

Distribution patterns of the crab *Ucides cordatus* (Brachyura, Ucididae) at different spatial scales in subtropical mangroves of Paranaguá Bay (southern Brazil)

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Abstract Heterogeneity in the distribution of organisms occurs at a range of spatial scales, which may vary from few centimeters to hundreds of kilometers. The exclusion of small-scale variability from routine sampling designs may confound comparisons at larger scales and lead to inconsistent interpretation of data. Despite its ecological and social-economic importance, little is known about the spatial structure of the mangrove crab *Ucides cordatus* in the southwest Atlantic. Previous studies have commonly compared densities at relatively broad scales, relying on alleged distribution patterns (e.g., mangroves of distinct composition and structure). We have assessed variability patterns of *U. cordatus* in mangroves of Paranaguá Bay at four levels of spatial hierarchy (10 s km, km, 10 s m and m) using a nested ANOVA and variance components measures. The potential role of sediment parameters, pneumatophore density, and organic matter content in regulating observed patterns was assessed by multiple regression models. Densities of total and non-commercial size crabs varied mostly at 10 s m to km scales. Densities of commercial size crabs differed at the scales of 10 s m and 10 s km. Variance components indicated that small-scale variation was the most important, contributing up to 70% of the crab density variability. Multiple regression models could not explain the observed variations. Processes driving differences in crab abundance were not related to the measured variables. Small-scale patchy distribution has direct impli-

cations to current management practices of *U. cordatus*. Future studies should consider processes operating at smaller scales, which are responsible for a complex mosaic of patches within previously described patterns.

Keywords *Ucides cordatus* · Spatial scale · Nested ANOVA · Variance components · Mangrove · Paranaguá Bay

Introduction

The description patterns of variation of abundance across spatial and temporal scales are essential to understand the factors and processes controlling its distribution (Underwood et al. 2000; Burrows et al. 2009). The scale-dependent nature of ecological processes (e.g., dispersion, predation) results in patterns of distribution of organisms varying across a hierarchy of scales, from a few centimeters to hundreds of kilometers (Morrisey et al. 1992; Archambault and Bourget 1996; Hughes et al. 1999; Underwood et al. 2000; Jenkins et al. 2001; Terlizzi et al. 2007).

When the variability at small scales is not estimated, the interpretation of results about patterns of distribution at larger scales may be wrong (Morrisey et al. 1992). Although well documented for the fauna from tidal flats (Ysebaert and Herman 2002), sandy beaches (James and Fairweather 1996), rocky shores (Benedetti-Cecchi et al. 2003; Fraschetti et al. 2005), and sublittoral soft-bottoms (Morrisey et al. 1992; Hewitt et al. 2002), small-scale spatial heterogeneity of mangrove benthic invertebrates has not been well addressed. Faunal distribution patterns from these environments are usually described at relatively large scales, from hundreds of meters to kilometers, and only recently they have been treated from a multiscale perspective

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(Chapman 1998; Chapman and Tolhurst 2007; Piou et al. 2009).

Distribution and density patterns of mangrove benthic species have been frequently related to sediment grain size, pneumatophore density, microphytobenthic biomass, and litter (Chapman and Tolhurst 2004; Piou et al. 2009). However, spatial variation in benthic invertebrates in mangroves is usually found at smaller scales (e.g., meters) than most sediment properties (Chapman and Tolhurst 2004) therefore making difficult their direct correlation. Sampling designs including several spatial scales are crucial to the adequate quantification and representation of mangrove benthic fauna and related environmental variables (Chapman and Tolhurst 2007). The application of hierarchical sampling design is a common way to ensure appropriate replication (Underwood 1997). These designs have become powerful tools when describing spatial variation of soft-bottom benthic assemblages (Morrissey et al. 1992; Ysebaert and Herman 2002; Giménez et al. 2005; Commito et al. 2006), since scales at which variability is higher can be identified through nested allocation of samples (Underwood 1997).

The crab *Ucides cordatus* (Linnaeus 1763) (Brachyura, Ucridae) is considered a key species of mangrove habitats for its high biomass (Koch and Wolff 2002) and its role in litter dynamics (Schories et al. 2003). Leaf removal by crabs through retention and consumption may reach up to 80% of the total litter produced (Nordhaus et al. 2006) and contribute to a significant decrease in its exportation to adjacent estuaries. In addition, *U. cordatus* supports a major mangrove fishery along the Brazilian coast (Glaser and Diele 2004; Diele et al. 2005; Legat et al. 2006; Magalhães et al. 2007). Particularly in Northern Brazil, over half of rural coastal households depend on the harvest, processing, transport, or marketing of *U. cordatus* for a main part of their income (Glaser and Diele 2004). Thus, the development of effective management strategies, including the determination of available stocks and sustainable harvesting practices, requires the identification of variability at scales relevant to *U. cordatus*.

Schories et al. (2003) recognized that the density of *U. cordatus* is extremely variable, but did not identify the spatial scales associated with this variability. Piou et al. (2009) showed that galleries are regularly spaced from each other at small scales (<10 m), but usually aggregated at larger scales (10–100 m). Unfortunately, most available surveys were based on a single spatial scale (Branco 1993; Blankensteyn et al. 1997; Schories et al. 2003; Diele et al. 2005; Wunderlich et al. 2008). Data interpretation from these designs is severely compromised by the lack of proper replication at relevant scales of variability. The identification of processes primarily responsible for variability in the abundance of *U. cordatus* will only be attained when its spatial structure is fully understood. At large scales, crab

distribution may be determined by estuarine salinity-energy gradients and hence mangrove typologies; while at smaller scales, biogenic structures, food availability, and intraspecific competition may be major structuring factors (Piou et al. 2009).

In this study, we have quantified *U. cordatus* variability in mangroves of Paranaguá Bay (Paraná, Brazil) at four spatial scales, from meters to 10 s km, using a hierarchical sampling design. This is the first time that the spatial distribution of this major mangrove resource has been analyzed in this way. Mangrove stands were sampled along a salinity-energy gradient that operates at the largest spatial scale (10 s km) and hence determines different forest types, from complex and well-structured to monospecific stands (Lana et al. 2001; Lana 2003). Since numerous studies have found large differences in the density of *U. cordatus* among distinct mangrove typologies (e.g., Blankensteyn et al. 1997), we hypothesized that the largest proportion of total variation in crab density would occur at the larger spatial scale (10 s km). At smaller scales, we have assessed the relative contribution of sediment characteristics, organic matter content, and pneumatophore density in regulating the observed distribution patterns.

Methods

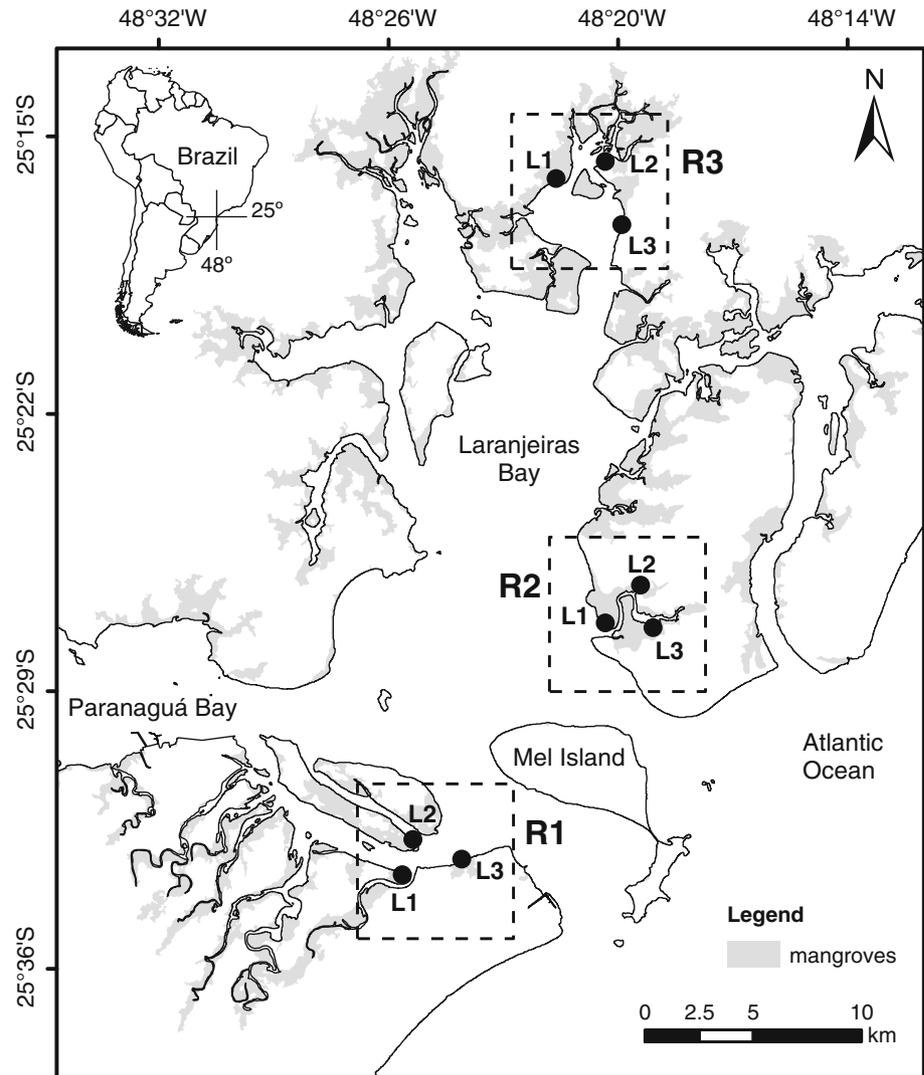
Study area

The study was conducted at Paranaguá Bay (25°30'S, 48°25'W), a semi-enclosed estuarine system in Paraná State, southern Brazil (Fig. 1). Tides are semi-diurnal with diurnal inequalities and may reach up to 2.7 m (Lana et al. 2001; Marone et al. 2005). A salinity-energy gradient from freshwater to marine conditions along the east–west and north–south main axes divides the bay into high energy, euhaline (salinity \approx 30) outer region, a middle polyhaline region, and oligo-mesohaline (salinity \approx 0–15) low-energy inner sectors (Lana et al. 2001). Local mangroves are usually made up of *Rhizophora mangle* L., *Laguncularia racemosa* Gaerth, and *Avicennia schaueriana* Stapf & Leechman and display distinct structural heterogeneity, establishing mono—as well as pluri-specific woods.

Sampling methods

The design included four spatial scales of variation: regions (10 s km), locations (km), sites (10 s m), and quadrats (m). Throughout January 2007, three regions (R1 to R3) tens of kilometers apart were sampled across the Paranaguá Bay salinity-energy gradient (Fig. 1). Regions were chosen because of its distinct mangrove typologies determined by vegetation composition and structure, sediment characteristics,

Fig. 1 Map of Paranaguá Bay showing sampling regions (R1, R2, R3; 10 s km apart) and locations within each region (L1, L2, L3; km apart)



topography, and drainage (Lana 2003). Mangrove stands from R1 and R3 are structurally more complex, with higher tree canopy heights and co-dominance of the three local tree species. Stands from R2, closer to the northern outlet of Paranaguá Bay, are structurally simpler, with lower tree canopy heights and dominance of *Laguncularia racemosa*. Within each region, three locations (1.5–3.5 km apart from each other) were randomly chosen. In each location, three sites of 10 × 10 m were randomized, and within these, five quadrats of 2 × 2 m were sampled.

Within each quadrat, burrow sizes were measured with a caliper (0.05 mm precision). *U. cordatus* burrows are easily recognized in the field and broadly used as a proxy of crab density and size (Piou et al. 2009). Only active galleries, identified by the presence of fluid mud, feces, and/or animal traces close to the opening, were considered. Closed burrows were not counted due to little occurrence during the sampling period (Wunderlich et al. 2008). Openings of 60 mm or more were attributed to commercial size crabs (Blankensteyn et al. 1997).

Sediment samples were collected with a PVC corer (10 cm diameter × 10 cm deep) in each site and frozen until analysis. Sediment analysis was conducted by pipetting and sieving and granulometric parameters (i.e., sediment grain size in phi, sorting and clay percentage) obtained using SysGran software, version 3.0 (Camargo 2006). Organic matter content was determined by differences between initial and final weights after burning 5 g of sediment in a muffle furnace for 1 h at 550°C. Pneumatophores were systematically counted in each quadrat. Dominant mangrove species were identified, and mean tree height was estimated in each site. Structure and composition of mangroves could only be assessed at larger scales than those used to estimate crab density, because the sampling units usually used to estimate mangrove stands' parameters are necessarily much larger. This description attempted to provide additional semi-quantitative or qualitative information on the structural heterogeneity of the sampled mangroves.

Data analysis

Total (non-commercial plus commercial size crabs), non-commercial (burrow size < 60 mm), and commercial size (burrow size \geq 60 mm) *U. cordatus* densities were analyzed separately using a pure random effects–nested ANOVA. The objective was to identify the scales that contributed most to the variation in crabs' density. Both statistical significance and variance components (magnitude of effect) were estimated. The latter were calculated using the residual maximum likelihood (REML) method, which is insensitive to negative estimates. Thus, the “pool-the-minimum-violator” procedure, recommended by Fletcher and Underwood (2002) for this particular case, was not necessary.

Normality and homogeneity of variances were, respectively, assessed by Kolmogorov–Smirnov and Bartlett tests. Data transformation of total and non-commercial size crabs densities was not necessary. Density of commercial size crabs was transformed to square root attempting to meet the homogeneity of variances assumption. Normality for this data was not possible to accomplish even when transformed. Even though this violates the assumptions of ANOVA, it does not represent a major problem to data processing and interpretation, which remains consistent notwithstanding the lack of normality (Underwood 1997).

Relationships between environmental factors and burrow density were evaluated at the scale of sites. Multiple regression was used, with burrow density as response variable and sediment grain size, sorting, clay percentage, organic matter content, and density of pneumatophores as predictor variables. Homogeneity of variances, non-collinearity among variables, and normality of errors assumptions were checked and no transformation was necessary. A stepwise forward procedure was used to determine the best model. Means from the five quadrats were taken to determine crab density and pneumatophores density, since only one sediment sample per site was available.

All statistical analysis and graphs were generated using R programming language (R Development Core Team 2009) combined with nlme (Pinheiro et al. 2009) and sciplot (Morales 2009) packages.

Results

Mangroves from Region 1 were mostly made up of *Rhizophora mangle* and *Avicennia schaueriana*, while *Laguncularia racemosa* occurred more often only at two sites. Mean height varied from 5 to 8 m at sites dominated by *A. schaueriana* and *R. mangle* and remained at 3 m at those dominated by *L. racemosa*. Mangroves from Region 2 showed a rather homogenous structure, consisting of *L. racemosa* mono-specific forests of ca. 3.5 m high. Region 3 mangroves were structurally complex, with pluri-specific stands and mean height ranging from 6 to 10 m.

About 60% of the total counted burrows belonged to non-commercial size crabs, which presented a higher density (1.35 ± 0.96 burrows m^{-2}) than commercial size crabs (0.86 ± 0.62 burrows m^{-2}). Total and non-commercial crabs' densities varied significantly ($P < 0.05$) among locations and sites, but were similar among regions (Table 1; Figs. 2a–c, 3a–c). Differences in commercial size density were marginally significant ($0.05 < P < 0.06$) among regions and sites, with lower densities at Region 2 (Table 1; Fig. 4a–c).

Generally, density patterns were strongly dominated by small-scale variability (i.e., among replicated quadrats few meters apart within each site) (Fig. 5). The large scale (regions tens of kilometers apart from each other) did not contribute significantly to the variability of total and non-commercial crab densities. However, the regions accounted for about 20% of commercial size crabs variance (Fig. 5). High variance components calculated for the quadrat level (i.e., the residual) indicated that total as well as non-commercial and commercial size crab abundance were patchy at the smaller spatial scale.

Stepwise forward multiple regressions selected models including a single independent variable and rather limited explanation of the total and non-commercial size crabs distribution patterns (Table 2). Mean sediment grain size (ϕ) accounted, respectively, for 16 and 15% of total and non-commercial variability. Despite the low coefficient of determination, the negative relation between these variables suggests a decrease in total and non-commercial *U. cordatus* abundance in areas with finer sediments. No variables

Table 1 Nested analysis of variance for spatial variation in mean number of crab burrows at different spatial scales

Source	df	Total crab burrows			Crab burrows < 60 mm			Crab burrows \geq 60 mm		
		MS	F	P	MS	F	P	MS	F	P
Region	2	7.050	1.366	0.324	3.629	0.954	0.437	1.897	4.826	0.056
Location (R)	6	5.162	2.741	0.045	3.804	3.243	0.024	0.393	2.146	0.098
Site (L(R))	18	1.883	2.130	0.009	1.173	1.746	0.042	0.183	1.691	0.052
Residual	108	0.884			0.672			0.108		

Fig. 2 Mean (SE, $n = 5$) number of *Ucides cordatus* burrows among **a** regions, **b** locations, and **c** sites

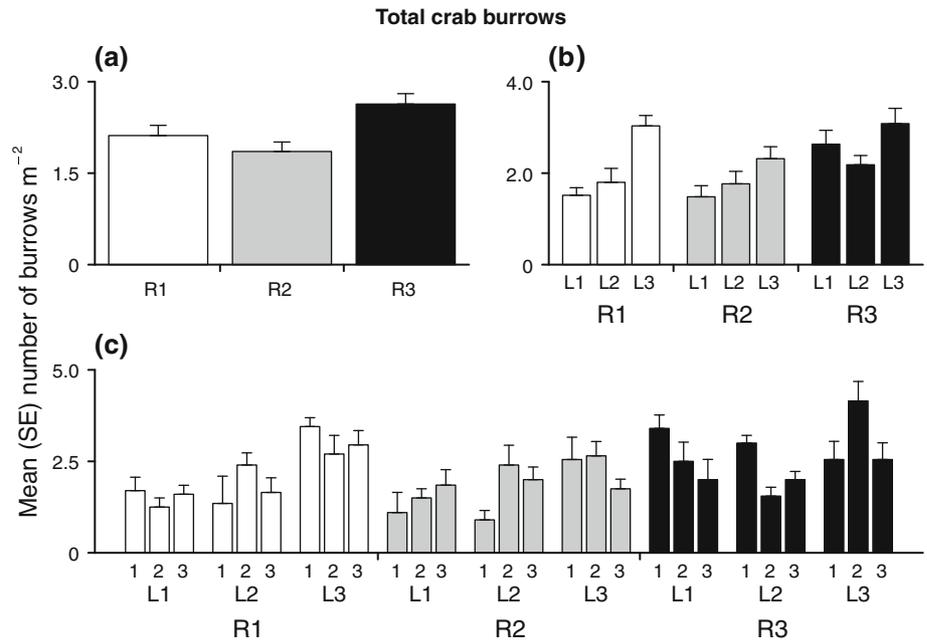
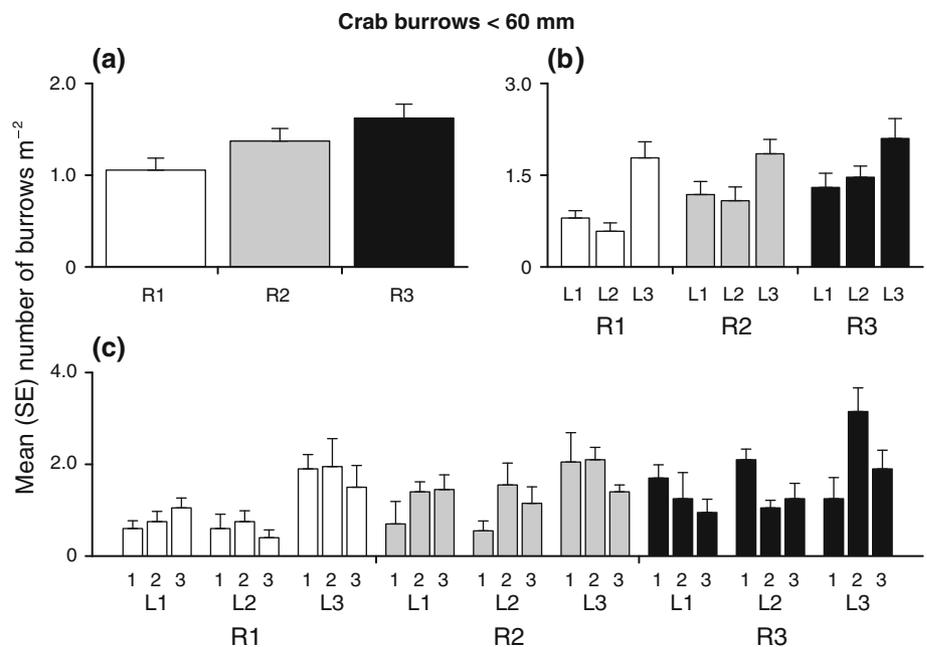


Fig. 3 Mean (SE, $n = 5$) number of non-commercial size *Ucides cordatus* burrows among **a** regions, **b** locations, and **c** sites



were selected that would explain the observed variability of commercial size crabs (Table 2).

Discussion

We rejected the hypothesis that the scale of tens of kilometers, which is responsible for the major variation in the structure of mangrove stands, accounts for most of the variation in crab density. Distribution of *U. cordatus* was patchy at the smallest spatial scale with the larger proportion of total

variance occurring among replicates. Thus, densities differed significantly among quadrats just a few meters apart and these differences were larger than those measured at larger scales. This small-scale variability, particularly in meters, is a well-known pattern in most benthic habitats (Morrissey et al. 1992; Underwood and Chapman 1996; Olabarria and Chapman 2001; Ysebaert and Herman 2002; Commito et al. 2006) including mangroves (Chapman 1998; Chapman and Tolhurst 2007) and stresses the need for the quantification of abundance patterns at a hierarchy of spatial scales.

Fig. 4 Mean (SE, $n = 5$) number of commercial size *Ucides cordatus* burrows among **a** regions, **b** locations, and **c** sites

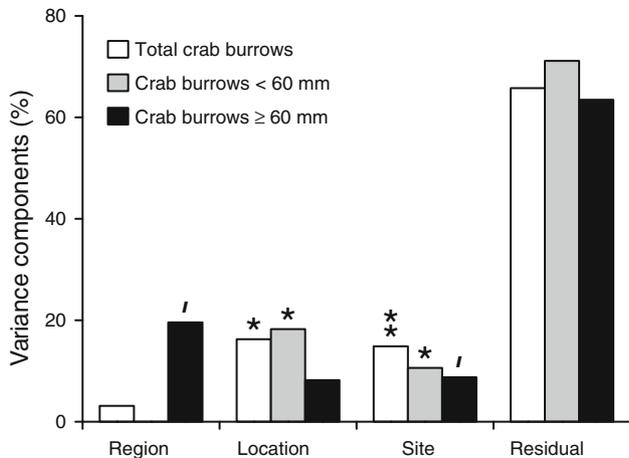
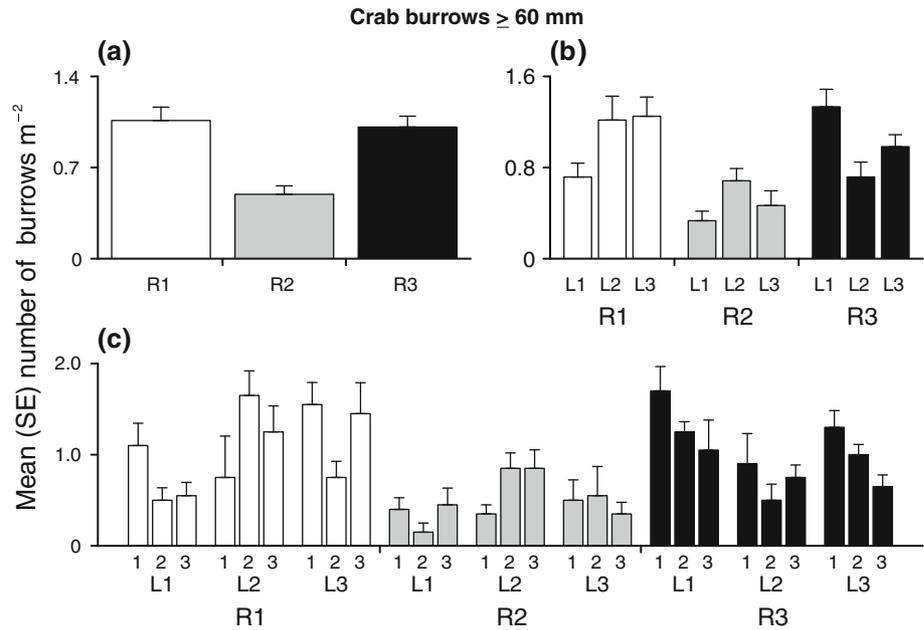


Fig. 5 Percent variance components for *Ucides cordatus* densities among regions, locations, sites, and residual (i.e., quadrats). *Marginally significant difference ($0.05 < P < 0.06$); * $P < 0.05$; ** $P < 0.01$

Such large small-scale variation should not be treated simply as uninteresting “noise” (Carroll 2003) but as relevant ecological information. Although apparently chaotic, small-scale patchiness results from specific ecological processes operating at very fine scales. These may be related to the patchy distribution of microhabitats, small-scale changes in environmental conditions, behavior and competition. For example, habitat choice and recruitment of *U. cordatus* megalopae are strongly induced by environmental cues associated with the presence of conspecific crabs and muddy sediments (Diele and Simith 2007), which is likely to be more important in regulating patterns of distribution at small scales. Other small-scale processes, such as intra-specific competition, may explain the differences in the

Table 2 Multiple regression analysis between burrow densities and environmental variables (mean grain size, sorting, clay percentage, organic matter content, and pneumatophore density)

Dependent variable	Effect	β	R^2	P
Total crab burrows	Mean grain size	-0.404	0.16	0.037
Crab burrows < 60 mm	Mean grain size	-0.383	0.15	0.048
Crab burrows \geq 60 mm	None			

The only variable selected in the stepwise forward procedure was mean grain size. β partial correlation coefficient; R^2 coefficient of determination

spatial patterns of non-commercial and commercial size crabs, since large crabs apparently exclude smaller ones from preferred habitats (Piou et al. 2009).

It is very unlikely that large-scale processes, such as wave-action or salinity gradients, regulate the distribution of fauna at smaller scales. Overall distribution of *U. cordatus* has been variously attributed to abiotic factors, such as sediment texture and flood rates, or biological factors, such as mangrove composition/structure and pneumatophore density (Blankensteyn et al. 1997; Schories et al. 2003; Nordhaus et al. 2009; Piou et al. 2009). However, most of these factors cannot explain spatial variations in burrow densities at the scales of sites and replicates. The size of the sampling units needed to adequately sample such variables is much larger than the scales mostly responsible for variation in crabs’ density. Mangrove composition and structure are mostly assessed at relatively large plots (typically 10×10 m or larger). The heterogeneity in the distribution and density of *U. cordatus* is greater within than between such putatively sources of variation. This implies that density comparisons among mangroves of different typologies are potentially confounded.

The amount of total variability in crab density explained by multiple regressions was low. Moreover, only one variable (i.e., mean sediment grain size) was selected in the stepwise forward procedure. The relationships between mangrove benthic fauna and sediment properties are usually weak and variable among different habitats and may display extremely complex patterns at scales ranging from a few meters to several kilometers (Chapman and Tolhurst 2007). This is a possible response to a number of processes operating at these scales, including sediment reworking by the fauna itself. Mangrove microtopography and sediment stability may be modified by crabs that bring fine and cohesive particles to the surface (Botto and Iribarne 2000). Multiple regression models showed the complexity of such interactions and the weak relation between sediment variables and crab density. The lack of paired measures of crab burrows and sediment also contributed to decrease the likelihood of significant correlations, even when considering that benthic animals in mangroves are more variable at the scale of meters while most sediment properties (e.g., grain size) differ at slightly larger scales (Chapman and Tolhurst 2004; Chapman and Tolhurst 2007).

The results of our multiscale approach have relevant implications for the current management procedures of *Ucides cordatus*. Crab densities are often calculated from unbalanced and poorly replicated designs to estimate regional standing stocks. Scale confounding may turn specifically relevant when densities estimated from single-scale surveys are extrapolated to other relevant scales (Morrisey et al. 1992). Most available studies in tropical and subtropical areas have extrapolated densities of *U. cordatus* measured at a single (usually large) spatial scale to whole mangrove areas (Branco 1993; Blankensteyn et al. 1997). An example of such confounding is shown by the results for total density of *U. cordatus*, in which significant variation was found at scales of sites (10 s m) and locations (km), but not among regions (10 s km). Any attempt to compare regions based on punctual or single-site samplings would be confounded by variation at these scales within each region. Estimates of densities at the scale of regions would have been extremely overestimated or underestimated, and spurious differences would have been found among regions, as previously shown by Morrisey et al. (1992) for other benthic species. This is particularly pertinent when defining a preferred habitat type or quantifying crabs' stocks at a regional level for fishery management purposes.

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