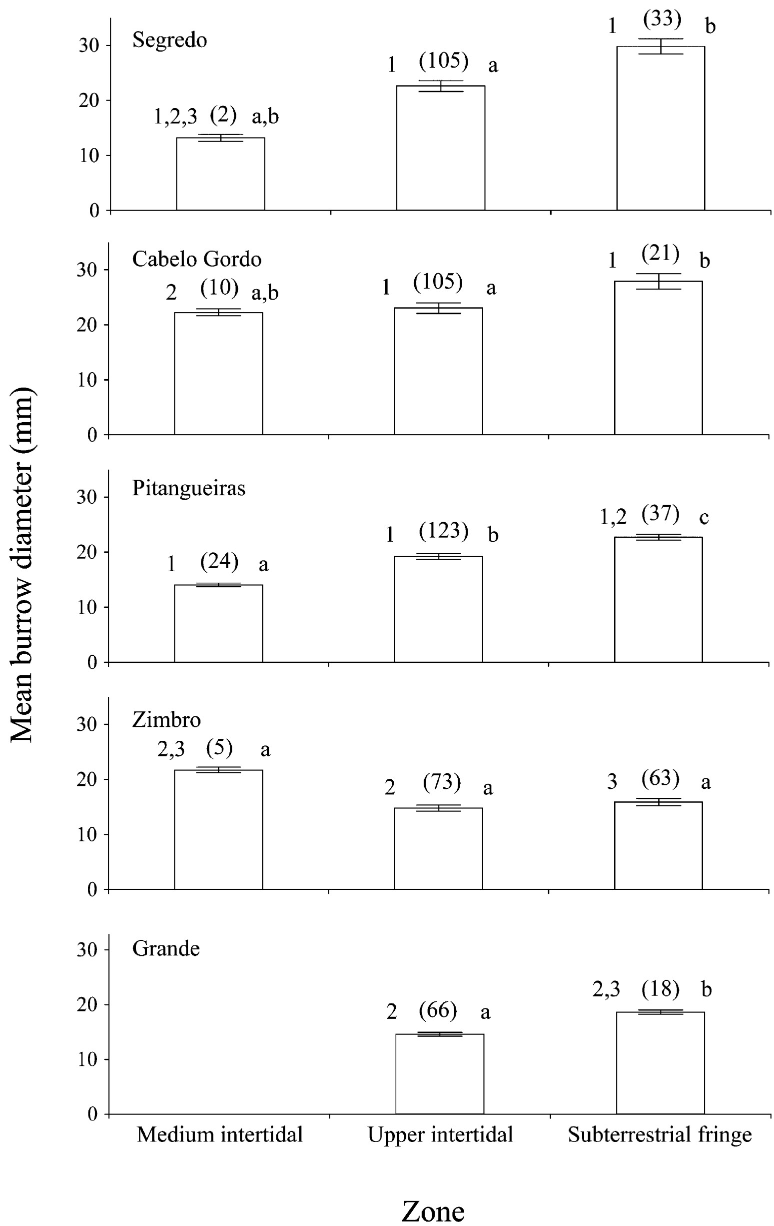

Figure 6. Comparison of the mean burrow diameter (±SE) of *Ocypode quadrata* among beaches and zones. Numbers in brackets represent the numbers of burrows sampled. Numbers at the left side of the bars indicate the results of the non-parametric Tukey-type test for multiple comparisons of zones among beaches. Letters at the right side of the bars indicate the results of the non-parametric Tukey-type test for multiple comparisons of zones within beaches. Identical labels (numbers or letters) indicate non-significant differences in the post hoc Scheffé's test. See Table IV for the results of the non-parametric Kruskal–Wallis tests.

Table V. Abundance and size of burrows of *Ocypode quadrata* and environmental characteristics in the studied sites.

	Beach				
Variable	Grande	Pitangueiras	Segredo	Zimbro	Cabelo Gordo
Abundance (individual per m^2)[a]	0.20	0.56	1.27	0.51	2.94
Size of burrows (mm)[a]	15.46	19.23	24.19	15.52	23.72
Grain size (phi units)[a, b]	3.18	1.86	2.05	0.42	2.61
	Very fine	Medium	Fine	Coarse	Fine
Sorting coefficient (phi units)[a, c]	0.40	0.76	1.12	0.57	0.54
	Good	Moderate	Poor	Moderate	Moderate
Slope (degrees)[d]	2.89	8.22	5.75	8.34	5.72
Tourism (urbanization)[e]	>1000/>100	100/40	3/3	7/8	2/3
Presence of Berm	−	+	−	+	−

[a]Mean values referent to the upper intertidal due to the higher number of individuals in relation to other tidal levels. [b]According to the Wentworth (1922) size scale (see Brown and McLachlan 1990). [c]According to Brown and McLachlan (1990). [d]Mean values of the five replicates taken on each site. [e]The two values represent 2 days of observation (vacation/out of vacation).

Table VI. Best models relating abundance and size of burrows of *Ocypode quadrata* with environmental variables (see Table V) through stepwise forward multiple linear regression using beaches as replicates (n=5).

Source of variation	Coefficient	Standard coefficient[a]	t	P (two-tail)
Abundance (individuals per m^2)				
Constant	7.704	0.000	3.351	0.185
Sorting coefficient (phi units)	−2.250	−0.568	−1.563	0.362
Slope (degrees)	−0.654	−1.327	−2.705	0.255
Tourism (urbanization)	−0.005	−1.852	−3.284	0.188
	r^2=0.916, F=3.629, df=3, P=0.364			
Size of burrows (mm)				
Constant	13.969	0.000	7.065	0.019
Grain size (phi units)	4.061	0.990	3.876	0.061
Tourism (urbanization)	−0.012	−1.187	−4.648	0.043
	r^2=0.920, F=11.574, df=2, P=0.080			

[a]The standard coefficient is dimensionless and evidences the relative effect of each independent variable.

into account in future sampling design to evaluate population densities of this species. As Defeo and Rueda (2002) pointed out, in such situations, estimates of density using cross-shore instead of along-shore transects are more adequate.

The cross-shore distribution of *O. quadrata* seemed to be related to ontogenetic development. There was a gradual increase of individual size from the water line to the terrestrial fringe, a fact also observed by Hill and Hunter (1973). This occurred probably because adult individuals were able to occupy a wider sandy beach moisture gradient than the younger/smaller ones, which were restricted to the moister areas due to their lower resistance to desiccation and lower ability to build deep burrows (Fisher and Tevesz 1979).

The dispersion pattern (mainly random) observed for *O. quadrata* on the sandy beaches of São Sebastião Channel contrasted with the results of Fischer and Tevesz (1979). These authors observed an evenly spaced (regular) distribution for the adults of *O. quadrata* and a clumped distribution for juveniles, which may reflect territorial behaviour of adults. Nevertheless, the validity of the data of Fischer and Tevesz (1979) was questioned by Leber (1981). Since regular dispersion is associated with territorial behaviour (Elliott 1977) it is possible to argue that territories are not a limiting resource in the populations studied here or that the eventually low population densities in the studied areas prevent strong intraspecific competitive interactions. The dispersion pattern in *O. quadrata* may be directly influenced by population density, which may be environmentally or anthropogenically modulated.

Our results indicated influence of beach on the zonation of *O. quadrata*, although the individuals were concentrated in the upper intertidal in all areas. Differences in crab size and abundance among areas were also reported and may be a consequence of beach-specific recruitment and mortality rates, which in turn may be associated with differences in morphodynamics, food availability, and human impact among beaches. The results of the present study also suggest that both sediment constitution and number of tourists may influence crab size and abundance but there is no information available evidencing the effect of beach morphodynamics either on food availability for, or on recruitment or mortality rates of, *O. quadrata*. In fact, the factors that regulate abundance of *O. quadrata* are still controversial (see Fisher and Tevesz 1979; Steiner and Leatherman 1981; Barros 2001).

The present study is the first attempt to understand the spatial structure of *O. quadrata* in low-energy tide-dominated sandy beaches but its low sample size did not allow a full understanding of the studied system. Two future sets of studies should be then employed: (1) more tightly spatially and temporally replicated field surveys and (2) unconfounded field manipulative experiments to test the hypothesis on the effect of specific factors on this species. In the first situation it would be difficult to find appropriate controls (e.g. beaches with same type of slope, grain size, and sorting coefficient) due to the high environmental variability among these kinds of beach. Such environmental parameters may then enter models to test for differences between impacted versus non-impacted areas as co-variables. Making this would lessen an eventual dependence between human impact, beach type, and initial crab abundances since intensity of human settlement might be related to beach type and different beaches might have different crab abundances before impact. In addition, a macro-scale replication (among different low-energy tide-dominated areas) would certainly strengthen the conclusions of future sampling surveys. As the crab abundance, size structure, recruitment, and activity may have a marked seasonality (Wolcott 1978; Alberto and Fontoura 1999; Corrêa 2001) and may be highly variable between subsequent years (Alberto and Fontoura 1999), temporal replication in such studies is fundamental. In the second situation, the effects of specific human activities, such as trampling, transit of vehicles, presence of food scraps, artificial removal of natural beach debris, and sea-wall building may be tested through field manipulative experiments.

Implications for conservation studies

The ghost crabs occupy areas of the beach frequently used by tourists and vehicles, and may be good indicators of impacts caused by urbanization and beach use. Steiner and Leatherman (1981) registered three negative effects on *Ocypode* caused by vehicle traffic: (1) by crushing or burying the crabs in their burrows in passing overhead; (2) by interrupting the reproductive cycle, since mortality prevented the individuals from reaching sexual maturity; or (3) by modifying the moisture content of the sand, possibly causing crab desiccation. Conversely, Steiner and Leatherman (1981) observed a greater density of crabs on swimming beaches, showing a positive effect of pedestrians on ghost crabs. A possible reason, according to these authors, was the food and scraps left by the bathers, which provided another food supply to the crabs. Barros (2001) warned about the data of Steiner and Leatherman (1981) because of the small spatial replication used by these authors. Since there were no vehicles on Grande beach, the intense recreational activities (trampling, beach excavation by children, and beach sports), mainly in the beach zone where the crabs were concentrated (upper intertidal), are thought to be causing such disturbance to crab populations. Barros (2001) also recorded a reduced density of *O. cordimana* on three recreational oceanic sand beaches near Sydney, Australia, in comparison to other beaches located in two non-urban areas. He attributed these differential densities to human trampling.

When oceanic sandy beaches are relatively homogeneous in their constitution, at least at small and medium scales, spatial controls alone may furnish accurate and precise information for decision-makers on the impact of human activities on benthic fauna. As shown above, this does not apply to tide-dominated embayed sandy beaches, such as those in the São Sebastião Channel, that show a marked small-scale variation in environmental constitution (sediment, slope, and hydrodynamism) and use history. Decision-makers may establish wrong frameworks and plans by classifying areas as impacted because the data on *O. quadrata* may be also influenced by other factors such as grain size and beach slope. A temporal control is fundamental in such cases mostly because different beaches may have different seasonal modifications in morphodynamics and in recruitment and size structure of *O. quadrata*. In addition, as the size and density of some species of this genus have been demonstrated to vary seasonally as a function of crab recruitment and growth (Alberto and Fontoura 1999) and crab activity (Wolcott 1978), the absence of temporal controls may confuse environmental managers. We argue that *Ocypode quadrata* may be used as a valuable conservation tool for assessing the degree of urbanization and environmental alteration in tide-dominated embayed sandy beaches (as on oceanic sandy beaches), but only under a well-planned hypothesis-free monitoring programme with both temporal (before and after impacts) and spatial (impacted versus non-impacted areas) controls (see Underwood 1991).

Acknowledgements

We would like to thank Centro de Biologia Marinha of the Universidade de São Paulo (CEBIMar-USP) for the technical and logistical support. We are also grateful to the two anonymous referees for comments that improved this manuscript.

References

Alberto RMF, Fontoura NF. 1999. Distribuição e estrutura etária de *Ocypode quadrata* (Fabricius, 1787) (Crustacea, Decapoda, Ocypodidae) em praias arenosas do litoral sul do Brasil. Brazilian Journal of Biology 59:95–108.

Amaral ACZ, Denadai MR, Turra A, Rizzo AE. 2003. Intertidal macrofauna in Brazilian subtropical sandy beach landscapes. Journal of Coastal Research 35:446–455.

Amaral ACZ, Pardo EV, Morgado EH, Reis MO, Salvador LB, Lima LH. 1993. Sobre a macroinfauna bêntica entremarés de praias da lha de São Sebastião (SP). Publicação da Academia de Ciências do Estado de São Paulo 3:330–337.

Barrass R. 1963. The burrows of *Ocypode ceratophthalmus* (Pallas) (Crustacea, Ocypodidae) on a tidal wave beach at Inhaca Island, Moçambique. Journal of Animal Ecology 32:73–85.

Barros F. 2001. Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. Biological Conservation 97:399–404.

Brown AC, McLachlan A. 1990. Ecology of sandy shores. Amsterdam: Elsevier. 328 p.

Corrêa MODA. 2001. Bioecologia de *Ocypode quadrata* (Frabricius, 1787) (Crustacea, Decapoda, Ocypodidae) no litoral norte do Estado de São Paulo [masters thesis]. Butucatu (Brazil): Universidade Estadual Paulista.

Dahl E. 1953. Some aspects of the ecology and zonation of the fauna on sandy beaches. Oikos 4:1–27.

Defeo O, Rueda M. 2002. Spatial structure, sampling design and abundance estimates in sandy beach macroinfauna: some warnings and new perspectives. Marine Biology 140:1215–1225.

Denadai MR, Amaral ACZ, Turra A, Structure of molluscan assemblages in sheltered intertidal unconsolidated environments. Brazilian Archives of Biology and Technology. Forthcoming.

Elliott JM. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association Scientific Publication 25:1–157.

Ewa-Oboho IO. 1993. Substratum preferences of the tropical estuarine crabs, *Uca tangeri* Eydoux (Ocypodidae) and *Ocypode cursor* Linne (Ocypodidae). Hydrobiologia 271:119–127.

Fisher JB, Tevesz MJS. 1979. Within-habitat patterns of *Ocypode quadrata* (Fabricius) (Decapoda Brachyura). Crustaceana Supplement 5:31–36.

Furtado VV, Mahiques MM. 1990. Distribuição dos sedimentos em regiões costeiras e plataforma continental norte do Estado de São Paulo (1). Publicação da Academia de Ciências do Estado de São Paulo 1:20–29.

Haley SR. 1972. Reproductive cycling in the ghost crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). Crustaceana 23:1–9.

Hill GW, Hunter RE. 1973. Burrows of the ghost crab *Ocypode quadrata* (Fabricius) on the Barrier Islands, south-central Texas coast. Journal of Sedimentary Petrology 43:24–30.

Lamparelli CC, Moura DO. 1999. Mapeamento dos ecossistemas costeiros do Estado de São Paulo. São Paulo: CETESB. 108 p.

Leber K. 1981. Spatial pattern of *Ocypode quadrata*: a re-evaluation (Decapoda, Brachyura). Crustaceana 41:110–112.

Leber K. 1982. Seasonality of macroinvertebrates on a temperate, high wave energy sandy beaches. Bulletin of Marine Science 32:86–98.

Melo GAS. 1996. Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. São Paulo: Plêiade. 604 p.

Nucci PR, Turra A, Morgado EH. 2001. Diversity and distribution of crustaceans from 13 sheltered sandy beaches along São Sebastião Channel, south-eastern Brazil. Journal of the Marine Biological Association of the United Kingdom 81:475–484.

Schober UM, Christy JH. 1993. Sand disposal of the painted ghost crab *Ocypode gaudichaudii* (Decapoda, Ocypodidae): a possible role in courtship. Marine Biology 116:53–60.

Shuchman E, Warburg MR. 1978. Dispersal, population structure and burrow shape of *Ocypode cursor*. Marine Biology 49:255–263.

Souza JRB, Gianuca NM. 1995. Zonation and seasonal variation of the intertidal macrofauna on a sandy beach of Paraná State, Brazil. Scientia Marina 59:103–111.

Steiner AJ, Leatherman SP. 1981. Recreational impacts on the distribution of ghost crabs *Ocypode quadrata* Fab. Biological Conservation 20:111–122.

Suguio K. 1973. Introdução a sedimentologia. São Paulo: Edgard Bluche/EDUSP. 321 p.

Trott TJ. 1998. On the sex ratio of the painted ghost crab *Ocypode gaudichaudii* H. Milne Edwards & Lucas, 1843 (Brachyura, Ocypodidae). Crustaceana 71:47–56.

Underwood AJ. 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. Australian Journal of Marine and Freshwater Research 42:569–587.

Warren JH. 1990. The use of open burrows to estimate abundances of intertidal estuarine crabs. Australian Journal of Ecology 15:277–280.

Wellins CA, Rittschof D, Wachowiak M. 1989. Location of volatile odor sources by ghost crab *Ocypode quadrata* (Fabricius). Journal of Chemical Ecology 15:1161–1169.

Wentworth CK. 1922. A scale of grade and terms for clastic sediments. Journal of Geology 30:377–392.

Wolcott TG. 1978. Ecological role of ghost crab, *Ocypode quadrata* (Fabricius), on an ocean beach: scavengers or predators. Journal of Experimental Marine Biology and Ecology 31:67–82.