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Sediment macrobenthos of mangrove flats at Inhaca Island, Mozambique

José GUERREIRO[1], Sara FREITAS[1], Pedro PEREIRA[1], José PAULA[1] & Adriano MACIA Jr.[2]
[1]*Laboratório Marítimo da Guia (IMAR) Faculdade de Ciências da Universidade de Lisboa*
Estrada do Guincho 2750 Cascais - Portugal - Fax 351 1 4869720
[2]*Departamento de Ciências Biológicas Faculdade de Ciências da Universidade Eduardo Mondlane*
CP 257 Maputo - Moçambique

Abstract : The composition of macroinvertebrate communities in the mangroves of Inhaca island, Mozambique, was analysed. Faunistic samples and sediment cores were collected in order to assess relationships between grain-size distribution, organic matter, phytopigments and the species distribution in two different mangroves: Saco and Ponta Rasa. Results showed the dominance of medium and fine sands rather than colloidal sedimentation, which is originated from the island itself. A clear zonation of benthic organisms is a function of several combined environmental factors which contribute to define mangrove communities. Here they are clearly dominated by polychaeta, in a similar situation as in the SW Madagascar mangroves. Grain-size, together with salinity and ground water were found to be the major factors affecting the macrobenthos distribution. The Saco mangrove constitutes a southern example of a subtropical mangrove with high diversity and production. The Ponta Rasa mangrove may be considered as an atypical one, or an extreme situation to subtropical mangrove, in which diversity is very low and several key-species are lacking. The differences between these two mangroves suggest that microenvironmental conditions, namely water content of sediments and phytobenthos, are determinant to the richness and faunal diversity of these ecosystems.

Résumé : *Macrobenthos des sédiments des mangroves de l'île d'Inhaca, Mozambique.*
Une étude détaillée de la macrofaune des sédiments, de la granulométrie, de la teneur en matière organique et des phytopigments a été faite dans deux mangroves différentes : Saco et Ponta Rasa. Les résultats indiquent une dominance des sables fins et moyens, au lieu des vases, ceci en raison de la nature sédimentaire de l'île. Une zonation très nette des organismes macrobenthiques a été établie, résultant de la combination des divers facteurs qui contribuent à la définition des communautés des mangroves. La granulométrie ainsi que la salinité, l'eau phréatique et le phytobenthos, sont les facteurs déterminants pour la distribution du macrobenthos où les polychètes sont dominantes comme cela a déjà été décrit pour le SW de Madagascar. La mangrove du Saco apparaît comme l'exemple de mangrove subtropicale le plus méridional d'Afrique orientale, avec une diversité et une production élevées. La mangrove de Ponta Rasa est considérée comme atypique, représentant une situation extrême de faible diversité, où sont absentes beaucoup d'espèces considérées comme caractéristiques des mangroves. Les différences faunistiques entre les deux mangroves seraient le résultat de conditions microenvironnementales déterminantes pour la richesse et la diversité de la macrofaune de ces écosystèmes, notamment la teneur en eaux des sédiments et le phytobenthos.

Keywords : mangroves, macrobenthos communities, sediment, phytobenthos.

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Introduction

Both eastern and western African mangroves received lately a good deal of descriptive attention in literature, focusing on several important aspects of economic, ecological and scientific relevance. As highly productive ecosystems, their role in providing breeding and "nursery" areas, their connection with adjacent marine ecosystems, namely seagrass beds, and their role in the stabilisation of coasts is well known (Howell & Semesi, 1982). John & Lawson (1990) stated that mangroves, which are constantly influenced and disturbed by seasonal freshwater and diurnal tidal flooding, exhibit a low species diversity and a high productivity, the huge organic production being exploited by many marine species, especially fishes and crustaceans that enter the mangrove environment as juveniles and return to the sea as adults for reproduction. Nevertheless, Thollot & Kulbicki (1988) and Thollot (1992) considered that these relationships are not fully demonstrated for fishes.

Although mangroves occur mainly in Tropics, they can sometimes be found outside these areas, on coasts along which warm oceanic streams occur, suggesting that water temperature has a determinant role in limiting the mangrove areas. Thus, as stated by Berjak *et al.* (1982), eastern African mangroves between Inhaca island (Mozambique) and Port Elizabeth (South Africa) could be considered as atypical because they are subtropical and lack the richness and diversity of "classical" mangroves. Inhaca island by its geographical location near the austral limit of the tropical eastern African fauna and flora and the septentrional limit of the southeast African coastal fauna and flora, is particularly relevant to assess the understanding of eastern African ecosystems.

Inhaca island, which extends 12.5 km nearby Maputo bay, is part of a large littoral fringe, developing from South to North in the SW coast of southern Africa. Although this area is located in a subtropical area (26° S), Macnae & Kalk (1969) and Lopes (1973) considered its climate as tropical. This is probably the consequence of both the influence of the warm current of the Mozambique channel, and of the atmospheric circulation from the East, which always dominates during the year. This atmospheric influence creates a mixing between the Mozambique warm current and cooler water masses coming from the South, thus causing sedimentation responsible for several north-pointing spits along the east coast of Africa, at Inhaca island.

This paper describes the composition of macrobenthic communities of mangroves at Inhaca island, and their interrelationships with sediment as defined by size, mineral composition, pigments and organic matter content. The results are then compared with a previous work by Macnae & Kalk (1969) on the mangroves' benthic epifauna of Inhaca island and also with studies on similar ecosystems at Madagascar (Kiener, 1965, 1973; Thomassin, 1978).

Material and Methods

Field techniques and sampling areas

At Inhaca, mangroves are restricted to sheltered bays in the northern and southern parts of the island, basically identical, and along a water stream on the West coast (Kalk, 1954; Freitas, 1960; Macnae & Kalk, 1969). An intensive survey has been made along two transects established in the mangroves of Saco da Inhaca (MIM/I) and Ponta Rasa (MIM/II) (Fig. 1) during low tides of June and July 1993.

Along each transect seven sampling points were defined according to biological and sediment characteristics. At the Saco mangrove, sampling points were defined as follow: **#0m**= upper level near terrestrial vegetation; **#RO**= presence of *Avicennia marina* and *Saccostrea cucullata* (on the roots); **#R**= presence of *A. marina*; **#VA**= a large muddy area with a visible fraction of sand; **#ADT**= high density of *Dotilla fenestrata* in crowds, within a sandy area; **#MW**= middle water - a sandy/muddy area; **#LW**= the upper limit of low water - a muddy area (low water line). At the Ponta Rasa mangrove sampling points were defined as follow: #**1**= upper limit of *Avicennia* sp.; #**2**= presence of *Rhizophora mucronata*, *Uca annulipes* and *Terebralia palustris*; #**3**= muddy area with *R. mucronata*; **4**= extremely dense association of *R. mucronata* and *A. marina*; #**5**= lower limit of the *Rhizophora/Avicennia* association in a sandy area; #**6** and #**7**= sandy platform towards middle water and low sea water, respectively.

To study infaunal macrobenthos (≥ 1 mm) in each station a total area of 0.25 m^2 (subdivided in four identical subsamples) was sampled using a PVC core or a spade, at a depth of 20 cm. The material was sieved through a 1 mm mesh-sieve, fixed in 10% formaldehyde-seawater solution and returned to the laboratory for sorting. Epibenthic species not sampled by these techniques were video-recorded for further identification/counting (*i.e. Uca* spp., *Cardisoma carnifex*, *Dotilla fenestrata*). A 50 g sediment sample was also taken with a 5 cm depth core and frozen to study the grain-size distribution, the organic matter content and pigments. Salinity and temperature of superficial sediments were measured using a refractometer and a thermometer, respectively.

Laboratory analysis

For grain-size analysis mud (<62 μm, >4ø), sand (62 μm-2000 μm, 4ø-1ø) and gravel (>2000 μm, <1ø) were separated by wet sieving (Buller & McManus, 1979 *in* Cancela da Fonseca *et al.*, 1987). The total organic matter content (OM $g.m^{-2}$) of the sediment was estimated by loss on ignition (500°C, 24 h period) after estimating the sediment water content (% H_2O), by drying for 24 h at 70°C.

The concentration of sediment phytopigments was evaluated by spectrophotometry, after 24 h cool extraction in 90% acetone. Concentrations ($\mu g.g^{-1}$ dry sediment) of

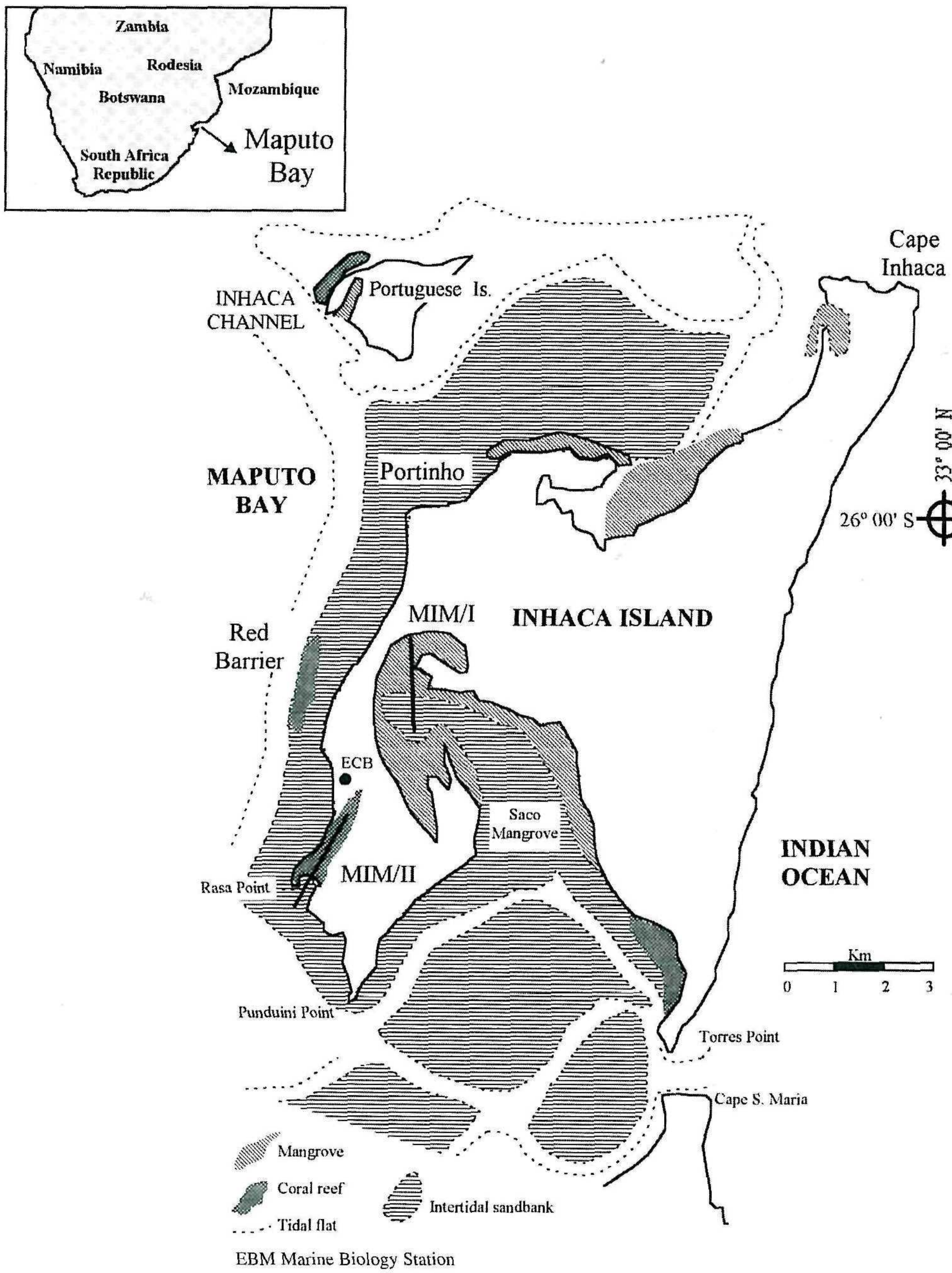

Figure 1. Localisation of transects MIM/I (Saco mangrove) and MIM/II (Ponta Rasa mangrove) at Inhaca island (Mozambique).

Figure 1. Localisation des radiales MIM/I (mangrove de Saco) et MIM/II (mangrove de Ponta Rasa) sur l'île d'Inhaca (Mozambique).

chlorophyll *a* (Chl.*a*), phaeopigments (Phaeop.), carotenoids (Car.), and chlorophyll *b* and *c*, were calculated from the modified equations from Lorenzen (Chl. *a*, Phaeop.), Parsons and Strikland (Car.) and Jeffrey and Humphrey (chl.*b* and *c*) (Plante-Cuny, 1974 *in* Cancela da Fonseca *et al.*, 1987). The Margalef index estimating pigment diversity and Chl *a* % degradation were used together (Plante-Cuny, 1978) to calculate the Moss index, as an indicator of productivity (Moss, 1967 *in* Cancela da Fonseca *et al.*, 1987). Phytopigment amounts per unit area ($mg.m^{-2}$) were deduced from phytopigment concentrations ($mg.g^{-1}$) by using a sediment specific weight estimate (Cancela da Fonseca *et al.*, 1987).

Data Analysis

As no quantitative studies have been done on macrobenthic communities in the mangroves of Inhaca island, a species/area curve was drawn for all the sampling stations, in order to provide a very simplistic way to find whether the number of a species is evenly represented in samples or not (Barbour *et al.*, 1980). The basic assumption is that the size of the sample is adequate when the slope of the curve reaches an asymptote.

Shannon-Weaver diversity index and Pielou evenness were also calculated (Daget, 1979). Data matrices containing sediment features and numbers of individuals per species and per station were used singly or in combination. Cluster analysis (Bravais-Pearson correlation coefficient) was used to define ecological patterns from biological and sediment characteristics (Pielou, 1984). Central value analysis (CVA) was also carried out to superimpose species' distribution and environmental gradients (Salen-Picard, 1987). In order to summarise the information, the principal component analysis (PCA - Sneath & Sokal, 1973) was used.

As there was a very clumped distribution of the abundance of species, it was not possible to perform a direct multivariate analysis (PCA and cluster analysis), and data were analysed in two steps. First, all the sediment components expressed in Table 1 were used as variables. Second, the eigenvalues from the first principal component were used as the new variables to perform a central value analysis (CVA) (Salen-Picard, 1987), in order to superimpose the distribution of species along an environmental gradient as defined by the first axis of the PCA. As a matter of fact, the first component extracts most of the variance due to the sediment characteristics and therefore represents the most probable gradient explaining the ecological variation along transects.

According to such an approach, it was therefore possible to relate all the sediment parameters and the biological features of the mangrove communities (*e.g.* abundance, diversity index, evenness) using PCA and cluster analysis, and to relate species onto the principal gradient axis by using CVA.

Results

Sediment parameters

The analysis of grain-size distribution within the Saco Mangrove - MIM/I (Table 1) indicates that the substratum of all stations associated with the transect is mainly made of medium and fine sands. In spite of being relatively similar

Table 1. Values of sediment, physico-chemical and biological parameters at the Saco mangrove (MIM/I).
Tableau 1. Valeurs des paramètres du sédiment, chimiques et biologiques à la mangrove du Saco (MIM/I).

			Sampling Stations - Transect MIM I						
Parameters	Unit	Abbreviation	Om	R	RO	VA	ADT	MW	LW
Temperature	°C		-	27.8	-	27.9	23.0	24.0	24.0
Salinity	‰		-	-	-	35	35	40	40
Organic Matter	$g.m^{-2}$	OM	152.0	234.0	258.4	127.2	99.0	65.6	139.5
% Water Content	%	%WATER	23.5	21.4	23.6	20.0	17.8	18.0	21.8
Chlorophyll *a*	$mg.m^{-2}$	Chl a	39.65	145.55	169.51	115.69	42.52	46.14	106.83
Chlorophyll *b*	$mg.m^{-2}$	Chl b	22.59	1.27	1.30	0.00	0.00	0.00	0.82
Chlorophyll *c*	$mg.m^{-2}$	Chl c	6.69	18.72	26.33	16.28	8.43	7.27	19.13
Phaeopigments	$mg.m^{-2}$	PHAEO	22.74	43.13	81.95	45.35	20.16	26.50	47.36
Carotenoids	$mg.m^{-2}$	CAR	39.99	178.55	158.06	102.59	32.13	38.23	104.05
Margalef Index		MARG	2.31	2.34	2.34	2.17	2.22	2.34	2.10
Moss Index		MOSS	1.09	1.21	1.11	1.22	1.22	1.18	1.07
% of Chlorophyll *a*	%	%DEGR	46.8	27.0	41.3	34.5	40.3	47.1	38.1
Gravel	%	GRAV	0.0	0.5	0.3	0.4	0.4	3.2	12.0
Very Coarse Sands	%	VCS	0.0	0.4	0.1	0.3	0.4	0.7	1.4
Coarse Sands	%	CS	3.0	11.1	13.9	11.2	7.2	5.3	4.4
Medium Sands	%	MS	35.3	61.7	44.6	59.9	67.6	67.9	67.5
Fine Sands	%	FS	35.4	24.3	36.2	26.2	23.9	21.3	13.6
Very Fine Sands	%	VFS	5.0	1.5	2.3	1.3	0.3	0.8	0.8
Silt and Clay %		SILT	1.2	0.5	2.6	0.7	0.2	0.8	0.4
Diversity Index		bits/ind.	1.56	0.42	3.00	2.80	1.24	2.03	3.61
Evenness Index			0.78	0.13	0.72	0.72	0.48	0.52	0.62
Abundance	$ind.m^{-2}$		88	1732	520	308	836	1120	5424

between stations, the fraction of coarser sediments increases towards the low water line of the spring tides (#LW), where the highest value of gravel was recorded (12%). Values of organic matter content are highest in stations #RO, #R and #0m, where very fine sand and mud dominate (low grain size) and are also correlated with higher percentages of pore water. Values of chlorophyll and pigments, together with the Moss index, seem to indicate that these tidal flats are a highly phytobenthic productive area, as the percentage of degraded Chl. *a* is always <50%. Levels of chlorophylls *a* and *b*, and carotenoids in stations #0m, #R, #RO, indicate the presence of macrophytes, such as mangrove trees *A. marina* and *R. mucronata*, and green algal epiphytes (Prézelin, 1981).

The sediments along the MIM/II transect (Table 2) show a rather homogeneous grain-size distribution, with mainly medium and fine sands, and at the lower end, the highest gravel contents. Lowest values of pore water were recorded near both ends of the transect and are associated with a silt plus clay content decrease. On the other hand the lowest organic matter contents is linked to higher fractions of medium sands, in the washed zones. Phytopigment analysis indicates a lower productivity in stations #1 and #6. Margalef index is maximum (>2.5) in stations #3, #4 and #5 and, according to Plante-Cunny (1978), indicates the occurence of stabilized communities of microphytobenthos. Otherwise, the average percentage of Chl. *a* degradation along this transect is higher than those recorded along the MIM/I transect, and may suggest a limitation in nutrients in the former.

Table 2. Values of sediment, chemical and biological parameters at the Ponta Rasa mangrove (MIM/II).
Tableau 2. Valeurs des paramètres du sédiment, chimiques et biologiques à la mangrove de Ponta Rasa (MIM/II).

Parameters	Unit	Abbreviation	Sampling Stations - Transect MIM II						
			1	2	3	4	5	6	7
Temperature	°C		19.6	20.3	19.5	20.0	20.1	20.9	21.6
Salinity	‰		-	-	60	40	39	35	
Organic Matter	$g.m^{-2}$	OM	236.6	329.4	919.8	928.8	95.4	101.4	136.8
% Water Content	%	%WATER	10.1	9.7	34.4	39.2	20.2	16.0	14.7
Chlorophyll *a*	$mg.m^{-2}$	Chl a	42.79	40.14	72.71	58.97	33.12	7.46	33.36
Chlorophyll *b*	$mg.m^{-2}$	Chl b	0.00	9.28	5.65	10.27	0.65	0.00	0.00
Chlorophyll *c*	$mg.m^{-2}$	Chl c	0.00	19.57	14.45	15.89	10.32	3.27	6.53
Phaeopigments	$mg.m^{-2}$	PHAEO	29.04	17.84	66.96	67.46	27.77	4.20	16.18
Carotenoids	$mg.m^{-2}$	CAR	0.00	42.59	92.43	97.70	42.64	2.93	32.39
Margalef Index		MARG	0.79	2.41	2.82	3.59	2.79	1.60	2.43
Moss Index		MOSS	0.89	1.02	0.98	0.87	1.02	1.24	1.10
% of Chlorophyll *a*	%	%DEGR	54.6	37.5	66.7	76.9	62.5	46.4	41.2
Gravel	%	GRAV	0.8	1.7	0.3	0.7	0.1	7.0	49.2
Very Coarse Sands	%	VCS	0.5	0.9	0.4	1.1	0.2	1.6	3.3
Coarse Sands	%	CS	3.2	3.7	3.2	5.9	1.9	5.8	5.9
Medium Sands	%	MS	50.3	63.4	29.9	35.5	83.6	44.5	23.3
Fine Sands	%	FS	41.3	25.6	41.7	35.1	12.7	39.1	15.7
Very Fine Sands	%	VFS	2.2	1.6	6.2	3.3	0.5	2.0	1.4
Silt and Clay	%	SILT	1.8	2.9	18.4	18.4	1.0	0.1	1.3
Diversity Index		bits/ind.	1.12	0.81	0.00	1.78	1.41	0.22	0.00
Evenness Index			0.71	0.81	0.00	0.69	0.44	0.09	0.00
Abundance	$ind.m^{-2}$		252	16	12	160	372	632	656

Minimal Sampling Area and Faunal Composition

Along both transects the species/area curves reach the asymptote at 0.19 m^2 , corresponding to the third of the four subsamples (Fig. 3a and b). Thus, and according to the concept of Barbour *et al.* (1980), such a sampling area is representative of the number of species that could be found in these communities and, as a consequence, the extension of sampling area would not add more information. Nevertheless, the primitive 0.25 m^2 area of sampling was kept, as the fourth subsample clearly stabilized the data concerning the number of species sampled. The analysis of Fig. 4 and Table 1 shows that the station #LW, on the transect MIM/I, displays the richest macrobenthos community in terms of density and diversity, although largely dominated by polychaetes. Low value of evenness reflects the fact that ≃ 50% of individuals are represented by 2 taxa, the polychaetes *Ceratonereis erythraensis* and

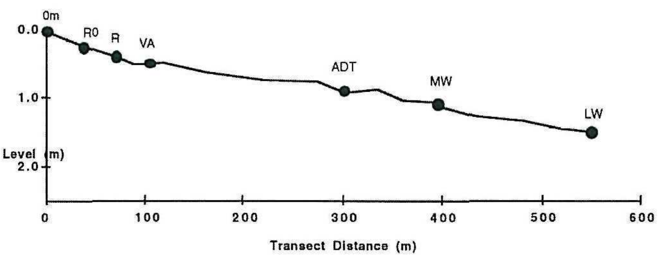

Figure 2. Sampling stations and profile at Saco mangrove (Transect MIM/I). **#0m=** upper level near terrestrial vegetation; **#RO=** presence of *Avicennia marina* and *Saccostrea cucullata*; **#R=** presence of *A. marina*; **#VA=** a large muddy area with a visible fraction of sand; **#ADT=** high density of *Dotilla fenestrata* within a sandy area; **#MW=** middle water - a sandy/muddy area; **#LW=** the upper limit of low water - a muddy area.

Figure 2. Stations d'échantillonnage et profil de la mangrove du Saco (Transect MIM/I). **#0 m** = niveau supérieur près de la végétation terrestre ; **#RO** = présence de *Avicennia marina* et *Saccostrea cucullata* ; **#R** = présence de *A. marina* ; **#VA** = large zone de vase avec une fraction de sable ; **#ADT** = densité élevée de *Dotilla fenestrata* dans une zone de sable ; **#MW** = médiolittoral - zone de sable/vase ; **#LW** = limite supérieure de l'infralittoral - zone de vase.

Parheteromastus tenuis as it is also shown in Annex 1. On the other hand, the epibenthic cirripede *Balanus amphitrite*, which uses stones and shells as substrate, clearly dominates the epifauna.

The lowest diversity occurs at station #R where *B. amphitrite* (very abundant on *R. mucronata* roots) represents 95% of the whole individuals sampled, forming a facies; also relevant is the presence of the epibiotic gastropod *Littorina scabra*. At #RO, the diversity index is higher, although the macrofauna is also clearly dominated by the epibenthic species *Saccostrea cucullata* (Bivalvia), living on the mangrove tree roots, and *Terebralia palustris* (Gastropoda), living on sediments and leaves. Polychaetes dominate at stations #VA and #LW, while oligochaetes, together with the crab *Uca annulipes*, are confined to #0m, and characterize this level. Station #ADT is dominated by *Dotilla fenestrata*, a crab typical of the upper infralittoral levels of sand banks according to Macnae & Kalk (1969), but also characteristic, as crowds, of the midlittoral level for the Tuléar region (Pichon, 1967); the presence of the polychaete *Glycera convoluta* is also relevant. The polychaete *Prionospio sexoculata* is the most abundant taxon in #VA, followed by the bivalve *Loripes clausus* and the crab *Macrophthalmus grandidieri* only present here. Gastropods and bivalves, namely *Setia* sp.1 and *Pseudophytina africana*, are dominant at #MW.

The Ponta Rasa mangrove (MIM/II) is clearly different from the Saco mangrove (MIM/I) and displays lower values of density and diversity. Gastropods are the most abundant group, followed by decapods, polychaetes and bivalves. In fact, *T. palustris* was only recorded at St. #3 and *Setia* sp.1 at St. #7, the latter reaching a density of 656 ind. m^{-2}. #6 is also dominated by *Setia* sp.1 and represents 96% of the whole collection. The highest values of diversity were recorded at St. #4 where the crab *Uca annulipes* dominates.

PCA and Cluster Analysis

The Principal components analysis (Figs. 6, 7 and Table 3) performed on MIM/I (Saco Mangrove) indicates a clear separation of the stations on the first axis, between coarse sediment (gravel, very coarse sand and medium sand) and the finest sediments (fine sands, very fine sand and silt plus clay, Fig. 6). On second factor, sediments are separated according to pigments in which Chl. *b* and the percentage of Chl. *a* degradation are opposed to other pigments (ie. Chl. *a* and *c*, phaeopigments and carotenoids). Stations #0m and #RO, containing the higher percentages of fine sediments are separated from station #LW, where coarser sediments dominate. Also, stations #MW and #ADT form a group associated with coarser sediments and higher biota abundance, compared to the finest sediments (#0m, #R and #RO), in which abundance is lower and diversity higher. These two factors explain 62.4% of the stations' variability.

Cluster analysis (Fig. 8) confirms the previous results and the role of grain-size and pigments in defining groups and sub-groups of habitats. Three groups could be defined

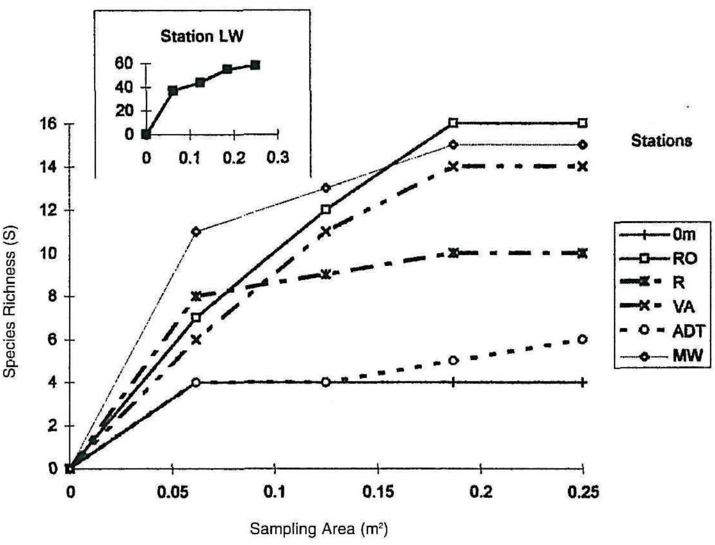

Figure 3 a. Species richness as a function of the area and level sampled at the Saco-Mangrove (Transect MIM/I). Abbreviations as in Fig. 2.

Figure 3 a. Richesse spécifique en fonction de la surface et du niveau échantillonnés dans la mangrove du Saco (Transect MIM/I). Mêmes abréviations que Fig. 2.

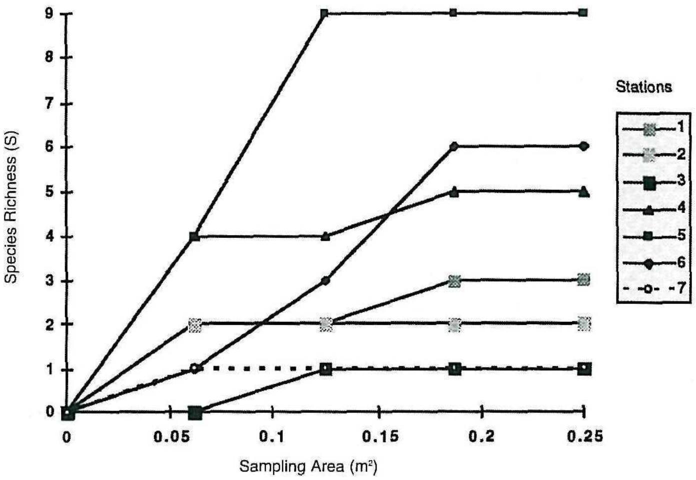

Figure 3 b. Species richness as a function of the area and level sampled at the Ponta Rasa mangrove (Transect MIM/II).

#1= upper limit of *Avicennia sp.*; #2= presence of *Rhizophora mucronata, Uca annulipes* and *Terebralia pallustris*; #3= muddy area with *R. mucronata*; 4= extremely dense association of *R. mucronata* and *A. marina*; #5= lower limit of the *Rhizophora/Avicennia* association in a sandy area; #6 and #7= sandy platform towards the sea, respectively middle water and low water

Figure 3 b. Richesse spécifique en fonction de la surface et du niveau échantillonnés dans la mangrove de Ponta Rasa (Transect MIM/II).

#1 = limite supérieure de *Avicennia sp.* ; **#2** = présence de *Rhizophora mucronata, Uca annulipes* et *Terebralia pallustris* ; **#3** = zone de vase avec *R. mucronata* ; **4** = association dense de *R. mucronata* et *A. marina* ; **#5** = limite inférieure de l'association *Rhizophora/Avicennia* dans une zone de sable ; **#6** and **#7** = large plateau de sable du médiolittoral à l'infralittoral supérieur.

according to the size of the grain, and within the fine grain group, three other sub-groups can be considered. The first gathers equitability, diversity and Chl. *a* % degradation; the second group the finest sediments, the % of pore water content and the Margalef index and the third the organic matter, pigments and the presence of coarse sand. As a matter of fact, these results confirm the PCA analysis, and oppose gravel and abundance to clay-silt and diversity.

The PCA performed from data collected on transect MIM/II (Ponta Rasa) (Figs. 9, 10 and Table 3), also indicates a separation on the first axis between coarse sands, gravel (associated with high abundances and Moss indices) and the fine sands associated with silt-clay, which also display the higher values of % of water, organic matter, carotenoids, Chl *a* degradation %, phaeopigments, Chlorophyll *a*, *b* and *c* (Fig. 9). The first two factors represent 66.5% of variability associated with the stations. Stations #1, #2 and #5 while located at the ends of transect MIM/II (Fig. 10), are grouped together on the first and second factor. In fact, both represent the boundaries of mangrove, the first being the dunar area, and the second the end of mangrove at the beach level, and so revealing the symmetric characteristic of grain-size distribution of this mangrove (see Table 1).

Cluster analysis (Fig. 11) provides a good relationships between the faunistic abundance at the

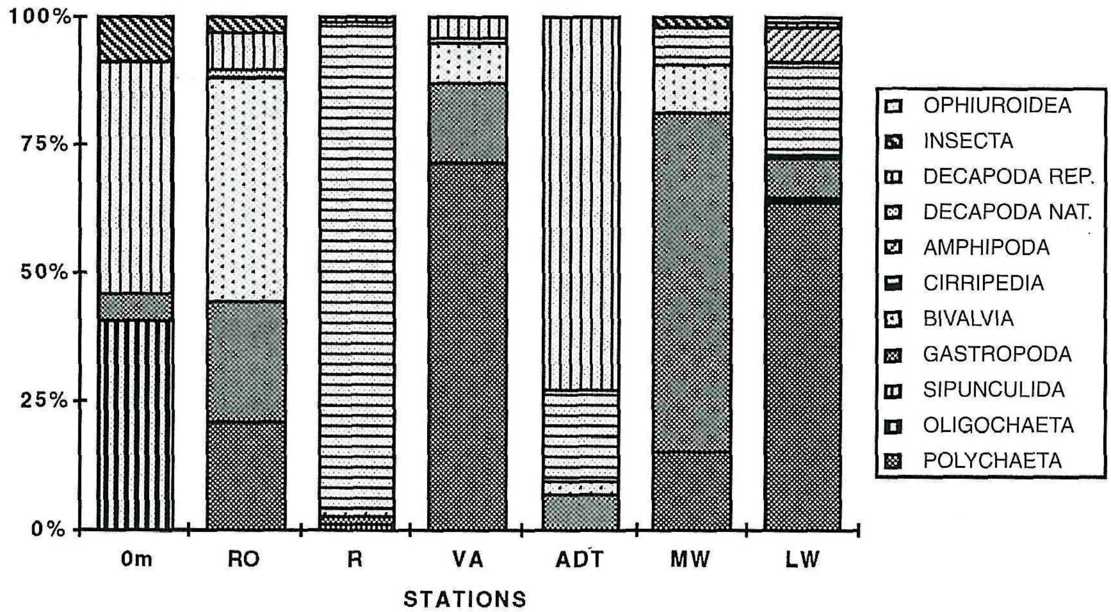

Figure 4. Relative frequencies of taxa in each station at the Saco mangrove (MIM/I).
Figure 4. Fréquences relatives des différents taxons à chaque station de la mangrove de Saco (MIM/I).

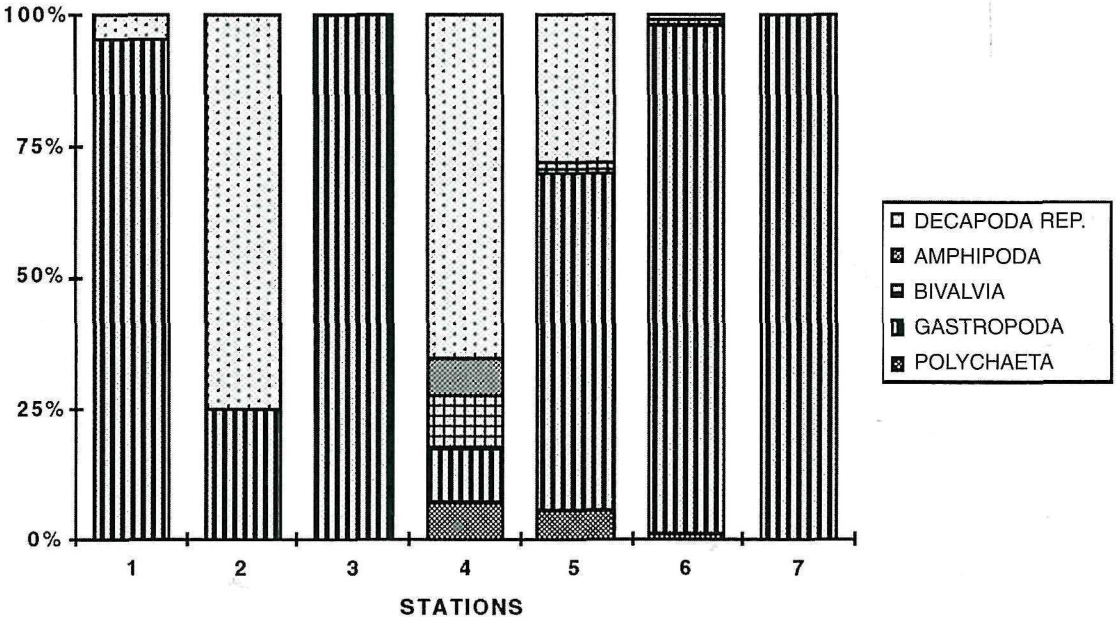

Figure 5. Relative frequencies of taxa in each station at the Ponta Rasa mangrove (MIM/II).
Figure 5. Fréquences relatives des différents taxons à chaque station de la mangrove de Ponta Rasa (MIM/II).

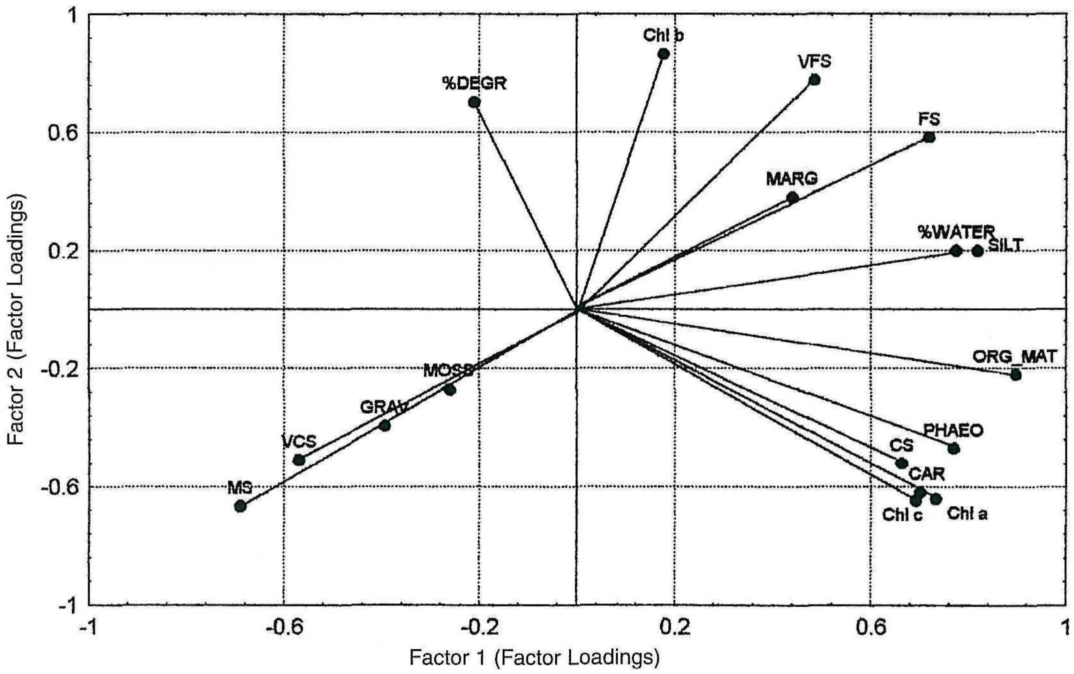

Figure 6. Principal Components Analysis (PCA) on chemical and sediment parameters at the Saco mangrove (MIM/I). Abbreviations in Table 1.

Figure 6. Analyse en Composantes Principales (PCA) des paramètres chimiques et ceux du sédiment de la mangrove de Saco (MIM/I). Abréviations dans le Tableau 1.

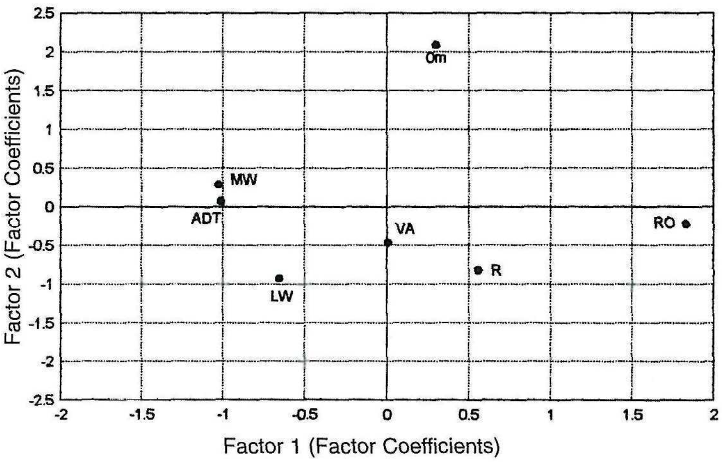

Figure 7. Principal Components Analysis (PCA). Representation of stations at the Saco mangrove (MIM/I).

Figure 7. Analyse en Composantes Principales (PCA). Représentation des stations à la mangrove de Saco (MIM/I).

level 0.4, and at about the same level, another major group including the Margalef index together with the finest sediments and the carotenoids, Chl. *a* degradation %, phaeopigments, Chlorophyll *a*, *b* and *c*. Thus, the basic structure of both mangroves remains identical, and is clearly orientated by the grain size of the sediment.

Central Values Analysis

As PCA did not reveal much information concerning the species zonation but only showed station aggregation as a function of sediment grain-size, central values were calculated by using the coordinates obtained from the first factor of PCA as the gradient profile. This approach allows the ordination of species in relation to a gradient (grain-size) that is more informative, as it also integrates the information of several variables. In the present case it is clear that grain-size distribution is, as usual in soft bottom communities, the major factor influencing faunal distribution. In this way, all taxa represented on the central axis (variation coefficient = 0), are species sampled only at a single point (exclusive), or at several stations but with identical values. In fact, a species which departs from the central axis the more could be considered as ubiquitous. The coefficient of variation was preferred to the standard deviation in order to eliminate the effect of large variation in densities between stations and between species.

The results of this analysis are presented in Figs. 12, 13 and Table 4, and set up the affinity of species to the different sediments. Concerning the Saco mangrove (Fig. 12 - Tab. 4), the first group corresponds to the lower fringe of the mangrove, where polychaetes dominate and where the presence of an important fraction of gravel and coarse sand is the most explanatory factor. This group matches previous results of the cluster analysis which gathers the coarser fraction of sediments with the faunistic abundance. Group XII (Table 4) clearly differs from other groups and displays species of polychaetes, *Saccostrea cucullata*, *Terebralia palustris* and *Clypeomorus caerulum*, which are linked to the finest sediments. *Dotilla fenestrata* is associated with medium sands and percentage of organic matter content, as it has been seen at the Ponta Rasa mangrove.

Actually, the Ponta Rasa mangrove presents a very low diversity, and several species which occur at the Saco mangrove are lacking. Nevertheless, groups VI and VII (MIM/II) are similar to group XII (MIM/I) found within the finest sediments. As in the Saco mangrove, *D. fenestrata*, *Glycera convoluta* and *Loripes clausus* are also related to the same kind of substratum.

Discussion

Environmental factors affecting mangrove's species distribution and its structure include climate, water temperature, sedimentation, tide relief, salinity and geology. Actually, there are strong climate differences between two nearby mangrove regions: Madagascar displays a humid tropical climate on its northeastern part, whereas its southwestern part is a dry tropical one. Conversely, the southern Mozambique is characterized by temperatures which could fall till 2°C during the southern hemisphere winter. As a consequence, a general characterization of macrobenthic communities seems unlikely and comparisons between communities still difficult to discuss.

Keeping in mind the general descriptions of mangroves by Chapman (1977) and Teas (1983), the most outstanding result in the present study is the clear dominance of medium and fine sands along transects rather than colloidal sedimentation (silt-clay). On these sites there is no station exclusively formed by silt plus clay, as it might be expected in a mangrove. This peculiar characteristic which influences the infaunal distribution, probably reflects both the hydrodynamic condition of the Inhaca island (the current regime mainly corresponds to the warm current of the Mozambique channel) and its sedimentary origin (Lopes, 1973). Nevertheless, a similar situation was already described by Kiener (1965, 1973) at Madagascar, where 98% of the mangroves are located in wide flats of the west coast and supported by the huge mass of alluvial sediments. The relative extension of mangroves between east and west coasts is also explained by the tidal regime of the Mozambique channel.

As stated by Macnae & Kalk (1969) "The composition of substratum, the water and tidal level combine to divide the mangrove into zones which have a pattern of zonation

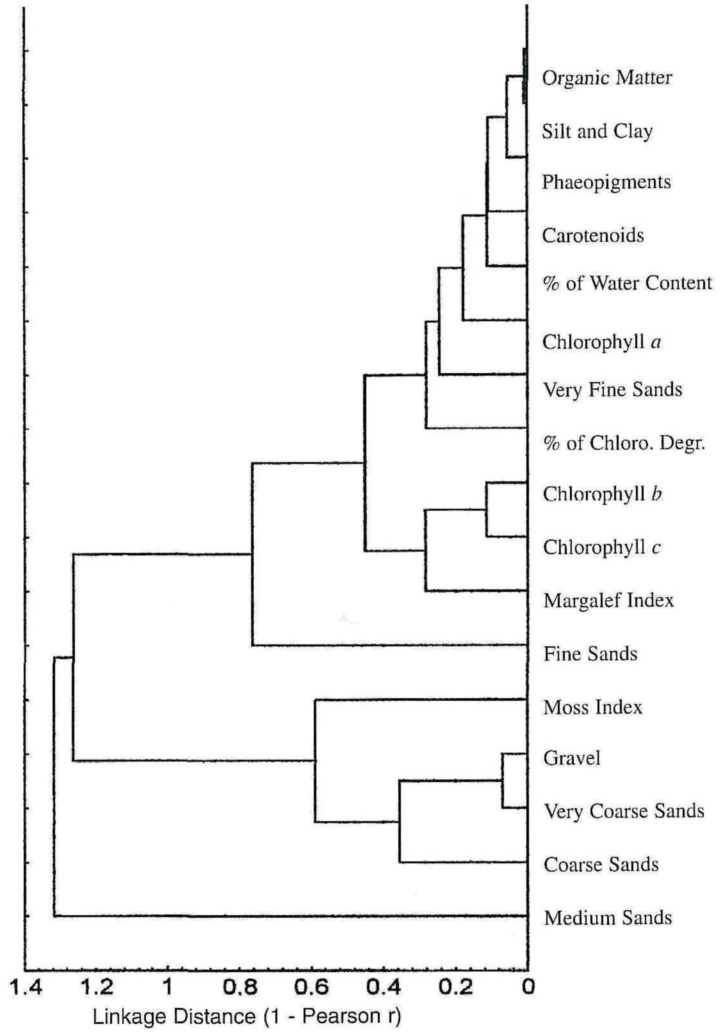

Figure 8. Cluster analysis on the sediment parameters and chemical parameters at the Saco mangrove (MIM/I).

Figure 8. Dendrogramme des paramètres du sédiment et chimiques de la mangrove de Saco (MIM/I).

closely paralleled by associations of animals". As a matter of fact, it can be added that water content and microphytobenthos seem to be a determining factor controlling diversity and zonation in these areas. It is generally accepted that along the coast a dynamic balance exists between the seaward outflow of groundwater, and salt water intrusion into coastal freshwater channels. The modification of water fluxes induces direct changes on the flux of nutrients (namely nitrogen and phosphorus), as well as on the oxygen levels and, consequently, on the mangrove's production. Tropical ecosystems are strongly dependent on the influx of terrestrial nutrients carried along by ground water (Clark, 1977). A similar situation has also been described for the mangroves of the SW of Madagascar (namely the Tuléar region) where the calcareous nature of the soil favours water resurgence and allows the occurrence of several littoral mangroves by reducing salinity (Weiss & Kiener, 1971). As a matter of fact, recent studies by Clough (1992) and Duke (1992), prone that the presence and the performed range of many mangrove's species are largely dependent upon salinity, and thus the ground water flux is presented as a modelling factor.

The lower diversity of the Ponta Rasa mangrove can thus be partly the consequence of the lower percentage of fresh water supply which increases salinity in sediments and reduces the amount of terrestrial nutrients. In fact, values recorded at the Ponta Rasa mangrove for both pigment diversity and percentage of Chl. *a* degradation, suggest a steady state in cellular division, that may be associated with the beginning of a limitation in nutrients as it was already shown by Plante-Cuny (1978). Furthermore, Lopes (1973) emphasized the role of freshwater fluxes within the island, which were undoubtedly affected by the excess of human pressure during the civil war, when the population of Inhaca increased by 3, reached 15000 people (Gove, *pers. com.*).

Nevertheless, considering both flora and fauna, there is a clear zonation which is a function of several environmental factors and contributes to define mangrove communities (Kiener, 1965; MacNae & Kalk, 1969; Weiss & Kiener, 1971; Daniel & Robertson, 1990). Grain-size, together with salinity, water percentage and microphytobenthos are the main factors affecting the macrobenthos distribution.

At the upper limit (high spring tides) near the halophyte vegetation, the substratum mainly composed of fine and very fine sands, is dominated by two animal taxa, oligochaetes and the burrowing crab *Cardisoma carnifex*, if we consider collections and videos of the supra and adlittoral communities. The area located between the inner edge of the mangrove flat bordered by *Avicennia marina* and the level characterized by *Rhizophora mucronata*, in which the silt-clay fraction predominates is characterized by epibenthic species: the oyster *Saccostrea cucullata*, the gastropods *Terebralia palustris* and *Clypeomorus caerulum*. Actually these two latter species have been referred to this kind of substrate at the western Indian Ocean by Cantera *et al.* (1983). The gastropod *Littorina scabra* (an epibiotic species on hard substrates, canopy and roots according to Cantera *et al.*, 1983), and the crab *Uca annulipes* display also their peaks of maximum of density at this level.

The barnacle *Balanus amphitrite* while occurring mainly on the trunks of *A. marina* and *R. mucronata*, has a wider repartition and could be found below the level of low tide on gastropod and bivalve shell debris.

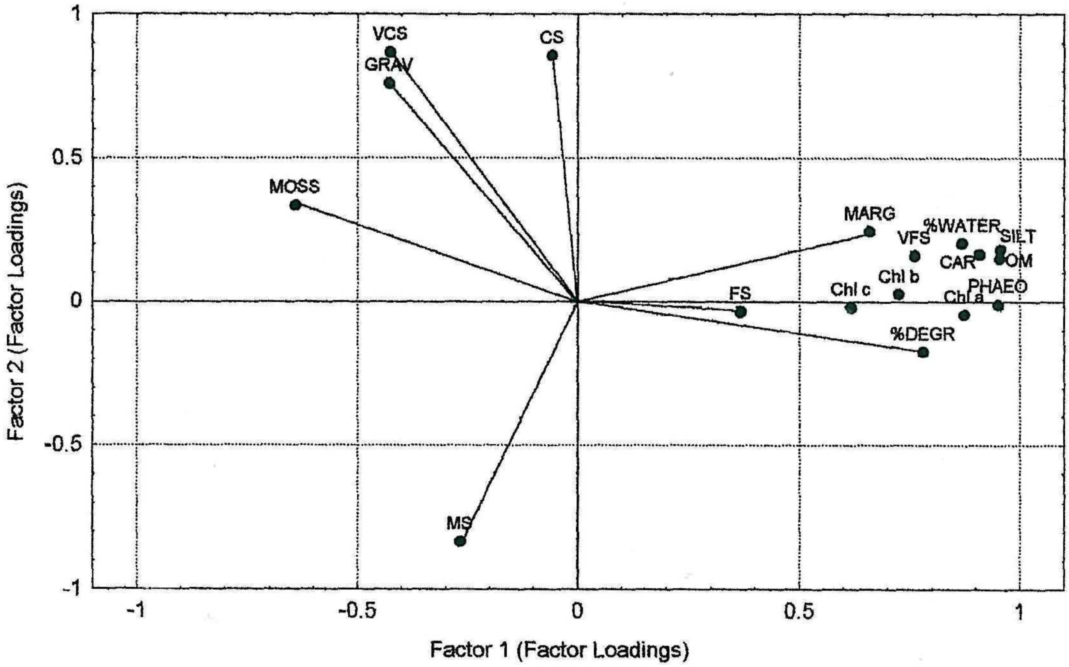

Figure 9. Principal Components Analysis (PCA) on sediment and chemical parameters at Ponta Rasa mangrove (MIM/II). Abbreviations in Table 2.

Figure 9. Analyse en Composantes Principales (PCA) sur les paramètres du sédiment et chimiques de la mangrove de Ponta Rasa (MIM/II). Abréviations dans le Tableau 2.

Although Macnae & Kalk (1969) asserted that polychaetes are rare in mangrove mud, our present results show that polychaetes represent the major zoological group, when the percentage of gravel and coarse sand increases towards low tide level. In fact, at the lower end of the mangrove and below the fringe of *R. mucronata*, the macrofauna is dominated by the polychaetes, *e.g.*, *Ceratonereis erythraensis*, *Dendronereis arborifera*, and *Parheteromastus tenuis*, the bivalves *Loripes clausus* and *Pseudophytina africana*, and the crabs *Dotilla fenestrata* (whereas they occur at a much lower density than in medium sands) and *Macrophthalmus grandidieri*.

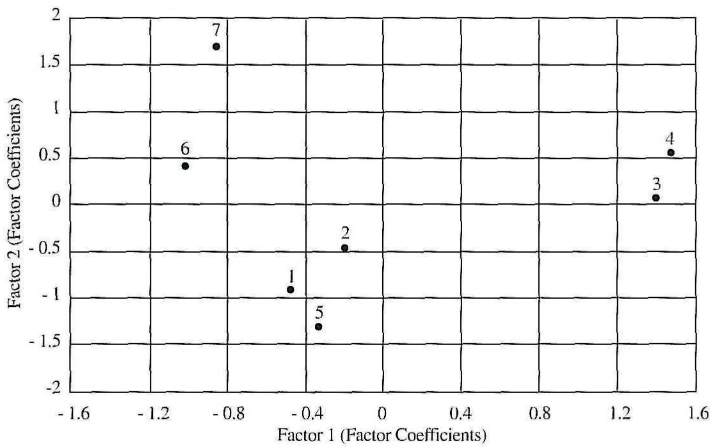

Figure 10. Principal Components Analysis (PCA). Representation of stations. Ponta Rasa mangrove (MIM/II).

Figure 10. Analyse en composantes principales (PCA). Représentation des stations de la mangrove de Ponta Rasa (MIM/II).

A similar community structure has also been recorded for the SW Madagascar mangroves by several authors (Thomassin, 1974, 1978), and for other parts of the world, such as the mangroves of the Missionary Bay adjacent to the Murray River estuary in Australia, in which Daniel & Robertson (1990) stated that epibenthos is dominated by polychaetes, bivalves and crustaceans. From these results it is possible to draw a scheme, as in Fig. 14, similar to that of Thomassin (1974) which is based on observations done on the mangrove belt located in the back area of Songoritelo fringing reef. The following zonation can be considered: i) a mangrove belt dominated by mean and fine sands and epibenthic species such as *Balanus amphitrite*, *Littorina scabra* and the crab *Uca annulipes*; ii) a belt boundary dominated by two epibenthic species, the oyster *Saccostrea cucullata* and the gastropod *Terebralia palustris*; iii) a midlitoral sand flat dominated by crowds of the crab *Dotilla fenestrata*, together

Table 3. Résumé of PCA analysis for Saco mangrove (MIM/I) and Ponta Rasa mangrove (MIM/II).
Table 3. Résumé de l'Analyse en Composantes Principales pour la mangrove du Saco (MIM/I) et de Ponta Rasa (MIM/II).

Transect MIM I

Eigenvalue	% of total variance	Cumulative	Eigenvalue	Cumulative %
1	9.269	46.3	9.269	46.3
2	4.072	20.4	13.341	66.7

Transect MIM II

Eigenvalue	% of total variance	Cumulative	Eigenvalue	Cumulative %
1	6.839	34.2	6.839	34.2
2	5.649	28.2	12.488	62.4

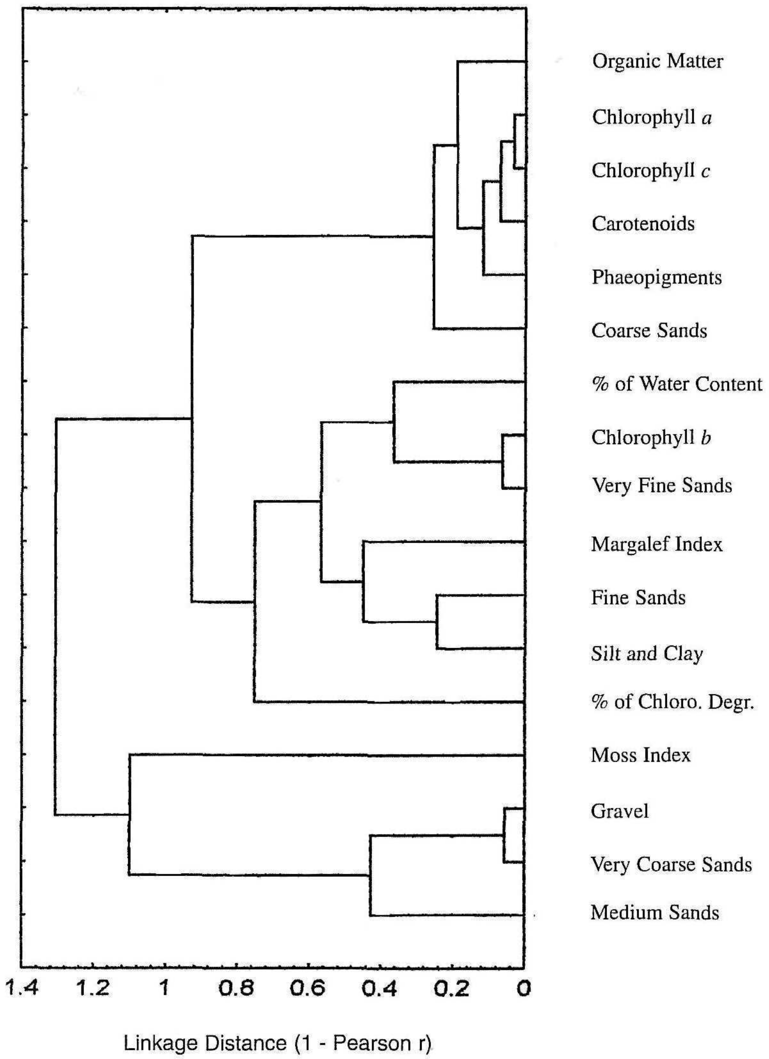

Figure 11. Cluster analysis on the sediment parameters and chemical parameters at the Ponta Rasa mangrove (MIM/II).
Figure 11. Dendrogramme des paramètres du sédiment et chimiques de la mangrove de Ponta Rasa (MIM/II).

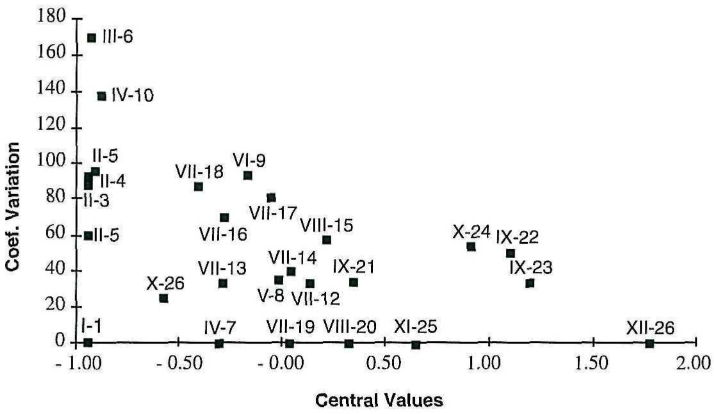

Figure 12. Central values analysis based on taxa distribution along PCA Factor 1 gradient. Saco mangrove (MIM/I). Roman numbers indicate groups of taxa. Arabic numbers indicate subgroups. For composition of groups and subgroups see Table 4.

Figure 12. Analyse des valeurs centrales de la distribution des taxons sur le premier axe de la PCA, à la mangrove de Saco (MIM/I). Les chiffres romains indiquent les groupes de taxons et les chiffres arabes les sous-groupes. Composition des groupes et sous-groupes dans le tableau 4.

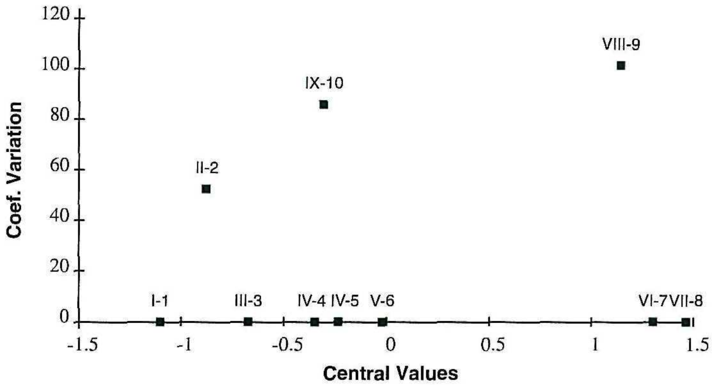

Figure 13. Central values analysis based on taxa distribution along PCA Factor 1 gradient. Ponta Rasa mangrove (MIM/II). Roman number indicate groups of taxa. Arabic numbers indicate subgroups. For composition of groups and subgroups see Table 5.

Figure 13. Analyse des valeurs centrales de la distribuition des taxons sur le premier axe de la PCA à la mangrove de Ponta Rasa (MIM/II). Les chiffres romains indiquent les groupes de taxons et les chiffres arabes les sous-groupes. Composition des groupes et sous-groupes dans le tableau 5.

with the polychaeta *Glycera convoluta*, a situation already described by Pichon (1967); iv) a muddy area, associated with gravel, matches what Thomassin (1978) called "la biocénose des sédiments vaseux de mode calme" with the bivalves *Loripes clausus* and *Pseudophytina africana* (here probably substituting *Tellina* spp.), the polychaetes *Dendronereis arborifera* and *Ceratonereis erythraensis* and the crab *Macrophthalmus grandidieri*. Nevertheless it can be noted that *C. erythraensis* also appears at Inhaca island when gravel is present.

If, as suggested by Berjak *et al.* (1982), the occurrence of mangroves, beyond tropical limits, mainly depends upon the presence of warm water currents, the Saco mangrove of Inhaca island represents a southern example of a highly diversified subtropical mangrove. Conversely, the Ponta Rasa mangrove is an example of mangrove with low diversity, as several typical macrobenthic species are lacking.

Bell & Westoby (1986), as well as several other authors, claimed that positive relationships between plant biomass or productivity and faunal density of the epibenthos in mangroves, should be understood as the result of a combination of three main factors: (1) food availability, (2) reduction of predation, (3) the increase of the living space. Concerning the infaunal species, other important factors such as the grain-size distribution pattern and the ground water fluxes have to be considered. For the epibenthos the adequate substratum is decisive, and for both communities the occurrence and frequency of exposure time related to tidal influence must be added. All these factors are therefore key processes in structuring these communities.

Acknowledgements

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Table 4. Central values analysis - grouping of taxa at the Saco mangrove (MIM/I)
Tableau 4. Analyse des valeurs centrales - groupement des taxons à la mangrove de Saco (MIM/I).

Transect MIM I Central Values Groups	***Taxa*** / Subgroups			
	Sub Group	*Taxa*	Sub Group	*Taxa*
	1	*Nereis falsa* (Quatrefages)	1	*Armandia* sp. (Fiippi)
	1	*Nereis operta* (Simpson)	1	*Loimia medusa* (Savigny)
	1	*Syllis cornuta* (Rathke)	1	*Polyophthalmus pictus* (Quatrefages)
	1	*Syllis ferrugina* (Langerhans)	1	Capitellidae nd.
	1	*Phyllodoce* sp (Savigny)	1	*Pulliella armata* (Fauvel)
	1	*Phyllodoce capensis* (Day)	1	*Owenia fusiformis* (Delle Chiage)
	1	*Glycera benguellana* (Augener)	1	*Isolda pulchella* (Muller)
	1	*Glycera longipinnis* (Grobe)	1	*Fabriciola mossambica* (Day)
	1	*Glycera natalensis* (Day)	1	*Sabella* sp. (Linnaeus)
	1	*Glycinde kameruniana* (Augener)	1	*Siphonosoma* sp. (Kef.)
	1	Eunicidae nd	1	Sipunculoida nd.
GROUP I	1	*Arabella iricolor* (Montagu)	1	*Diala conica* (Phillipson)
Gravel, very coarse sands.	1	*Diopatra cuprea cuprea* (Bosc)	1	*Setia* sp2 (Lamarck)
Taxa presents in only (at the utmost	1	*Diopatra neapolitana* (Delle Chiage)	1	*Tectonatica* sp2 (Sowerby)
in two) stations.	1	*Lumbrinereis latreilli* (Audouin & Milne-Edwards)		
	1			*Modiolus philippinarum* (Hanley)
	1	*Aonides oxycephala* (Sars)	1	*Ceradocus rubromaculatus* (Stimps)
	1	*Malacoceros indica* (Fauvel)	1	*Maera inaequipes* (Costa)
	1	Spionidae nd	1	Amphipoda sp1
	1	*Caulleriella acicula* (Day)	1	Amphipoda sp2
	1	*Cirratulus africanus* (Gravier)	1	Amphipoda sp3
	1	*Haploscoloplos fragilis* (Verrill)	1	*Dotilla fenestrata* (Hilgendorf)
	1	*Nainnereis laevigata* (Grube)	1	*Ophiocoma scolopendrina* (Lamarck)
	1	*Scoloplos johnstanei* (Day)	1	*Ophiocoma valenciae* (Muller)
	1	*Scoloplos* sp (Blainville)		
GROUP II	2	*Ophelia* sp (Savigny)		
Gravel, very coarse sands in larger	3	*Scoloplos madagascarensis* (Fauvel)		
quantity. Taxa can exist in other stations	4	*Parheteromastus tenuis* (Monro)		
in inferior proportions.	5	*Gibbula obscura* (Menke)		
GROUP III				
Gravel, very coarse sands in very larger quantity. Taxa can exit in other stations in very inferior quantities.	6	*Ceratonereis erythraensis* (Fauvel)		
GROUP IV	7	*Melongena pyrum* (Gmelin)		
Coarse sands. Taxa exists in only two stations in equal number.	7	*Paguridus* sp. (Fabricius)		
GROUP V				
Medium sands, but also in coarse sand. Taxa appear in more than one station.	8	Nereidae nd		
GROUP VI	9	*Balanus amphitrite* (Darwin)		
Medium sands in larger quantities. Ubiquitous taxa.	10	*Setia* sp 1 (Lamarck)		
GROUP VII	11	*Phyllodoce castanea* (Marenzeller)	15	*Macrophthalmus grandidieri* (Milne-Edwards)
Medium and fine sands. Taxa can	12	*Glycera alba* (Muller)	16	*Loripes clausus* (Phillipson)
exist in more than one station	13	*Tectonatica sp1* (Sowerby)	17	*Prionospio sexoculata* (Augener)
	14	*Dendronereis arborifera* (Peters)	18	*Pseudophytina africana* (Gmelin)

Table 4. Central values analysis - grouping of taxa at the Saco mangrove (MIM/I)
Tableau 4. Analyse des valeurs centrales - groupement des taxons à la mangrove de Saco (MIM/I).

Transect MIM I Central Values Groups	*Taxa* / Subgroups			
	Sub Group	*Taxa*	Sub Group	*Taxa*
GROUP VIII Medium and fine sands. Taxa appear in only one station.	19 19 19	*Glycera convoluta* (Keferstein) *Lumbrinereis meteorana* (Augener) Polychaeta nd.	20 20	*Glycera* sp. (Savigny) *Littorina scabra* (Linnaeus)
GROUP IX Fine sands. Taxa exists in more than one station.	21 22	Diptera larvae Xanthidae nd	23	Natantia nd
GROUP X Fine and very fine sands. Ubiquitous taxa.	24	*Uca annulipes* (Milne-Edwards)		
GROUP XI Very fine sands with some silts and clay.	25 25 26	Oligochaeta nd *Vitrinella* sp. (Gray) *Perinereis cultrifera* (Grube)	26	*Saccostrea cucullata* (Born)
GROUP XII Very fine sands with a larger quantity of sits and clay.	26 26 26 26	*Perinereis nigropunctata* (Horst) *Capitella capitata* (Fabricius) *Clypeomorus caerulum* (Sowerby) *Terebralia palustris* (Linnaeus)	26 26 26	*Alpheus crassimanus* (Heller) *Eurycarcinus natalensis* (Krauss) *Macrophthalmus* sp. (Latreilli)

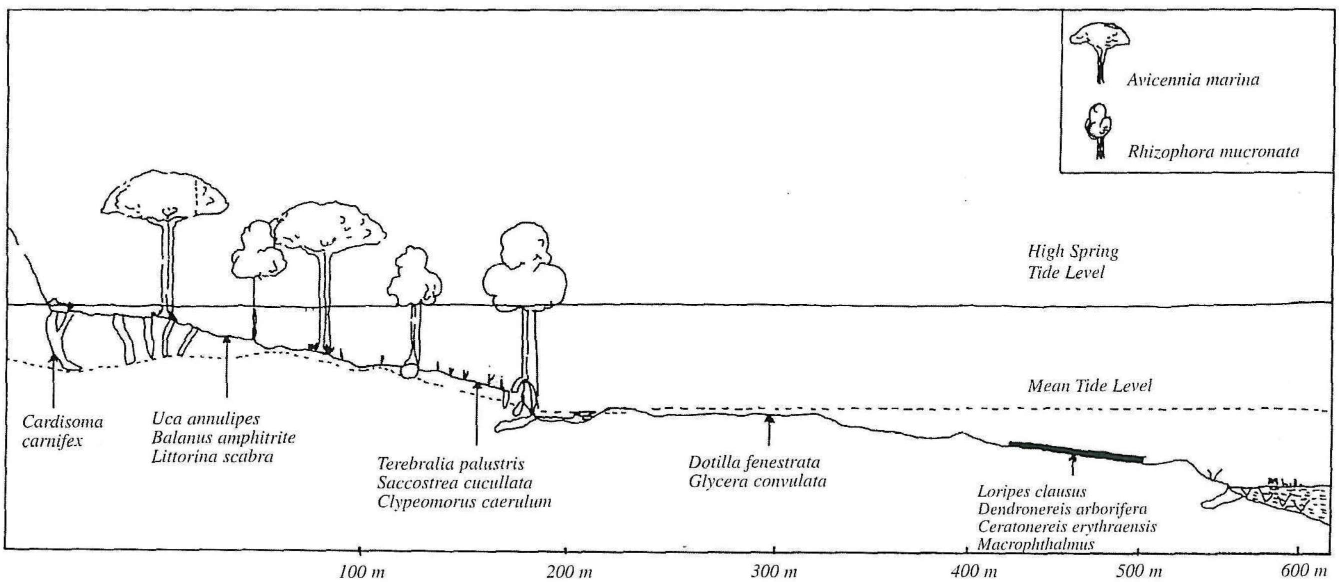

Figure 14. Schematic section and zonation of macrobenthos at the Saco Mangrove of Inhaca island (Mozambique).
Figure 14. Schéma de la zonation des peuplements macrobenthiques de la mangrove du Saco à l'île d'Inhaca (Mozambique).

Table 5. Central values analysis - grouping of taxa at the Ponta Rasa mangrove (MIM/II)
Tableau 5. Analyse des valeurs centrales - groupement des taxons à la mangrove de Ponta Rasa (MIM/II).

Transect MIM I Central Values Groups	***Taxa*** / Subgroups			
	Sub Group	*Taxa*	Sub Group	*Taxa*
GROUP I Medium and fine sands. Taxa present only in one station.	1 1	*Arabella iricolor* (Montagu) *Glycera convoluta* (Keferstein)	1	*Planaxis sulcatus* (Born)
GROUP II Ubiquitous taxa in stations with small quantity of silts and clay.	2	*Setia* sp1 (Lamarck)		
GROUP III Medium and fine sands. Taxa present in more than one station.	3	*Loripes clausus* (Phillipson)		
GROUP IV Medium sands with great % of silts and clay.	4 5 5 5	*Setia* sp2 (Lamarck) *Perinereis nigropunctata* (Horst) Neridae nd *Glycera alba* (Muller)	5 5 5	*Glycera natalensis* (Day) *Marphysa macintoshi* (Crossland) *Modiolus philippinarum* (Hanley)
GROUP V Fine and very fine sands	6	*Littorina scabra* (Linnaeus)		
GROUP VI Very fine sands, silts and clay, organic matter, water %, Cl *a*, phaeopigments, carotenoids, Margalef index, % of Chlorophyll degradation	7	*Terebralia pallustris* (Linnaeus)		
GROUP VII Great quantities of silts and clay. Taxa only in one station.	8 8 8	*Dendronereis zuzulandica* (Day) *Melampus acinoides* (Morelef) *Siliqua cf. radiata* (Wood)	8 8	*Alpheus crassimanus* (Heller) *Macrophthalmus* sp. (Latreilli)
GROUP VIII Great quantities of silts and clay. Ubiquitous taxa.	9	*Uca annulipes* (Mailne-Edwards)		
GROUP IX Medium sands with inferior quantity of silts and clay and organic matter.	10	*Dotilla fenestrata* (Hilgendorf)		

Annex 1. Original matrix of densities (ind.m^{-2}) at the Saco mangrove.
Annexe 1. Matrice originale des densités (ind.m^{-2}) à la mangrove de Saco.

	Sampling Sations - Transect MIM I						
	0m	R	RO	VA	ADT	MW	LW
Phyllodoce capensis (Day)							24
Phyllodoce castanea (Marenzeller)				12		20	
Phyllodoce sp. (Savigny)							4
Syllis cornuta (Rathke)							112
Syllis ferrugina (Langerhans)							80
Ceratonereis erythraensis (Fauvel)			4	4		16	1376
Dendronereis arborifera (Peters)			36	12		40	24
Nereis falsa (Quatrefages)							4
Nereis operta (Stimpson)							48
Perinereis cultrifera (Grube)			4				
Perinereis nigropunctata (Horst)			12				
Neridae nd			4	4			8
Glycera alba (Muller)		8		16			
Glycera benguellana (Augener)							4
Glycera convoluta (Kaferstein)					8		
Glycera longipinnis (Grobe)							4
Glycera natalensis (Day)						16	
Glycera sp. (Savigny)		8					
Glycinde kameruniana (Augener)							4
Eunicidae nd							8
Arabella iricolor (Montagu)							4
Diopatra cuprea cuprea (Bosc)							20
Diopatra neapolitana (Delle Chiage)							8
Lumbrinereis latreilli (A & M. Edwards)							4
Lumbrinereis meteorana (Augener)				8			
Aonides oxycephala (Sars)							148
Malacocerus indica (Fawel)							40
Prionospio sexoculata (Augener)				148		16	
Spionidae nd							8
Caulleriella acicula (Day)							4
Cirratulus africanus (Gravler)						4	4
Haploscoloplos cf. fragilis (Verril)							4
Nainnereis laevigata (Grube)						4	
Scoloplos johnstanei (Day)							12
Scoloplos madagascarensis (Fauvel)						4	60
Scoloplos sp. (Blainville)							16
Armandia sp. (Filippi)							28
Ophelia sp. (Savigny)						4	16
Polyophthalmus pictus (Quatrefages)							4
Capitella capitata (Fabricius)			48				
Capitellidae nd							16
Parheteromastus tenuis (Monro)						36	804
Pulliella armata (Fauvel)							8
Owenia fusiformis							8
Isolda pulchella (Muller)							4
Loimia medusa (Savigny)						12	
Fabriciola mossambica (Day)							4
Sabella sp. (Linnaeus)							4
Polychaeta nd				8			
Oligochaeta nd	36						
Siphonoma sp. (Kef)							12
Sipunculida nd							16
Clypeomorus caerulum (Sowerby)			80				
Diala conica (Phillipson)							76
Gibbula obscura (Menke)				4			140
Littorina scabra (Linnaeus)		4					

	Sampling Stations - Transect MIM I						
	0m	R	RO	VA	ADT	MW	LW
Setia sp1 (Lamarck)		20		36	52	736	148
Setia sp2 (Lamarck)							4
Tectonatica sp1. (Sowerby)				8	4		
Tectonatica sp2 (Sowerby)							4
Terebralia palustris (Linnaeus)			40				
Vitrinella sp (Gray)	4						
Melongena pyrum (Gmelin)		4					4
Saccostrea cucullata (Born)			208				
Loripes clausus (Phillipsin)		4		24	8	8	
Modiolus philippinarum (Hanley)							24
Pseudophytina africana (Gmelin)		24	20		16	100	
Balanus amphitrite (Darwin)		1648			148	84	824
Ceradocus rubromaculatus (Stimpson)							4
Maera inaequipes (Costa)							72
Amphipode sp1							228
Amphipode sp2							8
Amphipode sp3							24
Alpheus crassimanus			4				
Decapoda natantia nd			8	4			
Dotilla fenestrata (Hilgendorf)					608		
Eurycarcinus natalensis (Krauss)			4				
Macrophthalmus grandidieri (M. Edwards)		4	4	12			4
Macrophthalmus sp. (Latreilli)			4				
Pagurus sp. (Fabricius)		8					8
Thalamita sp. (Latreilli)							36
Uca annulipes (M. Edwards)	40		12				
Xanthidae nd			12				4
Insecta larvae	8		16			20	
Ophiocoma scolopendrina (Lamarck)							16
Ophiocoma valenciae (Muller)							12

Annex 2. Original matrix of densities (ind.m^{-2}) at the Ponta Rasa mangrove.
Annexe 2. Matrice originale des densités (ind.m^{-2}) à la mangrove de Ponta Rasa.

	Sampling Stations - Transect MIM II						
	1	2	3	4	5	6	7
Dendronereis zuzulandica (Day)				12			
Perinereis nigropunctata (Horst)					4		
Neridae nd					4		
Glycera alba (Muller)					4		
Glycera convoluta (Kaferstein)						4	
Glycera natalensis (Day)					4		
Arabella iricolor (Montagu)						4	
Marphysa macintoshi (Crossland)					4		
Littorina scabra (Linnaeus)		4					
Melampus acinoides (Morelef)				16			
Planaxis sulcatus (Born)						4	
Setia sp1 (Lamarck)	168				240	608	656
Setia sp2 (Lamarck)	72						
Terebralia palustris (Linnaeus)			12				
Loripes clausus (Phillipson)					4	4	
Modiolus philippinarum (Hanley)					4		
Siliqua cf. radiata (Wood)				16			
Alpheus crassimanus (Heller)				12			
Dotilla fenestrata (Hilgendorf)					104	8	
Macrophthalmus sp. (Latreilli)				4			
Uca annulipes (Milne-Edwards)	12	12		100			

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