



The influence of mangrove structure on the spatial distribution of *Melampus coffeus* (Gastropoda: Ellobiidae) in Brazilian estuaries

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Abstract. *Melampus coffeus* is a macro-detritivore pulmonate gastropod with an important role in energy transfer in mangroves, yet its distribution at different scales is still unknown. This study aimed to evaluate the relationship between the distribution of *M. coffeus* and mangrove vegetation structure and zonation in nine estuaries in the state of Ceará, northeastern Brazil. The distribution patterns of trees and snail densities were congruent in all sites except at the Ceará River where the density of *M. coffeus* was much higher than the density of trees. Similar results were recorded for tree and shell heights, which followed the same pattern in most of the studied mangroves except in the Barra Grande estuary. However, there was no clear zonation pattern among the mangrove sites themselves. The data herein presented suggest that the morphology and density of the *M. coffeus* shell vary considerably among different mangrove areas, and that such distribution is strongly related to the vegetation structure of each habitat. These data suggest that the deforestation of natural mangrove areas might have a significant influence on the distribution of *M. coffeus* with possible indirect effects on the functioning of these ecosystems.

Key words: Brazil, snails, *Pulmonata*, vegetation structure, zonation

Resumo. *Influência da estrutura vegetal dos bosques de mangue na distribuição espacial de Melampus coffeus (Gastropoda: Ellobiidae) em estuários brasileiros.* *Melampus coffeus* é um gastrópode pulmonado, macrodetritívoro, com um importante papel na transferência de energia em manguezais, mas sua distribuição em diferentes escalas ainda é desconhecida. Assim, este trabalho teve como objetivo estudar a distribuição de *M. coffeus* com relação à estrutura vegetal dos manguezais e sua zonação. Este estudo foi realizado em nove estuários no estado do Ceará, no nordeste brasileiro. Os padrões de variação da densidade das árvores e de caramujos foram semelhantes em todos os locais, exceto no rio Ceará, onde a densidade de *M. coffeus* foi muito maior do que a das árvores. Resultados semelhantes foram registrados para a altura árvore e da concha, que seguem o mesmo padrão na maioria dos manguezais, exceto no estuário da Barra Grande. No entanto, não foi encontrado um padrão claro de zonação para a espécie nos manguezais. Os dados apresentados sugerem que a morfologia da concha e densidade de *M. coffeus* variam consideravelmente entre os diferentes manguezais estudados e que essa distribuição está fortemente relacionada com a estrutura vegetal do habitat. Estes dados sugerem que o desmatamento pode influenciar diretamente a distribuição de *M. coffeus* com possíveis efeitos indiretos no ecossistema.

Palavras chave: Brasil, caramujos, *Pulmonata*, estrutura vegetal, zonação

Introduction

Trophic interactions involving plants and animals in mangrove forests play an important role in the control of populations and communities (Robertson, 1991). The zonation pattern of snail

populations in these environments can be influenced by the availability and quality of mangrove forest resources such as the production of leaves with differential palatability due chemical composition, species diversity, and varied degrees of senescence

(Rietsma *et al.*, 1988; Proffitt *et al.*, 1993). Roots and pneumatophores, which function both as food resources, substrate for algae and fungi, and refuge to extreme physical conditions and predation are also important because they create favorable microhabitats promoting increased snail densities (Chapman *et al.*, 2005). Thus, the distribution of mollusks is highly correlated with tree density and composition of vegetal species.

However, anthropic disturbances might be responsible for severe impacts in these ecosystems changing and completely disrupting the mangrove physical structure, and affecting the macrofaunal distribution and abundance (Fondo & Martens, 1998; Beasley *et al.*, 2005). Skilleter & Warren (2000) suggested that impacts generated by human activity led to changes in the dynamics of tidal flooding and, therefore, to different distribution of leaves on the substrate resulting in a decreased snail density in the affected areas. Chapman *et al.* (2005) also concluded that a widespread impact might greatly reduce snail densities due to changes in tidal flooding levels and amount of organic matter available in the sediment. However, according to the author, the density of snails can be altered by impacts causing fragmentation in the system because it affects intra- and inter-specific interactions.

Melampus coffeus (Linnaeus, 1758) (Ellobiidae) is a pulmonate macro-detritivore gastropod which plays an important role in energy transfer in neotropical mangroves, however, its distribution at different scales is still poorly known (Proffitt *et al.* 1993; Proffitt & Devlin, 2005). Salinity variations are the main determinant factors in the distribution and abundance patterns of *Melampus*; the highest population densities are found in areas with high salinity (Kerwin, 1972, Fell & Williams, 1985; Burnham & Fell, 1989, Martins 2001). Vegetation structure also plays an important role in their zonation (Kerwin, 1972, Martins 2001) because these snails prefer certain mangrove species and leaves at some degree of senescence; they are mainly attracted by older leaves of *Rhizophora mangle* (Proffitt *et al.* 1993; Proffitt & Devlin, 2005). Moreover, the roots of this mangrove trees are critical to the mollusk's distribution providing refuge from high tides; adult specimens climb these roots after feeding on the substrate during the low tide to avoid drowning during the high tide (Maia & Tanaka, 2007). Hence, in addition to the salinity effect, it is possible that the distribution of *M. coffeus* is influenced by tree composition, age, structure, and density; the trees are used both as a refuge and food source.

The goals of this study were to evaluate the relationship between the distribution of *M. coffeus* and mangrove vegetation structure and to verify the existence of zonation patterns for this species in mangrove areas. The working assumption was that low values of population densities and sizes of *Melampus coffeus* shells are found in mangroves with less developed structure, defined by measurements of tree height, basal area, number of trunks, and density, and evaluated along vertical (quadrats) and horizontal (sites) gradients.

Materials and methods

Study area

This study was carried out in nine estuaries in Ceará State, northeastern Brazil. Three estuaries were located in the metropolitan region of the state capital Fortaleza (Ceará, Cocó, and Pacoti Rivers), three were major basin rivers (Acará, Curú, and Jaguaribe Rivers), and three were second-order stream rivers (Aracatimirim, Guriú, and Barra Grande Rivers) formed by the union of small permanent flowing streams (Figure 1). The samples were collected in the middle estuary.

Sampling methods

The characterization of the vegetation structures in the mangroves was based on the methodology proposed by Schaeffer-Novelli & Cintrón (1986), which recommends the use of multiple quadrats with sample replication to increase representativeness and allow robust statistical analyses. Three sampling random sites were chosen in each river where a transect containing five 100 m² quadrats were set 5 meters apart from each other (Figure 2). Only three quadrats were set in the Guriú and Pacoti estuaries due to the small extension of the mangrove in these sites. The quadrats were established perpendicularly to the river and the first one at 10 meters from the waterline. The tree species were identified in each quadrat, their heights were estimated and diameters measured at breast height (approximately 1.30 m from the ground) (DBH) with the aid of a measuring tape. Only trees with a circumference greater than 2.5 cm were recorded; the number of trunks per tree was also recorded.

Five 1 m² quadrats were randomly established within each 100 m² quadrat, in which all *M. coffeus* specimens found were manually collected. In the laboratory, the specimens were fixed in 70% alcohol and measurements of shell height and width, and aperture height were taken with the aid of a caliper (precision = 0.01 mm). The mean snail density was calculated in each sample unit. Air, sediment, and water temperature and

humidity, and water salinity were recorded in each transect.

Three sediment samples were collected in the low tide for granulometric analysis, one in each transect. These samples were mechanically sifted, and fractions from 0.062 mm to 2.00 mm in diameter corresponding to the sandy fraction, and

fractions with a diameter larger than 2.00 mm corresponding to rock chips were obtained. The organic matter content was evaluated by the difference between the initial and final sediment mass after calcination in a muffle oven at 450 °C for 2 hours.

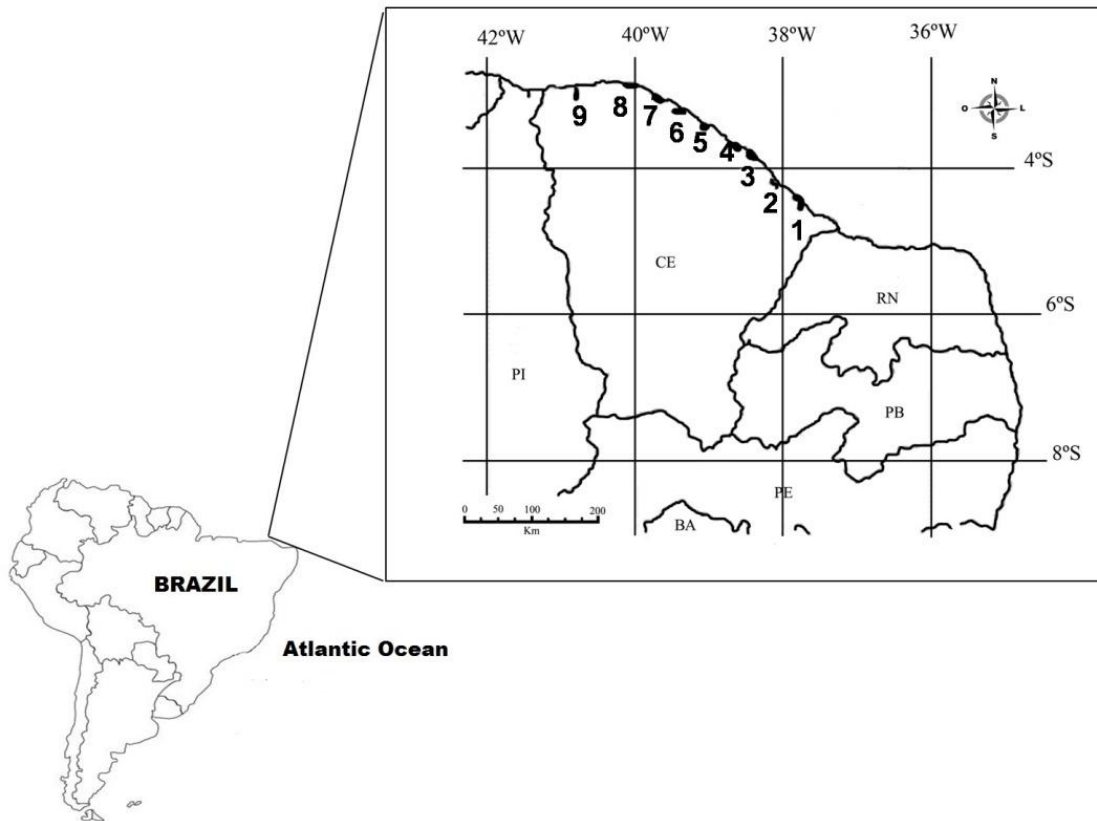


Figure 1. Map of the Ceará State with mangrove areas and sampling sites. 1. Barra Grande, 2. Jaguaribe, 3. Coco, 4. Pacoti, 5. Ceará, 6. Curú, 7. Aracatimirim, 8. Acaraú, 9. Guriú. Bold dots indicate sampled mangrove sites.

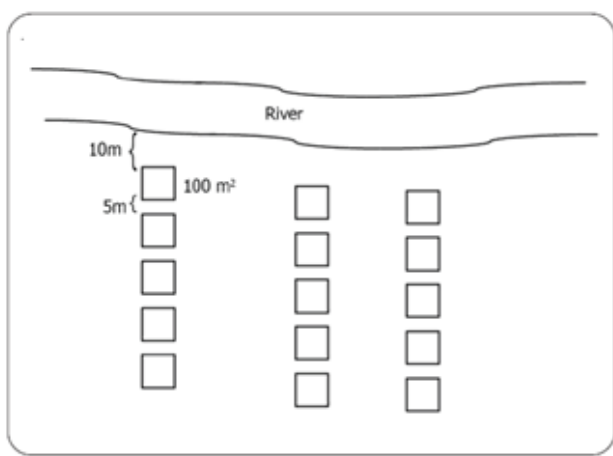


Figure 2. Schematic drawing of the methodology used for the characterization of the vegetation structure in mangrove forests in the study sites.

Data analysis

An Analysis of Variance (ANOVA) was performed to estimate differences in tree densities and *M. coffeus* densities among the study sites. The same analysis was used to evaluate differences in the densities of *M. coffeus* between quadrats to verify the existence of zonation patterns. All data were converted to Napierian logarithms to normalize the variances (Sokal & Rohlf, 1995). Differences between means ($p < 0.05$) were analyzed with the Tukey's HSD multiple comparisons test. The Kruskal-Wallis test was used to compare shell morphology (height, width, and aperture height) among the different study sites and quadrats because there was no data normality. The Multiple Comparisons Test was used when differences between samples were observed.

The relationships between the densities of *M. coffeus*, shell height, mangrove structural parameters (tree height and density, number of trunks, basal area and absolute density of each mangrove species), and sediment characteristics (percentages of gravel, sand, clay, and organic matter) were assessed through the Spearman's correlation analysis. The other size variables (width and aperture height) were not used in this analysis because they were highly correlated ($R \geq 0.95$). Statistical analyses were performed using the STATISTICA for Windows® software, version 7.0.

Results

Four mangrove species were sampled in nine estuaries: *Avicennia germinans* (Linnaeus) Stearn, *Avicennia schaueriana* Stapft & Leechman (Avicenniaceae), *Rhizophora mangle* Linnaeus

(Rhizophoraceae), and *Laguncularia racemosa* (Linnaeus) Gaertn (Combretaceae). *R. mangle* was the most dominant and frequent species in the studied sites considering the total basal area of individuals (Table 1). The tree density was not similar among sites ($F_{8,126} = 5.5161$; $p < 0.001$). The formation of 3 distinct groups of tree densities were observed; with high density and denser than the other 2 groups in Acaraú, Ceará, and Guriú, with intermediate values composed of Barra Grande, Jaguaribe, and Pacoti, and with low density including Aracatimirim, Cocó, and Curú. The Ceará estuary is threatened by impacts resulting from urbanization while Barra Grande is threatened by shrimp farming; both activities lead to the fragmentation of mangrove forests through the discharge of untreated effluents into the rivers.

Table I. Relative dominance (Do) and frequency (Freq) of mangrove species in the studied estuaries. Values are expressed in percentages.

Parameters/Estuaries	Barra Grande	Jaguaribe	Cocó	Pacoti	Ceará	Curú	Acaraú	Aracatimirim	Guriú
Do <i>R. mangle</i>	92.42	35.45	22.36	52.36	13.59	94.91	43.78	49.96	61.11
Do <i>A. germinans</i>	0	44	6.28	9.58	1.57	2.24	41.03	34.04	34.09
Do <i>A. schaueriana</i>	7.57	9.36	45.35	11.61	53.61	0.97	10.86	16	4.37
Do <i>L. racemosa</i>	0.01	11.19	26.01	26.45	31.23	1.87	4.33	0	0.42
Freq <i>R. mangle</i>	61.9	27.03	31.43	34.62	32.58	57.69	31.82	48	37.5
Freq <i>A. germinans</i>	0	29.73	8.57	19.23	12.36	11.54	29.55	20	37.5
Freq <i>A. schaueriana</i>	33.33	18.92	34.29	26.92	37.45	11.54	22.73	32	20.83
Freq <i>L. racemosa</i>	4.76	24.32	25.71	19.23	17.6	19.23	15.91	0	4.17

The *M. coffeus* mean density varied significantly among study sites ($F_{8,126} = 33,930$, $p < 0.0001$). According to the Tukey's HSD multiple comparisons test, the highest density values were recorded in the Ceará River estuary while the others were statistically similar (Figure 3). The mean shell size of *M. coffeus* specimens from the nine estuaries was statistically different considering the analyzed morphometric parameters. Thus, shell height ($H = 1715.557$, $df = 8$, $p < 0.001$), width ($H = 852.222$, $df = 8$, $p < 0.001$), and aperture height ($H = 735.212$, $df = 8$, $p < 0.001$) were high in the Barra Grande, Ceará, Curu, Aracatimirim, Acaraú, and Guriú sites and low in the Jaguaribe, Coco, and Pacoti sites (Figure 4).

After this analysis, positive correlations between *M. coffeus* shell height and snail density ($R = 0.66$), shell height and number of trunks ($R = 0.47$), and snail density and tree height ($R = 0.43$) were observed. Moreover, the density of *R. mangle* trees presented a statistically significant correlation

with shell height ($R = 0.41$) and snail density ($R = 0.40$). However, no significant correlations were observed between shell size or density of *M. coffeus* and the density of another tree mangrove species. Although the correlation analysis indicates low values of R the distribution pattern identified for the densities of trees and snails were similar in all studied sites, except in the Ceara River estuary, where the density of *M. coffeus* was exceedingly higher than the density of trees (Figure 3). Similar results were recorded for tree height and shell height, which followed the same pattern in most of the studied sites with similar values in all estuaries, except in the Barra Grande (Figure 4).

The density of *M. coffeus* was significantly correlated with the percentage of gravel ($R = 0.48$) and organic matter content ($R = 0.50$), while shell height was not correlated with any of the tested sedimentary variables. The snail density presented a significantly negative correlation with salinity ($R = -0.66$).

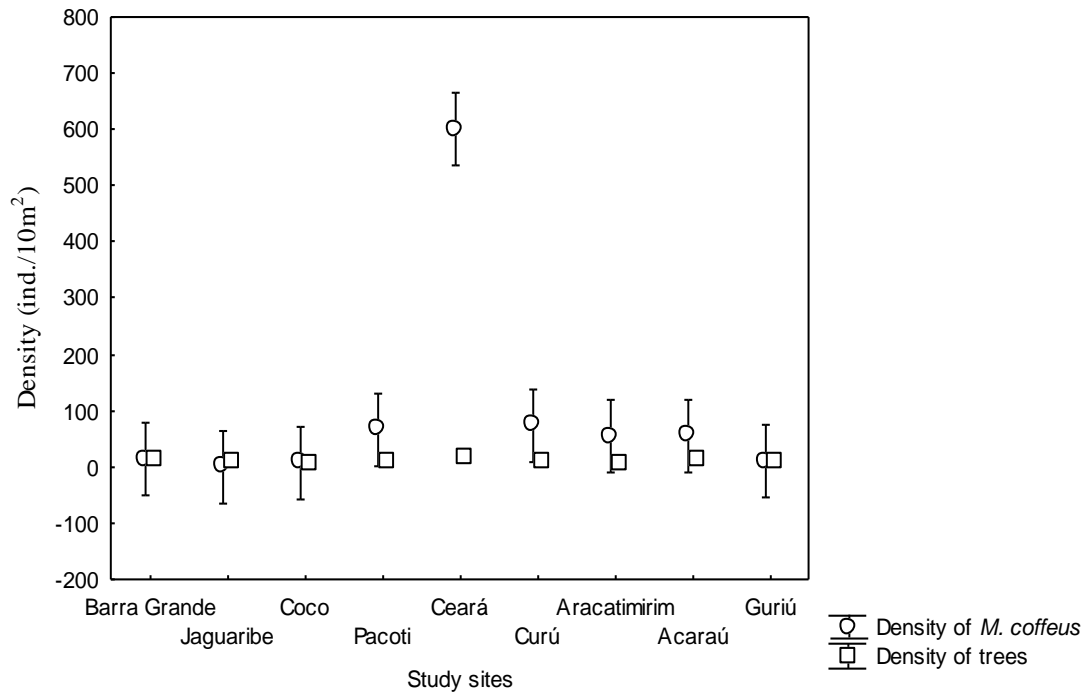


Figure 3. Variations in the densities of mangrove trees (□) and *Melampus coffeus* (○) ± standard deviation in the studied estuaries in Ceará State, Brazil.

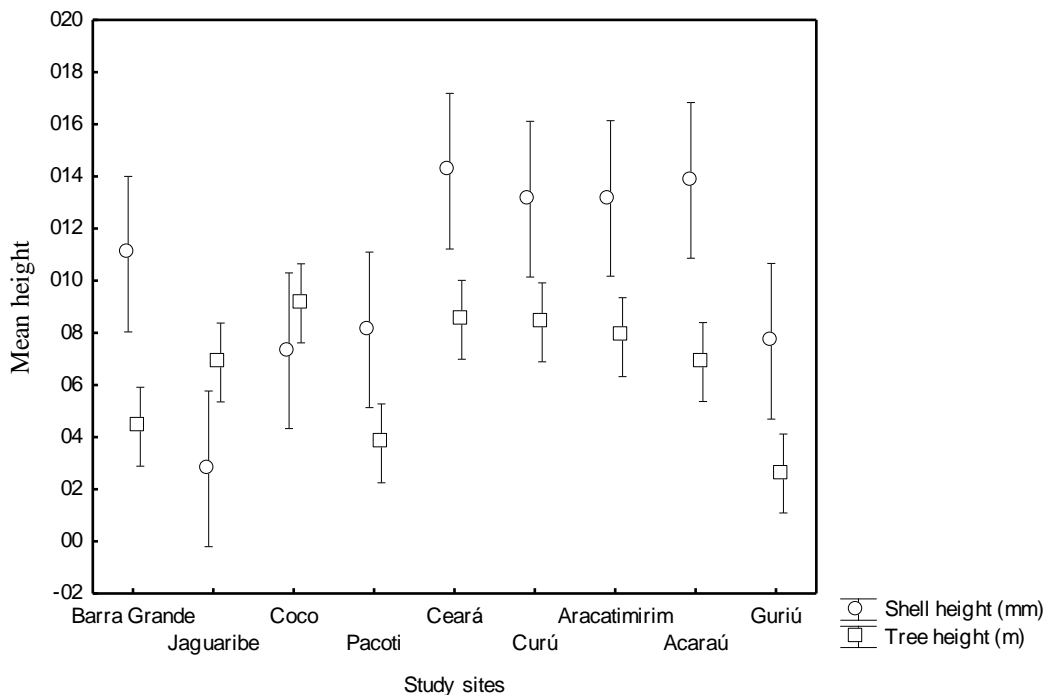


Figure 4. Variations in tree height (m) (□) and *Melampus coffeus* height (cm) (○) ± standard deviation in the studied estuaries in Ceará State, Brazil.

The density of *M. coffeus* was similar among the different quadrats in Barra Grande, Jaguaribe, Cocó, Ceará, Curú, Aracatimirim, and Acaraú estuaries. However, in the Guriú and Pacoti estuaries, the mean density was significantly lower

in the third quadrat than in the other quadrats (Table II). The third quadrat does not represent the interior of the forest but its end, due to the small extension of mangroves in the studied sites. The *M. coffeus* shell size showed significant statistical differences

among quadrats in all sites, except for the Guriú River, where shell height, width, and aperture height were similar in all quadrat (Table III). In the Barra Grande, Pacoti and Acaraú sites, the smallest individuals were found in quadrats one and two, while in the Jaguaribe River, the largest snails were found in the last quadrat. In the Coco river site only

quadrats two and five were not similar shell size. In the Ceará River, only the animals collected in quadrats three and four were similar shell size, while in the Curu River similar size specimens were found in quadrats three and five. In the Aracatimirim mangrove, the size of snails decreased with the increase in the distance from the river.

Table II. ANOVA results comparing the densities of *M. coffeus* between different quadrats in the studied sites in Ceará State, Brazil.

	Density		
	F	gl	p
Barra Grande	0.5544	4.10	0.700 ^{ns}
Jaguaribe	1.672	4.10	0.232 ^{ns}
Cocó	0.315	4.10	0.860 ^{ns}
Pacoti	4.712	2.6	0.05*
Ceará	0.592	4.10	0.675 ^{ns}
Curú	0.605	4.10	0.667 ^{ns}
Aracatimirim	1.571	4.10	0.255 ^{ns}
Acaraú	0.937	4.10	0.480 ^{ns}
Guriú	11.44	2.6	0.008*

^{ns} no significant variation; * significant variation

Table III. Results of the nonparametric Kruskal-Wallis test comparing the morphometric variables of *M. coffeus* between different quadrats in the studied sites in Ceará State, Brazil.

	Height			Width			Aperture height		
	H	gl	p	H	gl	P	H	gl	p
Barra Grande	18.2	4	0.001*	20.74	4	0.007	19.93	4	0.0005*
Jaguaribe	20.35	4	0.004*	20.98	4	0.0003	20.25	4	0.0004*
Cocó	15.88	4	0.032*	15.51	4	0.015	15.11	4	0.045*
Pacoti	225.2	2	<0.0001*	272.6	2	<0.0001	232.1	2	<0.0001*
Ceará	361.1	4	<0.0001*	305.6	4	<0.0001	346.7	4	<0.0001*
Curú	70.03	4	<0.0001*	78.5	4	<0.0001	81.51	4	<0.0001*
Aracatimirim	34.3	4	<0.0001*	38.07	4	<0.0001	35.29	4	<0.0001*
Acaraú	132.2	4	<0.0001*	128.4	4	<0.0001	138.1	4	<0.0001*
Guriú	3.15	2	0.26 ^{ns}	5.27	2	0.07	1.38	2	0.5 ^{ns}

^{ns} no significant variation; * significant variation

Discussion

Our results indicate congruent distribution patterns of mangrove trees and snails in most of the studied sites, that is, the greatest availability of food resources and shelter, provided by the mangrove vegetation, correlated with the greatest abundance of

M. coffeus. Similar results were reported by Kerwin (1972) who demonstrated the relationship between the abundance of snails of a congeneric species, *M. bidentatus*, and the density of trees. The trees serve as a food source by producing leaves and provide support during the high tides considering that these

pulmonate organisms need to go through a daily process of vertical migration to avoid drowning (Kerwin, 1972; Maia & Tanaka, 2007; Tavares *et al.* 2011). Physical factors such as sediment type also affect the distribution of mangrove mollusk species as the Ellobiidae snails (Cantera *et al.* 1999). This factor is determinant in the extremely high *M. coffeus* densities observed in the Ceara River estuary. This mangrove, compared to the other sampled ones, presented the highest levels of organic matter in the sediment. This region is close to a large city without an efficient domestic sewage treatment system resulting in an increased concentration of nutrients in the estuary. This might lead to increased primary production rates and biomass generation (Marques-Junior *et al.* 2002).

Melampus species present high densities in areas with high salinities (Price, 1980; McMahon & Russell-Hunter, 1981; Fell & Williams, 1985; Burnham & Fell 1989). In this study, variations observed in the densities of *M. coffeus* did not corroborate the patterns recorded for other species in this genus; instead, high densities were detected in areas with low salinities. This could be the result of the adopted criteria of sampling in the middle estuary where little variation in salinity was observed between samples.

The similar distribution pattern among trees and snail sizes, and the correlation between *M. coffeus* density and tree heights were also observed. Greater canopy heights provide favorable microhabitats for gastropods and correlates to higher values of shell height and snail abundance (Merkt & Ellison, 1998; Suzuki *et al.* 2002; Tanaka & Maia, 2006). Lower canopies are poor in nutrients and result in slower snail growth rate compared to estuaries with high mangrove trees, which are rich in nutrients (Merkt & Ellison, 1998). The correlation between the height of trees and organic matter content of the sediment, observed in the present study, corroborates to this fact, however, in mangroves that are rich in nutrients but disturbed by deforestation, the trees are lower and the shells taller (Merkt & Ellison, 1998). Mangroves with shorter trees have canopies that are more open and, therefore, more exposed to sunlight; taller shells would confer increased resistance to desiccation (Vermeij, 1972). This was probably the situation observed in the Barra Grande mangrove; an area historically disturbed by shrimp farming and the only sampled region that does not follow the pattern described above. Economic activities generate environmental impacts such as vegetation removal, alteration of water flows, effluent discharges from ponds, changes in the dynamics of currents,

landscape alterations, risks of erosion and siltation, changes in water quality, and others (SEMACE, 2004).

An additional important observation in this study was the tendency to areas with a predominance of *R. mangle* to present the highest *M. coffeus* density and size values indicated by the correlation analysis. These results might be related to the fact that these snails are macro-detritivores feeding on plant debris, preferably leaves of this particular mangrove species (Proffitt *et al.* 1993; Proffitt & Devlin, 2005). Thus, it is possible that the composition of mangrove tree species influences the distribution of *M. coffeus* as a function of the variation in the quantity of leaves available for consumption in different mangrove forests. These results corroborate the findings reported by Maia & Tanaka (2007) in another mangrove area in the State of Ceara. Other ellobiid species show similar distribution patterns related to the specific composition of the surrounding flora. Kerwin (1972) observed that the distribution and abundance of *Melampus bidentatus* is associated with the presence of some species of seagrass in the marine habitat, while Walthew (1995) showed that *Cassidula aurifelis* and *Ellobium polita* are restricted to sites with particular mangrove vegetation.

A clear zonation pattern for *M. coffeus* was not observed in the studied mangrove sites because the vegetation itself did not show a clear zonation pattern. Candra *et al.* (1999) stated that fauna inhabiting mangroves is often present in different sites in this environment due to the ecosystem's complexity expressed by a multitude of factors acting at the same time, and making the establishment of a zonation pattern almost impossible.

The data presented in this study indicate that the densities of *M. coffeus* are similar in all sampled sites with the exception of Pacoti and Guriu estuaries where the abundance decreased from the first to third sampling units. However, only three quadrats could be sampled due to fragmentation of the environment in these mangroves. Anthropogenic disturbances might alter the conditions that determine the distribution of snails in mangroves (Walthew, 1995; Chapman *et al.* 2005). The fragments differ from the original habitat by an increased number of edges per unit area, which might limit the potential for species dispersal and colonization and reduce the environmental feeding capacity for native animals (Primack & Rodrigues, 2002).

The identified shell size values were extremely variable among different sites. Only the

Guriu River mangrove showed similar values throughout the sampled area. This area is going through a maturation process with the land being occupied by a high density of trees with small diameters. Since this process was observed throughout the area, the shell sizes were not different among samples. Furthermore, the large edge effect due to this habitat's fragmentation, makes the conditions and resources between the center and edge of the fragments very similar (Primack & Rodrigues, 2002).

Our study suggests that the deforestation of natural mangrove areas might have a significant influence on the distribution of *M. coffeus* with possible indirect effects on the functioning of these ecosystems. This knowledge is essential to detect changes in the functioning of mangroves as these regions are increasingly subjected to human disturbance, and provide information for the management and conservation of these ecosystems.

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References

- Beasley, C. R., Fernandes, C. M., Gomes, C. P., Brito, B. A., Santos, S. M. L. & Tagliaro, C. H. 2005. Molluscan diversity and abundance among coastal habitats of northern Brazil. **Ecotropica**, 11: 9–20.
- Burnham, B. H. & P. E. Fell. 1989. Distribution of *Melampus bidentatus* (Say) and *Succinea wilsoni* (Lea) within a tidal marsh in eastern Connecticut. **The Nautilus**, 103: 109-112.
- Cantera, J. R., Thomassin, B. A. & Arnaud, P. M. 1999. Faunal zonation and assemblages in the pacific Colombian mangroves. **Hydrobiologia**, 413: 17-33.
- Chapman, M. G., Michie, K. & Lasiak, T. 2005. Responses of gastropods to change in amounts of leaf litter and algae in mangrove forests. **Journal of the Marine Biological Association of the United Kingdom**, 85: 1481-1488.
- Fell, P. E. & Williams, J. H. 1985. Distribution of the snail, *Melampus bidentatus*, and the mussel, *Geukensia demissa*, along the Pataguanset estuary (Connecticut) in relation to salinity and other tidal marsh invertebrates. **The Nautilus**, 99: 21-28.
- Fondo, E. N. & Martens, E. E. 1998. Effects of mangrove deforestation on macrofaunal densities, Gazi bay, Kenya. **Mangroves and Salt Marshes**, 2: 75-83.
- Kerwin, J. A. 1972. Distribution of the salt marsh snail (*Melampus bidentatus* Say) in relation to marsh plants in the Poropotank river area, Virginia. **Chesapeake Science**, 13: 150-153.
- Maia, R. C. & Tanaka, M. O. 2007. Avaliação de efeitos locais de espécies de mangue na distribuição **Iheringia, Série Zoologia**, 97: 379-382.
- Marques-Júnior, A. N.; Moraes, R. B. C. & Mourat, M. C. 2002. Poluição Marinha. Pp. 311 - 334. *In*: Pereira, R. C. & Soares-Gomes, A. (Eds). **Biologia Marinha**. Editora Interciência, Rio de Janeiro, Brasil, 382 p.
- Martins, A. M. de F. 2001. Ellobiidae – Lost between land and sea. **Journal of Shelfish Research**, 20: 441-466.
- McMahon, R. F. & Russell –Hunter, W. D. 1981. The effects of physical variables and acclimation on survival and oxygen consumption in the high littoral salt-marsh snail, *Melampus bidentatus* Say. **Biological Bulletin**, 161: 246-269.
- Merkt, R. E. & Ellison, A. M. 1998. Geographic and habitat-specific morphological variation of *Littoraria* (*Littorinopsis*) *angulifera* (Lamarck, 1822). **Malacologia**, 40: 279-295.
- Price, C. H. 1980. Water relations and physiological ecology of the salt marsh snail, *Melampus bidentatus* Say. **Journal of Experimental Marine Biology and Ecology**, 45: 51 - 67.
- Proffitt, C. E., Johns, K. M., Cochrane, C. B., Devlin, D. J., Reynolds, T. A., Payne, D. L., Jeppesen, S., Peel, D. W. & Linden, D. 1993. Field and laboratory experiments on the consumption of mangrove leaf litter by the macrodetritivore *Melampus coffeus* L. (Gastropoda: Pulmonata). **Biological Sciences**, 56: 211-222.
- Proffitt, C. E. & Devlin, D. J. 2005. Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove leaf litter degradation rates. **Marine Ecology Progress Series**, 296: 209-218.
- Primack, R. B. & Rodrigues, E. 2002. **Biologia da Conservação**. Editora Vida, Londrina, 328 p.
- Rietsma, C. S. & Valiela, I. 1988. Detrital chemistry, growth and food choice in the salt-marsh snail (*Melampus bidentatus*). **Ecology**, 69: 261-266.
- Robertson, A. I. 1991. Plant-animal interactions and

- the structure and function of mangrove forest ecosystems. **Australian Journal of Ecology**, 16: 433-443.
- Schaeffer-Novelli, Y. & Cintrón, G. 1986. **Guia para estudo de áreas de manguezal: estrutura, função e flora**. Caribbean Ecological Research, São Paulo, 25p.
- SEMACE, 2004. **Demonstrativo das ações de ordenamento, controle e monitoramento ambiental da atividade de carcinicultura no estado do Ceará**. SEMACE/SOMA, Fortaleza, Ceará, 240p
- Skilleter, G. A. & Warren, S. 2000. Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. **Journal of Experimental Marine Biology and Ecology**, 244:107-129.
- Sokal, R. R. & Rohlf, F. J. 1995. **Biometry**. 3th edition. W.H. Freeman and Company, New York, 88p.
- Suzuki, T.; Nishihira, M. & Paphavasit, N. 2002. Size structure and distribution of *Ovassiminea brevicula* (Gastropoda) in a Thai mangrove swamp. **Wetlands ecology and management**, 10: 265-271.
- Tanaka, M. O. & Maia, R. C. 2006. Shell Morphological Variation of *Littoraria angulifera* among and within mangroves in NE Brazil. **Hydrobiologia**, 559: 192-202.
- Tavares, D. S., Maia, R. C. & Rocha-Barreira, C. A. 2011. Contribuição de *Melampus coffeus* (Gastropoda, Ellobiidae) na degradação da serapilheira do médio estuário do rio Pacoti, Ceará, Brasil. **Iheringia, Série Zoologia**, 101:56-60.
- Vermeij, G. J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. **Ecology**, 53: 693-700.
- Walthew, G. 1995. The distribution of mangrove-associated gastropod snails in Hong Kong. **Hydrobiologia**, 295: 335-342.

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