

MOLLUSCAN DIVERSITY AND ABUNDANCE AMONG COASTAL HABITATS OF NORTHERN BRAZIL

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Abstract. There is a lack of basic information about the distribution and abundance of molluscs along the northern coast of Brazil. Many coastal habitats are under threat from development and uncontrolled exploitation of natural resources. Between 1999 and 2003 surveys were carried out along the Ajuruteua peninsula (north-eastern Pará state, Brazil) in mangrove forest, sandy beach and estuarine habitats. A total of 30 species of bivalves in 18 families and 19 species of gastropods in 15 families were recorded, and these numbers are similar to those obtained in surveys of intertidal molluscs in other parts of the northern and north-eastern coast of Brazil. Seasonal variation in molluscan density may be linked to rainfall and its effect on salinity as well as the effects of desiccation during the dry season. Molluscs have important ecological roles as well as economic importance in the region but habitat deterioration along with overexploitation may threaten this natural resource in the Ajuruteua Peninsula.

Resumo. Há uma falta de informações básicas sobre a distribuição e abundância de moluscos na costa norte brasileira. Muitos habitats costeiros estão ameaçados pelo desenvolvimento e exploração desenfreada de recursos naturais. Entre 1999 e 2003, levantamentos foram realizados na península de Ajuruteua (nordeste do Estado do Pará, Brasil) em manguezal, praias arenosas e habitats estuarinos. Um total de 30 espécies de bivalves em 18 famílias e 19 espécies de gastrópodes em 15 famílias foram registradas e estes números são similares aos obtidos em levantamentos de moluscos das entremarés em outras partes das costas norte e nordeste do Brasil. Variação sazonal em densidade de moluscos pode ser ligado a precipitação e seu efeito sobre salinidade bem como os efeitos de dessecação durante a estação seca. Moluscos têm papéis ecológicas significativas bem como importância econômica na região mas deterioração do habitat junto com sobre exploração pode ameaçar este recurso natural na Península de Ajuruteua. *Accepted 15 March 2005.*

Keywords: density, mangrove, Mollusca, number of species, tropical estuary.

INTRODUCTION

The documentation of the distribution and magnitude of biodiversity is an essential task for any program involving sustainable development and should be a fundamental part of each region's development (Mittermeier *et al.* 1998). Since coastal ecosystems are responsible for a large proportion of fish and shellfish yields, the evaluation and conservation of their biodiversity should protect their productivity. Practical conservation depends on obtaining reliable information about the distribution and abundance of the organisms present in each ecosystem or habitat. Recently, invertebrates have been attracting attention regarding their importance in terms of conservation and monitoring (New 1998). Despite their ecological

and economic importance, many species of molluscs are suffering from the threat of extinction (Kay 1995) and there is a distinct lack of basic information regarding their occurrence and conservation status in Asia, Africa and South America (Kay 1995).

In Brazil, the mangrove forests, as well as the estuaries and beaches associated with them, are coming under increased pressure from exploitation and development (Vannucci 1998). Recent estimates suggest that the most extensive and structurally complex mangroves remaining in Brazil are those found along the northern coast, especially between Belém (Pará state) and São Luís (Maranhão state) (Lacerda 1999). However, along the coast of the state of Pará, northern Brazil, the cutting of mangrove trees for charcoal production (Barros 2001), the uncontrolled collection of crabs and mussels (Blandtt & Glaser 1999, Glaser 2003), as well as badly planned urban development

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(Souza-Filho 2001) are examples of non-sustainable developments that threaten this habitat. For example, the removal of mangrove vegetation for fuel and fish-trap construction may increase the negative impact of erosion at naturally dynamic coastal settlements (Krause & Glaser 2003). Such activities may increase the loss of other natural resources since mangrove habitats provide shelter for the reproduction and development of many species of fish, shrimp, crab and mollusc (Neumann-Leitão 1995). In particular, many molluscs are economically important as food items, such as mussels, oysters, clams and some shipworm species (Grasso & Tognella 1995). Human populations in northern and north-eastern Brazilian coastal areas may depend heavily on certain molluscs as sources of food (Pereira-Barros & Pereira-Barros 1987), especially low-income households (Glaser 2003). Molluscs are also being increasingly used as biological monitors of pollution (Carvalho *et al.* 2000, Castro *et al.* 2000). Besides anthropogenic impacts, changes to the coastline and vegetation caused by erosion and sedimentation have been recorded (Cohen & Lara 2003) but little is known of their effect on the fauna of mangroves and adjacent beaches and estuaries.

The present study aims to provide data on molluscan diversity and abundance among coastal habitats from the Ajuruteua Peninsula, northern Brazil, that may be useful in the selection and planning of areas of conservation and help contribute to the evaluation of biodiversity in the region.

METHODS

The Ajuruteua Peninsula is located in the municipality of Bragança in the state of Pará, northern Brazil. The region and its habitats are described in detail in Barletta *et al.* (1998), Wolff *et al.* (2000) and Cohen & Lara (2003). *Avicennia* trees are the tallest vegetation and found on the landward side of the mangrove whereas *Rhizophora* occurs on the seaward side. In certain areas, a fringe of *Spartina brasiliensis* is found as a pioneer species at the shoreline. Large intertidal areas are submerged daily and are also subject to high levels of precipitation during the rainy season (Lacerda 1999). Bivalve species (except shipworms) from the sandy and muddy-sandy beaches were surveyed monthly at Canela Island (00°47' S, 46°43' W) between December 2001 and November 2002 using a 1-m² quadrat within which the substrate was dug to a depth of 30 cm and sieved through a 1-mm mesh. A random stratified sampling strategy was used in

which a first stage sampling area of 100 m² within the habitat was chosen randomly, and within this first stage area 10 random positions were chosen for placing the quadrats (second stage sampling units) on each sampling occasion. The survey of *Mytella guyanensis* took place in the mangrove at Canela Island between September 2001 and August 2002. Random stratified sampling of the mussel bed, which has a total area of 7500 m², was carried out using a 1-m² quadrat. Without disturbing the sediment, a total of 50 quadrats were visually inspected for the presence of *M. guyanensis* each month. The survey of shipworm species took place in an area measuring 100 m by 50 m delimited at the beach and mangrove at Canela Island, and at the Furo Grande mangrove (00°50' S, 46°38' W) between August and October 2002. Each area was divided into 10 adjacent, parallel transects measuring 10 by 50 m. On each sampling occasion, a single transect within each area was chosen randomly and searched for logs. All logs measuring between 18 and 23 cm in circumference were marked and numbered *in situ* and of these 10 were randomly selected for examination. The selected logs were cut so as to measure 30 cm in length. The logs were carefully opened and shipworms removed with a forceps. Density was expressed as the number of individuals per cm³.

Gastropods

In the mangrove and on the beach at Canela Island, a 100-m² area was selected randomly within which 5 *Rhizophora mangle* trees were selected randomly. In the mangrove, gastropods were counted on the roots and trunk of each tree in a 10-minute search, whereas on the beach dry tree trunks were examined in a similar fashion. Within *currais*, which are traditional wooden structures used to capture fish (Barletta *et al.* 1998), a 10-minute search was carried out within a randomly selected 100-m² area.

Identification and statistical analysis

Species were identified using Rios (1994) and Warmke & Abbott (1961) as well as other publications. In some cases identifications had to be verified by specialists.

One-way analysis of variance was used to compare mean bivalve density among monthly samples using suitable transformations ($\log x+1$, or x^2) where necessary. Where variances remained heterogeneous after transformation, tests were carried out using the Welch approximation. *Post-hoc* Tukey Honestly Significant Difference tests were carried out to compare pairs of sample means.

RESULTS

Molluscan diversity. A total of 30 species of bivalves distributed among 18 families was found among the three habitats, of which 6 species are from sandy beaches, 11 from the mangrove, and 13 from muddy-sandy habitats (Table 1). Species of economic importance are the mussels *Mytella* sp., the mangrove oyster *Crassostrea* sp., and the shipworms (Teredinidae). Other edible species such as *Lucina pectinata*, *Tagelus plebeius*, *Iphigenia brasiliana*, and *Anomalocardia brasiliana* appear to be of minor economic importance in the region.

A total of 19 gastropod species from 15 families was recorded, of which 3 were from the mangrove, 9 from sandy beaches, and 3 from muddy-sandy habitats (Table 2). A single specimen of the genus *Diodora* sp. was found washed up on the beach at Aju-ruteua. All members of the Thaididae were found in all three habitats. None of the gastropod species is considered edible by the inhabitants of the region.

Bivalve density. Significant differences in mean densities (number of individuals per m²) of the following bivalve species were found between months of the year at Canela Island: *Donax striatus* ($x^{0.3375}$ transformed

TABLE 1. List of bivalve species and their typical habitats, muddy-sandy substrate (MS), sandy beach (S) and mangrove (M), found in surveys on the Ajuruteua Peninsula.

Order	Family	Species	Edible	Habitat
Arcoidea	Arcidae	<i>Anadara brasiliana</i> (Lamarck, 1819)	N	S
Mytiloidea	Mytilidae	<i>Mytella falcata</i> (d'Orbigny, 1846)	Y	M
		<i>Mytella guyanensis</i> (Lamarck, 1819)	Y	M
Ostreoida	Ostreidae	<i>Crassostrea</i> sp. Sacco, 1897	Y	M
Veneroidea	Lucinidae	<i>Lucina pectinata</i> (Gmelin, 1791)	Y	MS
	Crassatellidae	<i>Crassinella lunulata</i> (Conrad, 1834)	N	S
	Mactridae	<i>Mactra isabelleana</i> d'Orbigny, 1846	N	S
		<i>Mulinia cleryana</i> (d'Orbigny, 1846)	N	S
	Tellinidae	<i>Tellina alternata</i> Say, 1822	N	MS
		<i>Strigilla carnaria</i> (Linnaeus, 1758)	N	S
		<i>Macoma constricta</i> (Bruguière, 1792)	Y	MS
	Donacidae	<i>Donax striatus</i> Linnaeus, 1767	N	S
		<i>Iphigenia brasiliana</i> (Lamarck, 1818)	Y	MS
	Psammobiidae	<i>Sanguinolaria sanguinolenta</i> (Gmelin, 1791)	N	MS
	Solecurtidae	<i>Tagelus plebeius</i> (Lightfoot, 1786)	Y	MS
	Veneridae	<i>Chione subrostrata</i> (Lamarck, 1818)	N	MS
		<i>Anomalocardia brasiliana</i> (Gmelin, 1791)	Y	MS
		<i>Protothaca pectorina</i> (Lamarck, 1818)	N	MS
<i>Petricola stellae</i> (Narchi, 1975)		N	MS	
Myoidea	Corbulidae	<i>Corbula caribaea</i> d'Orbigny, 1842	N	MS
	Myidae	<i>Sphenia antillensis</i> Dall & Simpson, 1901	N	M
Pholadina	Pholadidae	<i>Martesia striata</i> (Linnaeus, 1758)	N	M
		<i>Martesia fragilis</i> Verrill & Bush, 1890	N	M
		<i>Cyrtopleura costata</i> (Linnaeus, 1758)	N	MS
	Teredinidae	<i>Neoteredo reynei</i> (Bartsch, 1920)	Y	M
		<i>Lyrodus pedicellatus</i> (Quatrefages, 1849)	Y	M
		<i>Teredo</i> sp. Linnaeus, 1758	Y	M
		<i>Bankia fimbriatula</i> Moll & Roch, 1931	Y	M
Pholadomyoidea	Periplomatidae	<i>Periploma ovata</i> d'Orbigny, 1846	N	MS
	Lyonsiidae	<i>Anticorbula fluviatilis</i> (H. Adams, 1860)	N	M

TABLE 2. List of gastropod species and their typical habitats, muddy-sandy substrate (MS), sandy beach (S) and mangrove (M), found in surveys on the Ajuruteua Peninsula.

Order	Family	Species	Habitat	
Archaeogastropoda	Fissurellidae	<i>Diodora</i> sp. Gray, 1821	S*	
	Neritidae	<i>Neritina virginea</i> (Linnaeus, 1758)	MS	
Mesogastropoda	Littorinidae	<i>Littoraria angulifera</i> (Lamarck, 1822)	M	
		<i>Littoraria flava</i> (King & Broderip, 1832)	S	
		<i>Epitonium</i> sp. Röding, 1798	S	
	Calyptraecidae	<i>Calyptraea centralis</i> (Conrad, 1841)	S	
	Naticidae	<i>Natica marochiensis</i> (Gmelin, 1791)	S	
	Cassidae	<i>Phalium granulatum</i> (Born, 1778)	S	
	Bursidae	<i>Bufo naria bufo</i> (Bruguière, 1792)	S	
Neogastropoda	Thaididae	<i>Thais haemastoma</i> (Linnaeus, 1767)	S, MS, M	
		<i>Thais trinitatensis</i> (Guppy, 1869)	S, MS, M	
		<i>Thais coronata</i> (Lamarck, 1816)	S, MS, M	
	Columbellidae	<i>Anachis helena</i> Costa, 1988	MS	
	Nassariidae	<i>Nassarius vibex</i> (Say, 1822)	S	
	Melongenidae	<i>Pugilina morio</i> (Linnaeus, 1758)	MS	
	Olividae	<i>Olivella minuta</i> (Link, 1807)	S	
	Terebridae	<i>Terebra imitatrix</i> Aufenberger & Lee, 1988	S	
	Basommatophora	Ellobiidae	<i>Ellobium pellucens</i> (Menke, 1830)	M
			<i>Melampus coffeus</i> (Linnaeus, 1758)	M

* A single empty shell of *Diodora* sp. was found on the beach at Ajuruteua.

data; $F_{11,42.4} = 7.65$, $p < 0.001$), *Macoma constricta* ($x^{0.502}$ transformed data; $F_{11,42.4} = 17.1$, $p < 0.001$), *Lucina pectinata* ($\log_{10}(x+1)$ transformed data; $F_{11,42.4} = 9.91$, $p < 0.001$), *Anomalocardia brasiliiana* ($\log_{10}(x+1)$ transformed data; $F_{11,42.4} = 56.08$, $p < 0.001$), *Tagelus plebeius* ($\log_{10}(x+1)$ transformed data; $F_{11,42.2} = 8.264$, $p < 0.001$), *Mytella guyanensis* ($\log_{10}(x+1)$ transformed data; $F_{11,230.3} = 74.2432$, $p < 0.001$).

Variation in mean density of bivalves during the 12-month period is shown in Fig. 1. Density of *D. striatus* was lower during the drier months of the year (October–December) and was higher during the rest of the year (March–September). Significant differences occurred between February and all other months except December, October, and November (Tukey, $p < 0.05$). The densities of *M. constricta*, *L. pectinata*, and *A. brasiliiana* were generally low between December and July and were higher between August and November. Density of *M. constricta* was significantly greater in October and November than during the rest of the year (Tukey, $p < 0.05$). Density of *L. pectinata* was significantly greater in October in comparison

with December, February and the period between April and July (Tukey, $p < 0.05$). Densities of *A. brasiliiana* were significantly greater between August and November in comparison with the rest of the year. Similarly, the density of the mangrove mussel *M. guyanensis* was higher between the drier months (September–November), while densities in December, April and June were significantly lower than for other months. In contrast, the density of *T. plebeius* tended to be greater during the wetter months (January–April). In the case of *D. striatus*, *L. pectinata*, and *T. plebeius*, significantly lower densities were recorded in February, the month with the heaviest rainfall.

Overall, highest densities were recorded for *D. striatus* on sandy beaches, for *M. constricta* and *A. brasiliiana* on muddy-sandy beaches, and for *M. guyanensis* in the mangrove (Table 3).

Density of Neoteredo reynei (the mangrove shipworm)

There were no differences in the mean density of *N. reynei* between sampling dates, whereas there was

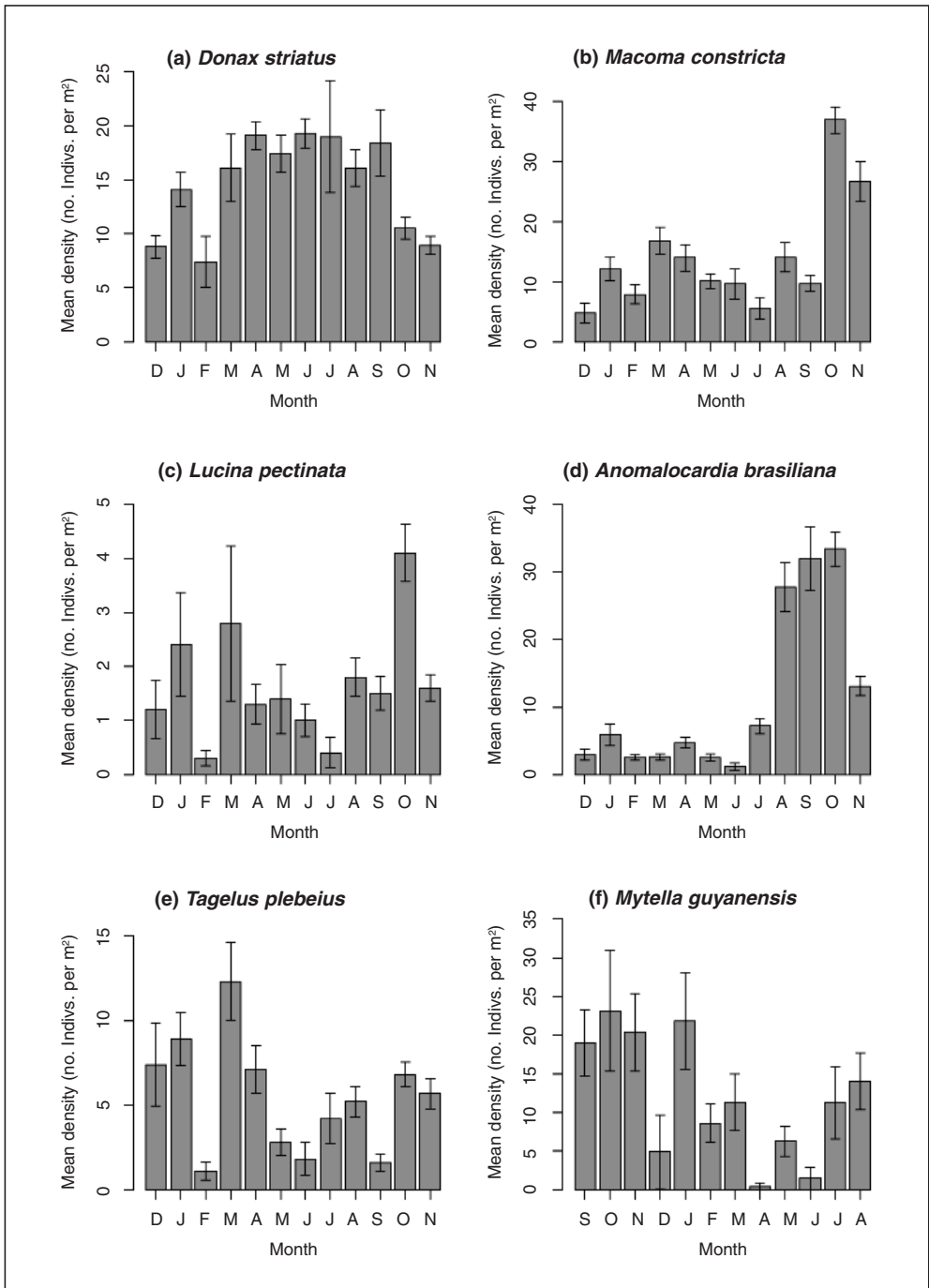


FIG 1. Mean density (\pm s.e.) of bivalve species at Canela Island between December 2001 and November 2002. Note *Mytella guyanensis* was sampled at the Canela mangrove forest between September 2001 and August 2002.

TABLE 3. Summary of 12 months data on the density (mean \pm sd) of bivalve species from Canela Island. n is the total number of 1-m² quadrats examined during the study.

Species	Minimum	Mean \pm sd	Maximum	n
<i>Donax striatus</i>	1	14.6 \pm 8.9	57	120
<i>Macoma constricta</i>	0	14.0 \pm 11.3	46	120
<i>Lucina pectinata</i>	0	1.6 \pm 2.3	16	120
<i>Tagelus plebeius</i>	0	5.4 \pm 5.5	31	120
<i>Anomalocardia brasiliiana</i>	0	11.3 \pm 13.7	69	120
<i>Mytella guyanensis</i>	0	11.9 \pm 16.7	162	600

a difference in density between the three habitats (Tables 4 & 5). Mean densities of *N. reynei* in logs from the mangrove at Canela Island were significantly greater than those from the beach at Canela (Tukey, $p < 0.05$) (Table 5). There was no difference between densities of *N. reynei* from the mangroves at Canela and Furo Grande (Table 5). Furthermore, the interaction between habitat and date was not significant

(Table 4). Mean densities of *N. reynei* ranged from 0.0015 to 0.0219 individuals per cm³ (Table 5), corresponding, to estimates of between approximately 3 and 52 individuals colonizing a 10 x 30 cm log (2356.2 cm³), for example. *Bankia fimbriatula* was rarely encountered at Canela Island and did not occur at the Furo Grande mangrove. Mean densities of *B. fimbriatula* were low (0.0002–0.0034 individuals per cm³).

TABLE 4. Analysis-of-variance summary of $x^{0.135}$ -transformed data on density (number of individuals per cm³) of the shipworm *Neoteredo reynei* from mangrove and beach habitats at Canela Island and the Furo Grande creek on the Ajuruteua Peninsula between August and October 2002.

Source of error	df	Sum Squares	Mean Square	F	p
Month	2	0.02	0.01	0.27	n.s.
Habitat	2	0.42	0.21	5.22	<0.001
Interaction Month X Habitat	4	0.16	0.04	0.97	n.s.
Residuals	81	3.24	0.04		

TABLE 5. Density (number of individuals per cm³) of *Neoteredo reynei* in logs collected from mangrove and beach habitats at Canela Island (CN) and the Furo Grande creek (FG) on the Ajuruteua Peninsula between August and October 2002. For all samples the number of logs examined (n) was 10.

Sampling date	Habitat	Min	Mean \pm s.e.	Max
August	Mangrove CN	0.0021	0.0085 \pm 0.0019	0.0186
	Beach CN	0.0000	0.0029 \pm 0.0013	0.0103
September	Mangrove FG	0.0000	0.0132 \pm 0.0045	0.0362
	Mangrove CN	0.0000	0.0219 \pm 0.0149	0.1550
	Beach CN	0.0000	0.0051 \pm 0.0022	0.0209
	Mangrove FG	0.0000	0.0126 \pm 0.0035	0.0348
October	Mangrove CN	0.0009	0.0047 \pm 0.0017	0.0184
	Beach CN	0.0000	0.0015 \pm 0.0003	0.0035
	Mangrove FG	0.0000	0.0040 \pm 0.0013	0.0128

TABLE 6. Mean density of gastropods on *Rhizophora mangle* in the mangrove on Canela Island. The number of trees searched was 25.

Species	Minimum	Mean density \pm s.e.	Maximum
<i>Littoraria angulifera</i>	0	9.68 \pm 1.89	33
<i>Melampus coffeus</i>	0	0.32 \pm 0.21	5
<i>Thais trinitatensis</i>	0	7.24 \pm 1.72	30

Gastropod density. Three species were frequently encountered on leaves, trunk and branches of the red mangrove *Rhizophora mangle*, *Littoraria angulifera*, *Melampus coffeus*, and *Thais trinitatensis* (Table 6). At the beach habitat, *L. angulifera* and *Littoraria flava* were the most frequent gastropods present on the trunks and roots of dead mangrove trees (Table 7).

At fishing *currais*, the mean density (\pm s.e) of *Thais trinitatensis* was 61.8 (\pm 1.5) individuals per 100 m². Counts at five different 100 m² areas varied between 57 and 65 individuals, indicating a high density of this species for this particular habitat.

DISCUSSION

Surveys of bivalves from soft-sediment coastal habitats in Brazil reveal similar numbers of species and families to those found in the present study. At the Mundaú-Manguaba lagoon complex in Alagoas state, 18 species from 13 families were found (Silva & Pereira-Barros 1988). At the Paraíba do Norte estuary, Paraíba state, 8 (+7 shell only) species of bivalves in 5 families and 8 (+10 shell only) gastropods from 7 families were encountered during a survey of the intertidal area of the Ilha da Restinga (Dijk 1980). A survey of the Pirapama river, southern Pernambuco state, found 7 bivalves in 5 families and 7 gastropod species in 7 families (Silva Mello 1993). An extensive initial survey (Matthews *et al.* 1977) of the Ilha de São Luís, Maranhão state, in the 1970s revealed a total of 32 bivalve species in 15 families, while 29 gastropod spe-

cies in 17 families were recorded. The higher diversity, especially in terms of gastropods, in comparison with the Bragança region, may be due to sampling in subtidal areas in São Luís. A later study, between 1982 and 1983 (Costa & Silva Mello 1983/84), restricted to the intertidal area of three sections of an estuary in the south-eastern part of São Luís Island, showed a lower overall diversity. A total of 11 gastropods in 8 families and 8 bivalves in 6 families was found. An offshore survey in March 1984 from the same area (Silva Mello & Costa 1993) found 12 bivalves in 8 families and 24 gastropods in 10 families. The intertidal areas of the Santa Cruz Canal (Pernambuco state) were found to contain 12 species of bivalve and 15 species of gastropod. However, considering the infralittoral region, the number of species increased to 144 in 56 families, including 2 species of Scaphoda (Silva Mello & Tenório 2000).

Thus considerably greater molluscan species richness is recorded when sampling both intertidal and subtidal areas. Fewer species of molluscs are found in mangroves from the Bragança region in comparison with other mangroves. Ashton *et al.* (2003) found 44 molluscan species, mostly gastropods, in a well-conserved mangrove in Sarawak, Malaysia, and a similar study in a mangrove in southern Thailand recorded 33 molluscan species (Macintosh *et al.* 2002). At a Venezuelan mangrove, Marquez & Jimenez (2002) found 45 species (22 gastropods, 15 bivalves and 8 chitons). A review of Brazilian mangroves listed 10 gastropod species and 22 bivalve species (Aveline 1980).

TABLE 7. Mean density of *Littoraria angulifera* and *L. flava* on dry tree trunks from the beach habitat at Canela Island.

Species	Minimum	Mean \pm s.e.	Maximum
<i>Littoraria angulifera</i>	0	8.76 \pm 1.53	39
<i>Littoraria flava</i>	2	10.64 \pm 1.31	25

Seasonal changes in density

Concentrations of physiologically important cations (K⁺, Mg⁺⁺, Ca⁺) in a creek in the Caeté mangrove estuary were higher during the dry season, and were influenced by tidal state, evaporation, rainfall and groundwater input (Cohen *et al.* 1999). Through phytoplankton uptake, seasonal and diurnal variation in cation concentrations (Cohen *et al.* 1999), as well as dissolved organic carbon and dissolved inorganic nitrogen (Dittmar & Lara 2001), may occur. Wolff *et al.* (2000) found that in the Caeté estuary energy flow appears to cycle within the mangrove forest itself and little material export occurs. However, when the supply of inorganic nutrients exceeds the demand of the mangrove trees and epibenthos, tidal outwelling of nutrients and dissolved organic carbon can occur, mediated by porewater flow into the creeks and estuary (Dittmar & Lara 2001). Cation and nutrient dynamics may cause seasonal variation in infaunal bivalve densities through regulation of food (organic matter and phytoplankton) and physiological tolerance to cation variation. However, experimental enrichment of sediments with mangrove detritus showed a negative effect on macrobenthic species richness and the total number of individuals, probably due to increasing concentrations of tannins associated with the detritus that may interfere with colonization (Lee 1999).

Salinity values in the Bragança region are highest at the end of the dry season (December) and lowest during the wet season (between the end of March and May) (Cohen *et al.* 1999, Marques-Silva 2002) and several species showed marked seasonal variation in density. The survival rate of *M. guyanensis* is over 80% at salinities between 5 and 35 (Leonel & Silva 1988) and it is thus considered a euryhaline species. However, mortality is greater at very low or very high salinities (Leonel & Silva 1988). Thus, mortality in sedentary or sessile bivalves may occur during the wet season in places where rain water collects, as well as during dry periods when evaporation may cause porewater to become hypersaline. In the Mundaú/Manguaba lagoon complex, the occasional disappearance of stocks of *M. falcata* has been related to almost zero salinity due to flooding of the lagoon during the rainy season (Pereira-Barros 1987). Mobile molluscs, however, may change their behavior to avoid unfavorable conditions. During the wet season, the neogastropod *Pugilina morio* is rarely found and appears to bury itself in the sediment, only to reappear soon after the rains end (Matthews-Cascon *et al.* 1990a). Tolerance to variation in salinity allows the shipworm *Neoteredo*

reynei to colonize wood along the estuary of the Tocantins river in waters ranging from 0 to 14 (Reis 1995).

Some species may have seasonal reproductive cycles that influence recruitment and density. Egg capsules of *Neritina virginea* on red mangrove leaves from Ceará state were most abundant during the dry season (Matthews-Cascon & Xavier-Martins 1999). The density of *Tagelus peruvianus* was highest between April and November at two sites from the Gulf of Nicoya, Costa Rica (Rojas *et al.* 1988), and the increase in density was attributed to increased recruitment since greater numbers of smaller individuals were found during this period. During a three-year study of *Anomalocardia brasiliana* in Guadeloupe, only a single successful recruitment event was recorded and this was accompanied by a decrease in adult density (Monti *et al.* 1991). At two sites on the Cururuca estuary (Maranhão state) the mean density of *A. brasiliana* ranged from 855 to 2613 individuals per m². Based on condition index values, the clams appear to have spawned in both areas at least twice a year and in both dry and wet seasons but without any marked effect on density (Fernandes *et al.* 1983).

A decrease in the proportion of lipids, proteins and caloric content occurred in *Mytella guyanensis* from Costa Rica during the reproductive period due to gamete production and spawning (Cruz & Vila-lobos 1993). Such variation in condition as a result of reproductive effort could lead to mortality and changes in density, especially during unfavorable environmental conditions.

The density of *Mytella falcata* in two locations on the Cururuca estuary (Maranhão state) varied between 300 and 9000 individuals per m². However, there was a steady decrease in density during the study period until stocks at both sites disappeared completely in November 1981 and, despite monitoring up to June 1982, stocks did not subsequently reappear (Fernandes *et al.* 1983). The authors suggested that disease or predation may have been responsible for the decline. The presence of a protoctistan parasite in a related species *Mytella guyanensis* (Azevedo & Matos 1999) may cause mortality and sterility in adults.

The uncontrolled exploitation of *M. falcata* in the Caeté mangrove estuary causes rapid depletion of stocks that only reappear again after 10 months (Marques-Silva 2002). Increased harvesting of *Tagelus peruvianus* in the Gulf of Nicoya due to a greater demand during the tourist season may have caused a reduction in density during that period since clam stocks recovered afterwards (Rojas *et al.* 1988).

Habitat complexity and environmental impacts. The effects of erosion and sedimentation on coastal vegetation may affect molluscs and other benthic organisms. Areas of mangrove may die due to sand invading and asphyxiating the vegetation (Cohen & Lara 2003). Mussels and certain epibenthic gastropods may disappear from degraded areas. However, the trunks and roots that remain for some time in the substrate provide habitat for *Martesia*, Teredinidae, *Neritina* and *Littoraria*. Compacted peat remaining from degraded mangrove areas is a habitat for burrowing Pholadidae. Changes in sediment characteristics due to currents and wave action may cause the dislocation of banks of *Mytella* and other species that burrow in soft intertidal sediments.

At the Cururuca estuary, Maranhão state, oyster (*Crassostrea rhizophorae*) density was considered low in comparison with other studies, and substrate availability did not appear to be a limiting factor (Fernandes *et al.* 1983). In the Bragança region, adult oysters are not commonly encountered, despite a ready abundance of larvae settling during the dry season (Marques-Silva 2002) and abundant available substrate in the form of mangrove roots. Predation by small mammals (Fernandes 1991), birds, and humans may have eliminated many oyster populations and reduced others to deeper waters where predator access is difficult. There appear to be three *Crassostrea* species along the Brazilian coast that overlap considerably in their habitat preferences (Lapègue *et al.* 2002). Comparisons of oyster DNA sequences by one of us (CHT) show that the oysters from the Ajuruteua Peninsula are not *C. rhizophorae* and further studies are being carried out to establish their identity, thus our list refers to oysters as *Crassostrea* sp. for the moment.

Deposit-feeding molluscs of the intertidal zone of beaches of the São Sebastião Canal (São Paulo state) were most abundant where highest silt-clay and organic matter content values were recorded (low flow and high nutrient levels), whereas suspension feeders were correlated with very fine, homogeneous sediments (little active sediment transport and stable flow) and with lower salinities associated with sewage outflow (but also greater amounts of organic matter) (Aruda *et al.* 2003). In Bragança, sheltered beaches with muddy sediment have the highest number of species of molluscs, both suspension-feeders (e.g., *Anomalocardia*, *Tagelus*) as well as deposit-feeders (e.g., *Tellina*, *Macoma*) in comparison with exposed sandy beaches where the bivalve suspension-feeder (*Donax*) and its gastropod predator (*Natica*) were the predominant components of the fauna.

In the Paraiba estuary, the density of *Mytella guyanensis* varied between 1.7 and 7.8 individuals per m²; substrates with a higher proportion of fine sand and a higher water content had lower densities of mussels (Nishida & Leonel 1995). Density of *Anomalocardia brasiliiana* in a mangrove lagoon in Guadeloupe ranged between 20 and 1370 individuals per m², and the species was not found in anoxic parts of the lagoon where decaying vegetation had accumulated (Monti *et al.* 1991).

Gastropod density in a mangrove in southern Thailand was negatively correlated with the number of senescent leaves, mangrove tree diversity, and associate species number, but was positively correlated with sapling species number and diversity as young leaves on saplings may provide a better food source or habitat (Ashton *et al.* 2003). High diversity and abundance of *Littoraria* species were observed at one location where plantation trees were still very young, low numbers were observed at an older plantation, and they were absent in mature forest. In contrast, pulmonate snails (Ellobiidae) tended to be associated with mature forest, upper shore and back mangrove (Macintosh *et al.* 2002). Koch & Wolff (1996) found that juveniles of *Thais kioskiformis* from the Golfo de Nicoya (Costa Rica) were more abundant inside the forest than adults, which were more abundant at the mangrove edge, and cited reduced rates of desiccation and predation inside the forest as a possible explanation.

In a subtropical Australian mangrove, reduction of pneumatophore density and epiphytic algae cover was associated with significantly lower abundance and diversity of molluscs relative to control areas. The presence of pneumatophores and algae may reduce flow rates near the bottom causing deposition of material suitable as food for deposit feeders and/or providing protection from predatory fish (Skilleter & Warren 2000). The presence of epibenthos, such as oysters on trees in an Australian mangrove, may provide habitat for other molluscs (Minchinton & Ross 1999).

Among members of the mangrove epibenthos in the Caeté estuary, the predators (the gastropod *Thais* and a carnivorous crab) appear to make a small contribution to the overall epibenthic energy budget. However, their role in regulating prey species (other crabs and teredinid bivalves) may be significant, though a lower food supply in the creek as opposed to the mangrove forest may account for lower productivity of *Thais* in the former (Koch & Wolff 2002). Although present in all major habitats, we found high densities of *Thais* at fishing *currais* where the remains of fish

were readily available. *Thais* may also feed on barnacles encrusted on mangrove roots and predation pressure by these snails may influence mangrove root growth by cleaning the aerial root system (Koch & Wolff 1996).

Shipworms (Teredinidae) are highly specialized wood-boring bivalves (Turner & Johnson 1971). The teredinids, along with fungi, are important decomposer organisms in mangroves, but differences in the time taken to completely break down the wood varies with the nutrient status of the water, which may be important for bacterial symbionts, and differences in tidal fluctuations that may limit the development of certain species due to desiccation (Kohlmeyer *et al.* 1995). Leonel *et al.* (2002) recorded *Neoteredo reynei*, *Teredo bartschi*, *Nausitoria fusticula*, and *Bankia fimbriatula* from the Mamanguape river estuary, Paraíba state. Lampert (2000) found *Neoteredo reynei*, *Bankia gouldi*, and *Teredo bartschi* in the mangrove of the Furo Grande, Ajuruteua Peninsula. *N. reynei* was the most abundant species, accounting for between 94% and 100% of the density and over 99% of the biomass in examined logs. Overall density ranged from 0.00054 to 0.00584 individuals per cm³ (Lampert 2000); these values are generally lower than the ones we report for *N. reynei*.

Anatomical features of *N. reynei*, the most common shipworm in the Bragança region, indicate that this species primarily consumes wood and to this end depends on nitrogen-fixing and cellulase-producing bacteria in specialized pouches in the gill (Morães & Lopes 2003). Reduced dependence on suspended food allows *N. reynei* to occupy wood in parts of the mangrove that are less frequently inundated by the tide.

Economic importance. Many molluscan species along the northern coast of Brazil are of economic importance. The mussels *Mytella* sp. and the mangrove oyster (*Crasostrea* sp.) are among the most important of these (Dijck 1980, Costa & Silva Mello 1983/84, Silva & Pereira-Barros 1988). Pereira-Barros & Pereira-Barros (1987) show that around 40% of households from two districts near Lagoa Mundaú (Alagoas state) depend on the extraction of *Mytella falcata*. Commonly, coastal communities depend on such resources as a direct source of food. Glaser (2003) showed that of the molluscan species collected from the mangrove at Bragança, over 40% of households collected *Mytella* and shipworms (Teredinidae) for subsistence production, whereas less than 10% com-

mercially harvest these species. In the north-east of Brazil, *Anomalocardia brasiliiana*, *Chione pectorina* and *Tagelus plebeius* are also commercially exploited where abundant (Dijck 1980, Silva & Pereira-Barros 1988). There is growing interest in aquaculture so mangrove mussels and oysters are potential target species (Mora & Alpizar 1998, Proença *et al.* 2001).

In Bragança, gastropods are rarely acceptable as food items for humans (Glaser 2003), although *Pugilina morio* is considered edible in Paraíba state (Matthews-Cascon *et al.* 1990a) but not in Maranhão (Costa & Silva Mello 1983/84). *Neritina virginea* is an abundant species in estuarine areas (Dijck 1980), the shells of which have highly diverse polymorphic patterns and are used to make jewelry (Matthews-Cascon *et al.* 1990b).

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