

INTERLINKAGES BETWEEN EASTERN-AFRICAN COASTAL ECOSYSTEMS

Contract No. TS3*-CT92-0114
FINAL REPORT (DECEMBER 1995)

Participating institutes

The Netherlands

Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, Yerseke

Catholic University, Laboratory of Aquatic Ecology, Nijmegen

Kenya

Kenya Marine and Fisheries Research Institute, Mombasa

Belgium

Free University, Laboratory of Analytical Chemistry, Brussels

Portugal

University of Lisbon, Guia Marine Laboratory, Cascais

Mozambique

Eduardo Mondlane University, Department of Biological Sciences, Maputo

Sweden

Stockholm University, Department of Zoology, Stockholm

Tanzania

University of Dar es Salaam, Institute of Marine Sciences, Zanzibar

General coordinator

Dr. M.A. Hemminga

Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology,
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PREFACE

This final report on the STD-3 project "Interlinkages between Eastern-African coastal ecosystems" marks the end of a joint enterprise involving researchers from four European and three African countries. Some two and a half years ago, teams of researchers of these countries together set out to elucidate the functional interdependence of mangroves, seagrass beds and coral reefs, with the ultimate goal to contribute to the scientific basis that is necessary for the formulation of sound management and exploitation policies concerning the coastal fringe ecosystems in Eastern-Africa.

The reader will find this final report has been arranged according to four concrete scientific objectives which have been formulated at the onset of the project:

- (1) To assess the nutrient sink or source function of mangroves.
- (2) To make a comparison of the functioning of seagrass meadows in two contrasting situations, i.e., in the proximity of mangroves, and outside the influence of these intertidal forests.
- (3) To elucidate the hydrodynamics and fluctuations in nutrient contents in the tidal waters flushing mangroves and seagrass meadows
- (4) To study the biological diversity of the coastal zone and the population dynamics of (economically) relevant species.

The total data output generated in the course of the project has been considerable. In several parts of the research area covered by the project a clear integration of the collected data already has been achieved, allowing very interesting and relevant conclusions to be drawn. A number of these have already found their way to the international scientific literature. Other topics, particularly those studied in the later phases of the project, need further consideration. However, undoubtedly a series of other scientific publications is still to follow.

A second aim of the project was to support further development and strengthening of marine institutes involved in strategic marine research in East-Africa by the cooperation with European universities and research institutes. This cooperation in general has been perceived as being very positive by most participants, European and African scientists alike.

It is revealing in this respect that all participating institutes, without exception, have expressed the wish to continue the existing cooperation, and already have taken concrete steps to achieve this cooperation in the years to come.

Hopefully, this final report gives the reader clear insight in the scientific progress that has been made as a result of the joint efforts of African and European scientists, all of whom hold the view that increasing the insight in the functioning of tropical coastal ecosystems is an aim definitely worthwhile pursuing!

Dr. M.A. Hemminga
(general coordinator)

Part 1: The nutrient sink or source function of mangroves

NITROGEN TRANSFORMATIONAL PROCESSES IN SEDIMENTS OF A TROPICAL MANGROVE ECOSYSTEM (GAZI BAY, KENYA)

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INTRODUCTION

Mangrove swamps are common coastal ecosystems in many tropical and subtropical countries. They are highly productive marine ecosystems and are believed to enhance near-shore primary and secondary production (Wattayakorn et al., 1990). Tropical ecosystems such as mangroves, seagrass meadows and coral reefs sustain intense biological production despite low ambient concentration of nutrients (O'Neil & Capone, 1989). Mangroves produce considerable quantities of organic matter, primarily as leaves but the fate of this organic detritus is still not very clear. Do mangroves export their organic detritus and therefore nutrients to adjacent seagrass meadows and coral reefs or do they act as a sink for imported material with detritus being buried or degraded and recycled in the sediments?

In order to understand the role of mangroves in the overall nutrient budget of these tropical coastal ecosystems, we investigated as part of the KMFRI/VUB contribution to the EC STD-3 Project "Interlinkages between Eastern-African coastal Ecosystems" (1) the sediment characteristics and pore-water chemistry of mangrove sediments; (2) the major factors affecting water column nutrients concentration, focusing on the epibenthic fluxes or sediment/water nutrient fluxes; (3) the main nitrogen transformational processes in the sediments: organic nitrogen remineralization, ammonification, nitrification, nitrogen fixation and denitrification.

METHODS

Study area

Rhizophora mucronata and *Ceriops tagal* species are the two most common species in Gazi mangrove forest, covering almost 70% of the total area of the mangrove vegetation. Areas covered by these two species were therefore selected for the nitrogen-transformational process studies. A *Ceriops tagal* and a *Rhizophora mucronata* plot (referred to as nrs. 1 and 2 respectively). The *Rhizophora* stands are inundated twice a day because of their low elevation compared to the one of the *Ceriops* stands which are inundated only during the spring high tides. These two different flooding rates are bound to reflect different physico-chemical patterns in the two sediment types. A sub plot covering an area of 20 by 20m was established at each of the two study plots and all sediment samples for the various analysis were picked from those sub plots. Exact description of the whole study area is given elsewhere in this report (Kitheka et al.).

Geological parameters

Peat comprises larger amounts of organic matter relative to humus (Ranjan and Rao, 1991). Humus, quartz sands and carbonate have densities of 1.3 - 1.5 g cm⁻³, 2.5 - 2.8 g cm⁻³ and 2.7 - 4.30 g cm⁻³ respectively (Deer et al. 1974; Hakanson and Jansson, 1983). Based on this, about 100 to 150g of sediment sample was placed in 1 litre measuring cylinder, to which distilled water was added until the sample was covered. The mixture was thoroughly shaken, after which it was stirred for about 4 hrs at intervals of 1 hr for mud to form on top of the sand. The samples were left overnight for all material to settle down. After this, the column heights of sand and mud were determined, from which percentage of each by volume was determined. The mud was then removed carefully by decanting, after which the sand was dried and stored for further analysis.

A sieve shaker and a set of sieves of mesh sizes ranging from 0.063 to 1 mm were used to determine mean grain size from the sand obtained above. Levels of various grain sizes were

determined as percentages by weight. Sorting, skewness and kurtosis were then calculated as described by Babu and Sinha, 1987. Grain shapes and lithology of the sand fraction were also investigated using an ordinary microscope at a magnification of 12.

Nutrient stocks and physico-chemical parameters

The sediment samples for the analysis of the nutrient stocks, processes and other physico-chemical parameters were collected by hand using clear acrylic cores (i.d. 3.6 cm, length 25 cm) and immediately transported to the laboratory. The sediments were then sectioned to cover seven depth intervals; 0-1, 1-2, 2-4, 4-6, 6-8, 8-10 and 10-12 cm. Interstitial water sample from each segment was then obtained by KCl extraction (10 g wet sediment: 40 ml of 1N KCl) and centrifugation at 2000 x g for 10min (Henriksen et al. 1981). The KCl-porewater extracts were then filtered (0.42 µm GF/F millipore fibre filter) into vials and frozen immediately for subsequent analysis of NH_4^+ , and $\text{NO}_3^- + \text{NO}_2^-$. Nitrate determination was done using a Technicon Autoanalyzer using the standard methods of Armstrong et al. (1967) and Chan & Riley (1970) while ammonium determination were performed manually using the phenol hypochlorite method (Solorzano, 1969). Pore-water for salinity determination was obtained from the sectioned segments by pressure suction using N_2 gas. Since porewater volumes were very small, salinity was determined mainly by using a refractometer. Pore water content (porosity) was determined from the weight loss of known volume of sediment dried to constant weight at 105 °C. Organic content was determined as the Ignition loss (LOI) of dried sediment after 24 hr at 450°C. Carbon and Nitrogen contents were determined (at Free University, Brussels) from the dried (105°C) sediments by the use of an NA 1500 Carbon-Nitrogen Analyzer (Carlo Erba Instrumentazione) while the $\delta^{13}\text{C}$ isotope signature was determined using the NA 1500 C/N Analyzer in line with a Finnigan Delta E Isotope Ratio Mass Spectrometer interfaced with a Finnigan Mat CT CN-NT trapping box. Results are expressed relative to the PDB limestone reference.

Nitrogen transformational processes

Ammonification rates in sediments were measured using a technique similar to that described by Aller and Yingst, 1980. In principle, this technique involved incubating (under anaerobic condition) approx. 10g of sediment (replicate samples) from each section with 30ml of distilled water in a 100 ml serum vials on a shaker table. The increase of ammonium concentration with time was calculated as the ammonification rate.

Potential nitrification rates in the sediments were assessed using the technique described by Henriksen et al., 1981 and Caffrey and Kemp, 1990. Duplicate samples (about 2 g) from different depths were incubated in 50 ml of filtered sea water (from the water overlying the sediment station) for 24hr under aerobic conditions at ca. 25°C on a shaker table. The seawater used was enriched with NH_4Cl (0.5 mmol l⁻¹) and KH_2PO_4 (0.1 mmol l⁻¹). After the incubation period of 24 hrs (and sometime 72 hrs), sediment from replicate flasks were centrifuged and the water filtered and analyzed for $\text{NO}_3^- + \text{NO}_2^-$. Potential nitrification rates of sediment at different depth were then calculated from the accumulation of $\text{NO}_3^- + \text{NO}_2^-$.

Actual nitrification rates were measured on undisturbed sediment cores using ATU inhibition method as described by Hall, 1984. In each case about 10 cores (sediment adjusted to about 6 cm) were used. Five cores were injected with the ATU at 1 cm interval diagonally while the other five were used as controls. Incubation time was 24 hrs in the dark.

Ammonium regeneration and assimilation rates were investigated using the ^{15}N isotope dilution technique (Blackburn, 1979; Izumi et al. 1982; Blackburn and Henriksen, 1983; Bowden, 1984; Selmer, 1988). In this technique the rate of ammonium regeneration and uptake is determined by labelling the product, i.e ammonium. The ^{15}N labelled is initially added to the sediment sample and the dilution of the atom % ^{15}N with regenerated ammonium of only the natural background ^{15}N abundance (0.366%) is monitored with time. By determining the initial and final ammonium concentration and atom % ^{15}N of the ammonium pool, the rate of dilution of ammonium pool (equal to the rate of ammonium regeneration) and uptake rate of ammonium were calculated according to Blackburn (1979).

In each case 10 g wet sediment from 0-1 and 1-6 cm depth were used for regeneration studies. These sub-samples were spiked (in duplicate) with 0.1 ml of $^{15}\text{NH}_4\text{Cl}$ spike (750 µM) and

ammonium extracted with KCl as discussed earlier. Ammonium pool was determined using the phenol-hypochlorite method while samples for ^{15}N % atom determination were analyzed using the JASCO NIA-1 ^{15}N analyzer after trapping the ammonium using a micro diffusion technique described by Kazungu and Goeyens, 1989.

Nitrogen fixation was investigated using the acetylene reduction incubation technique (Hardy et al. 1973) which is an indirect method. Perplex tubes fitted with silicone filled holes along the tube, were used to perform the acetylene reduction technique on undisturbed cores of sediments. During each sampling, ten cores were collected in each plot. *Rhizophora* and *Cerriops* plots were investigated at low and high tide respectively. The cores were brought back to the laboratory and injected with acetylene-saturated water, calculated to give 10% saturation, through the silicone filled holes. Three cores were injected from 0 to 1 cm depth, three others from 0 to 3 cm and the last three, from 0 to 5 cm. Each core was also injected with 5 ml C_2H_2 gas in the headspace. One core didn't receive any acetylene to check for natural production of ethylene. Reduction of acetylene into ethylene was followed by hourly analyses of 100 μl gas phase samples during 6 to 8 hours, with a Varian model 3300 gas chromatograph, set up at KMFRI during the last STD-2 programme.

The method used for measuring denitrification is the recently described nitrogen isotope-pairing technique (Nielsen, 1992). This method allows to determine both denitrification and coupled nitrification-denitrification processes in sediments. It consists in spiking of the water overlaying the sediment with enriched $^{15}\text{NO}_3^-$ and the mass spectrometric analysis of the isotopic distribution of ^{29}N and ^{30}N in N_2 formed by denitrification.

Eight intact sediment cores were collected at high tide in the *Cerriops* and *Rhizophora* plot. The cores were kept in the fridge for one night. Next morning, the overlaying water of each core was replaced, by 80 ml of filtered seawater left 3 days in the lab to exhaust the nitrates. After 30 minutes of stabilization, the cores were incubated in the dark, with addition of 3.2 ml of a stock solution 1000 μM of 99.8% $^{15}\text{NO}_3^-$ to reach a final concentration of 40 μM . In each core, the overlaying water was stirred by small magnetic stirring bars rotating via a 12 V micromotor during incubation. Incubation time was 30', 2 h, 4h and 6h. At the end of the incubation period, a few drops of ZnCl_2 solution (1g ml^{-1}) were added to the core to stop the denitrification. The whole core was then thoroughly mixed and the sediment allowed to settle for 10 minutes. The overlaying water was sampled with a syringe and stored in 10 ml serum vials to which 50 μl of ZnCl_2 solution (1g ml^{-1}) was added to stop the denitrification process. Analysis of ^{29}N and ^{30}N was done by mass spectrometry at the University of Aarhus, Denmark (Dr. L. P. Nielsen). The production of ^{29}N and ^{30}N in each core, expressed in $\mu\text{mol N h}^{-1} \text{ m}^{-2}$, was calculated knowing the distribution coefficient of N_2 in water and gas, the total volume of water in the cores and the slope value of the linear regression between incubation time and production of ^{29}N and ^{30}N .

Sediment - water nutrient fluxes

For the investigation of sediment - water fluxes of NH_4^+ and NO_3^- intact core incubations (4 to 6h) were performed using a technique similar to that described by Henriksen et al. (1981). About 12 cm of sediment depth was sampled with Perspex tubes of 3.6 cm I.D. and 30 cm length and with the overlaying water replaced with 80 ml of filtered seawater collected from the sampling location. This overlaying water was also gently bubbled with clean air (passed through H_2SO_4 acid) to maintain oxygen gradients. For every experiment, about five sediment cores were incubated. Two more empty cores were filled with the filtered water from the same sampling station and used as controls. The increase (or decrease) of the NH_4^+ and NO_3^- over the incubation time was used to calculate the flux rates.

For repeated incubations, intact sediment cores (diameter = 4 cm, height = 35 cm) were collected in the field. In the laboratory, the overlaying water was replaced by filtered water collected from the sampling site. The cores were incubated in the dark during 2 to 4 hours while the overlaying water was continuously stirred by small magnetic stirring bars rotating via a 12 V micromotor. The overlaying water was sampled for ammonium analysis and replaced by a new aliquot of filtered water from the field. All cores were incubated again for 4 to 8 h. Then the overlaying water was sampled again, replaced by new filtered water and the cores were incubated for another period of 9 to 13 hours. The slope value of the linear regression between incubation time and ammonium accumulation was used to calculate the flux of ammonium from the sediments to the overlaying water column.

RESULTS

Geological parameters

Determination of the mud and sand levels for the surface (0-10 cm) and bottom (10-20 cm) sediment for the two study biotopes indicated slight differences. *Cerriops tagal* had a percentage mud level of 48% (by volume) for the surface which increased to 78% (by volume) at 20 cm depth while for *Rhizophora* the surface mud portions was 70% which increased to 98% at 20 cm depth (Fig. 2). Lithological analysis of the sediment revealed that carbonate forms only about 1% while the rest of the mangrove sediment is composed of quartz (Table 1). Generally, the mangrove sand were found to be medium to fine grained with grains mean diameter ranging from 2.04 - 2.17 and 1.68 - 2.11 on the phi scale in surface and bottom sediments respectively (table 1 and 2). The sediments are also poorly sorted with sorting ranging from 1.78 to 1.88 and 1.60 - 1.84 on the phi scale for the surface and bottom sediments, respectively. The largest portion of the sediment's sand (both for *Cerriops* and *Rhizophora*) were found to have grain size of 2.39 on phi scale which corresponds with grain size width of 0.18 mm (Fig. 3 and table 2). Table 1 also shows sorting, skewness and kurtosis values as calculated from cumulative curves using mathematical formulars given by Babu and Sinha (1987).

Physico-chemical parameters

Fresh riverine water is introduced into the bay by river Kidogoweni and river Mkurumuji whose maximum discharge in rainy season is $5 \text{ m}^3\text{s}^{-1}$ and $12 \text{ m}^3\text{s}^{-1}$ respectively, (Kitheka et al., this issue). This discharged volume is rather low compared to the volume of sea water which fills the bay and creeks during high tide. Due to this low discharged volume of riverine water into the bay during rainy season, salinity fluctuations in the bay do not change very much (especially at high tide) with seasons. The main salinity changes are noticed on water column within the creek leading to the Kidogoweni river.

The lowest salinity recorded at the water column above the *Rhizophora* study plot during rainy season was about 32 ppt while the highest recorded in dry season was about 36‰ (Table 3). This low salinity fluctuation range (ca 4 ppt) within the water overlying the *Rhizophora* study plot was found not to have a significant effect on the pore water salinity of *Rhizophora* sediment (Table 3). During the dry season (February/March) pore water salinity at the 0-1 cm depth was 38.0 ± 2 ppt and did not change much with depth while in wet season it was 34.0 ± 4.0 ppt at the surface and increased slightly with depth. The relatively high standard deviation noticed for the 0-1 and 1-2 cm depth during rainy season reflects the variability of the salinity with sampling time. Heavy down pour on exposed (low tide) sediment had an effect of slightly lowering the surface pore water.

For the sediment of the *Cerriops* plot, the surface salinities were found to be 46 ± 5 ppt and increased to 58 ± 3 ppt at 12 cm depth (Fig. 5) during dry period. During rainy season, the surface salinities were found to be slightly lower (42 ± 6 ppt) but also increased slightly to 57 ± 2 ppt at 12 cm depth. These samples were taken during spring high tide when the water column height was about 30 cm. However during neap tides, the surface (0-1 cm) salinities were found to increase upto 58 ± 3 ppt. In this case, flooding during spring tide reduces the sediment's salinity mainly by dilution while evapotranspiration of surface porewater during neap tide raises the salinity of the sediment's porewater.

Rhizophora mucronata sediments (RMS) were found to have a higher water content than that of *Cerriops tagal*. The 0-1 cm sections of the RMS has a water content of 68% (fig. 6a) which decrease gradually to 50% at 12 cm depth. For *Cerriops tagal* sediment (CTS), the surface sediment (0-1 cm) had a water content (fig. 6b) of 24% which increased gradually to 48% at 12 cm depth. Due to these differences in water content, porosity values for the two sediments were different. The surface porosity for the RMS was 0.92 ± 0.04 (v/v) which decreased to 0.74 ± 0.02 (v/v) at 12 cm depth while for CTS, it was 0.46 ± 0.05 for the surface and increased gradually to 0.65 ± 0.02 at 12 cm depth (Tables 4a & b).

Density for RMS increased slightly from $1.35 \pm 0.05 \text{ g cm}^{-3}$ at the surface to $1.48 \pm 0.05 \text{ g cm}^{-3}$ at 12 cm depth while for CTS it was slightly higher, being $1.91 \pm 0.14 \text{ g cm}^{-3}$ at the surface decreasing to $1.48 \pm 0.07 \text{ g cm}^{-3}$ at 12 cm depth (Tables 4a and 4b).

Organic Matter

Organic matter in sediments plays a very key role in fuelling most of the oxidation processes in

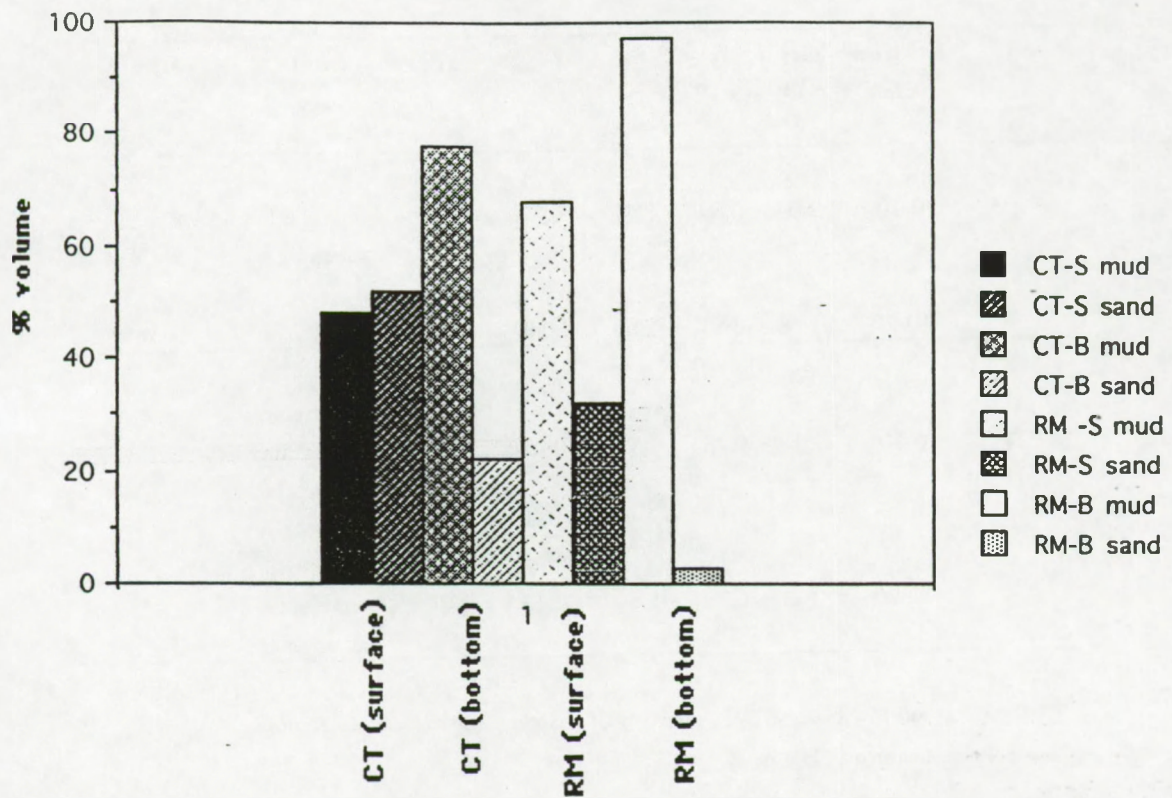


Fig. 2 : A bar graph showing mud and sand levels for the surface (S: 0-10 cm) and bottom (B: 10-20 cm) sediments of *Ceriops tagal* (CT) and *Rhizophora mucronata* (RM) biotopes of Gazi Bay.

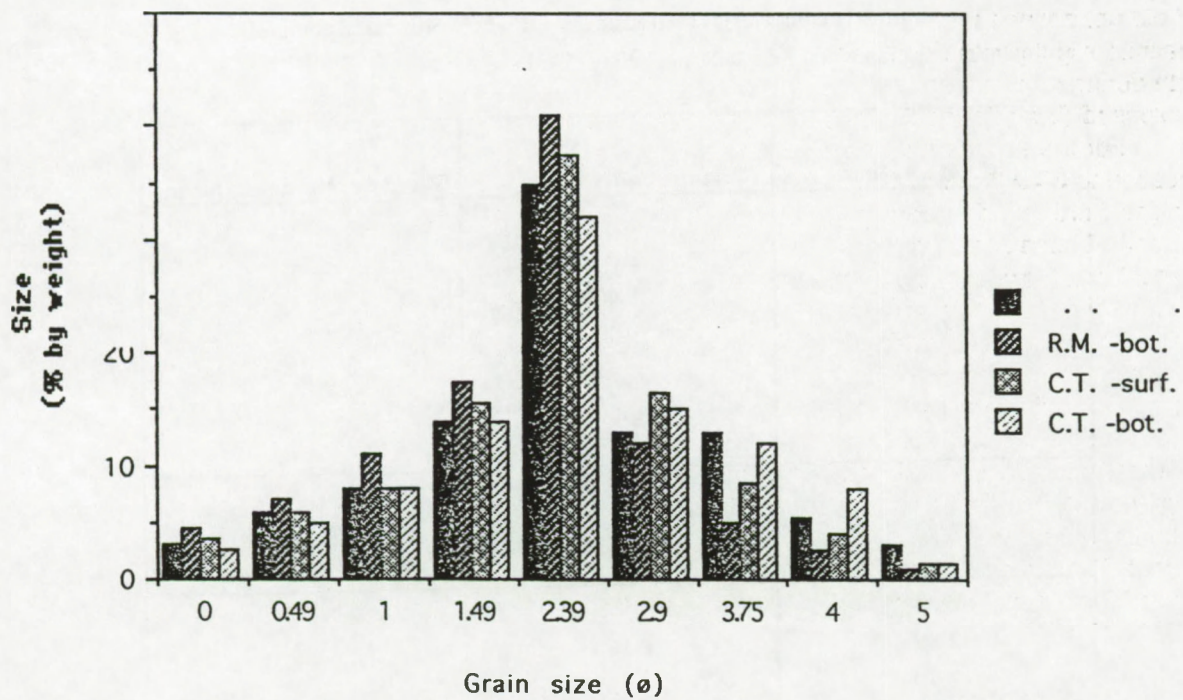


Fig. 3 : Histograms showing percentages by weight of various grain sizes of surface (0-10 cm) and bottom (10-20 cm) sediments of the *Ceriops* (CT) and *Rhizophora mucronata* (RM) biotopes.

Table 1 : Statistical parameters of grain size analysis, shape and lithology of sediments inhabited by *Rhizophora mucronata* and *Ceriops tagal* mangrove species.

St.	Section (cm)	Grain size ($\phi \pm S.D.$)	S_0	ϕ_k	K	Shape	Lithology
R. M.	0-10	2.04 ± 0.80	1.88	0.23	0.61	angular to subangular	99 % quartz, 1 % CO_3^{2-}
	10-20	1.68 ± 0.63	1.60	- 0.04	1.14	"	"
C.T.	0-10	2.17 ± 0.43	1.78	0.45	1.16	subangular larger grains and angular smaller grains	"
	10-20	2.11 ± 0.79	1.84	0.13	1.01	angular to subangular	"

R.M.:- *Rhizophora Mucronata*; C.T. :- *Ceriops tagal*; S_0 :-Sorting; ϕ_k :-skewness; K:- Kurtosis .

Scale of measurements is Phi (ϕ).

Table 2: The millimeter equivalents of phi scale and the wentworth descriptions of sediment grains diameters. Adapted from Selley (1981).

phi (ϕ) values	mm equivalents	Wentworth descriptions
- 1.00 - 0.49 0.00 0.49 1.00	2.00 1.40 1.00 0.71 0.50	coarse
1.49	0.355	medium
2.39 2.90	0.180 0.125	fine
3.47 4.00	0.090 0.063	very fine

Table 3: Salinity readings obtained from the water column and the sediment within the Rhizophora study plot during dry (February/March) and rainy season (May/June) of 1992/1993/1994. The water column salinities were taken when the water above the sediment was about 30 cm. Means \pm S.D. shown.

Section (cm)	Dry season S \pm S.D. (ppt) (n = 13)	Rainy season S \pm S.D. (ppt) (n = 17)
water column	35.0 \pm 1.0	34.0 \pm 2.0
0 - 1	38.0 \pm 2.0	34.0 \pm 4.0
1 - 2	39.0 \pm 1.0	36.0 \pm 3.0
2 - 4	40.0 \pm 1.0	38.0 \pm 3.0
4 - 6	40.0 \pm 2.0	40.0 \pm 1.0
6 - 8	40.0 \pm 1.0	39.0 \pm 1.0
8 - 10	41.0 \pm 1.0	40.0 \pm 1.0
10 - 12	40.0 \pm 1.0	40.0 \pm 1.0

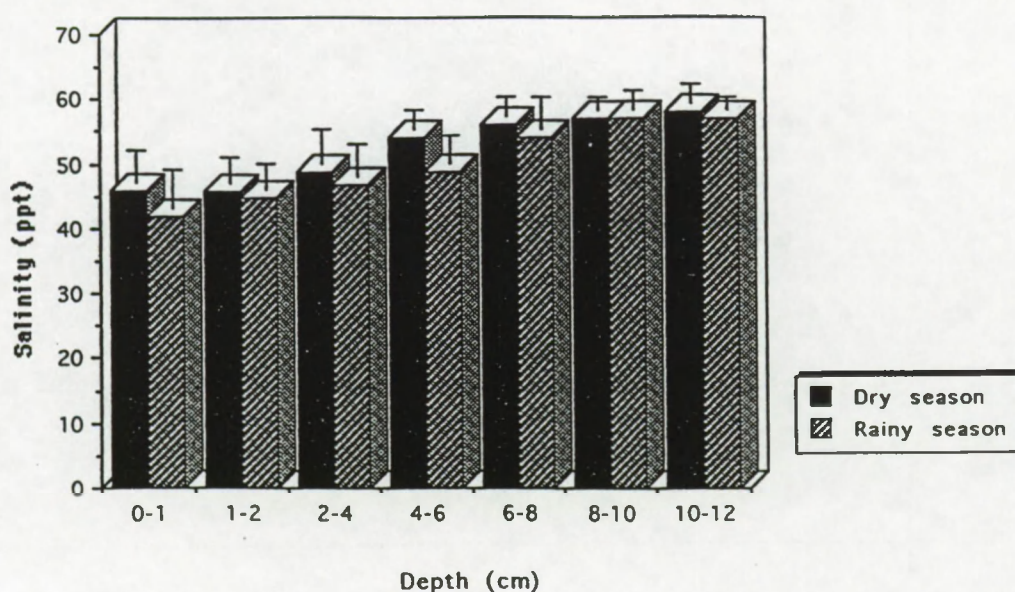


Fig. 5: Average (\pm S.D.) salinity values for the 0 - 12 cm depth of *Ceriops tagal* sediments during dry and rainy seasons of 1992/3/4. n = 12.

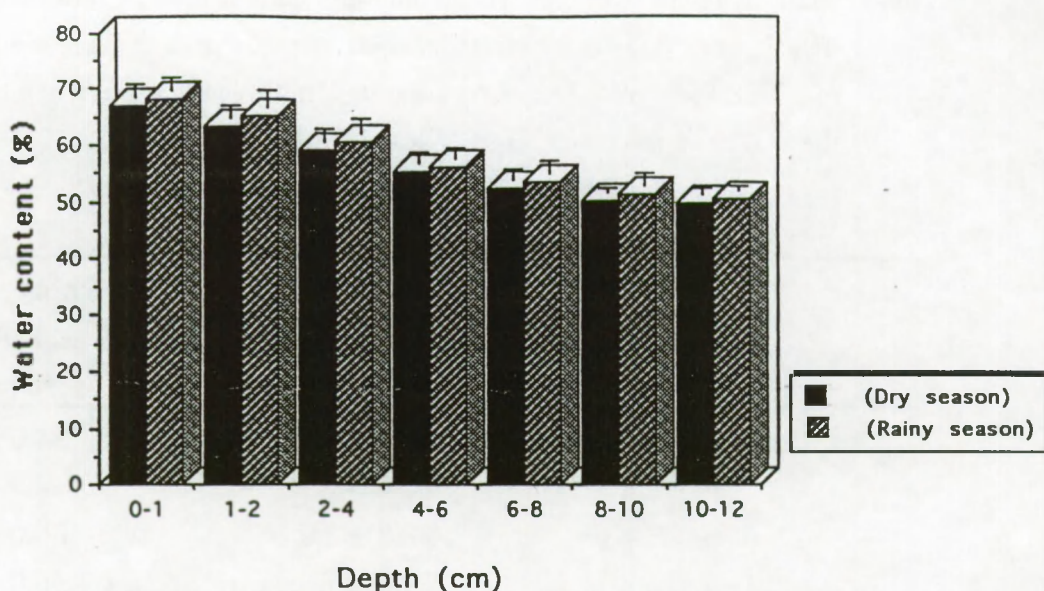


Fig. 6a: Average water content (%) of *Rhizophora mucronata* sediment during dry (Feb./Mar.) and Rainy (May/June) seasons between 1992 and 1994. $n=24$.

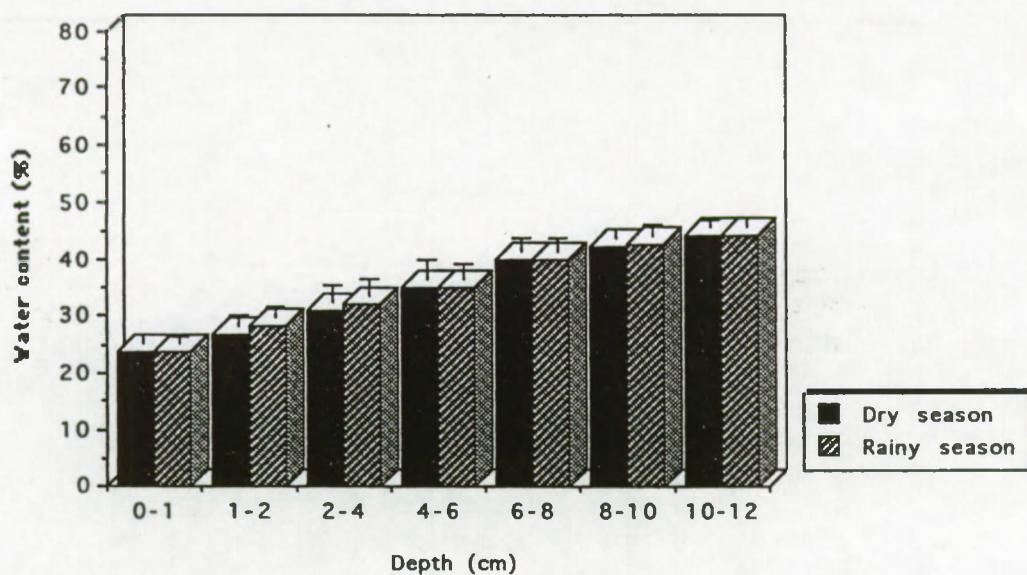


Fig. 6b: Average water content (%) of *Ceriops* sediment during dry (Feb./mar.) and rainy (May/June) seasons between 1992 and 1994. $n= 24$.

sediments. As organic carbon is oxidised, nitrogen is re-mineralised hence becoming available for uptake by plants or release into the water column by diffusion. Source determination of carbon in Gazi *Rhizophora* sediments using carbon - 13 isotope abundance (Rao et al. 1993) revealed that the mangrove vegetation was the major contributor of organic carbon in the sediments. In order to investigate whether there is a seasonal variation of organic matter in mangrove sediments, samples were analysed for organic matter contents during both - the dry (February and March) and rainy (May/June) seasons of 1992/1993/1994.

For *Rhizophora* sediment, the highest organic matter (LOI) content ($21 \pm 1\%$ D.W_{sediments}) were found at the surface and decreased gradually to $13 \pm 2\%$ DW_{sediments} at the 12 cm depth. Organic matter contents for *Ceriops* sediment were much lower, being $2.40 \pm 0.5\%$ D.W_{sediment} at the surface and increasing to $10.46 \pm 1.20\%$ D.W_{sediment} at 12 cm depth (Tables 4a & 4b). One striking observation in both sediments is the lack of significant variation ($p \leq 0.05$ for all corresponding sections) of organic matter content with seasons. Tables 4a & b shows the other parameters : total organic carbon (TOC); total organic nitrogen (TON), and C:N atom ratio which were measured and determined on some of the sediment samples analysed for organic matter content. *Ceriops* sediment is seen to be poorer in organic nitrogen than the *Rhizophora* sediment. The C:N ratio for the *Rhizophora* sediment increased from $23.1 \pm 1\%$ at the surface to about $30 \pm 1\%$ at 12 cm depth while for *Ceriops*, it increased from $19 \pm 2\%$ at the surface to about $39 \pm 2\%$ at 12 cm depth. A slight increase (becoming less negative) was noticed for $\delta^{13}\text{C}$ biotope signature from bottom (12 cm) to the surface. In both cases, the $\delta^{13}\text{C}$ signature obtained for sediment were close to those obtained for the mangrove leaves at the specific study plots (Rao et al., 1994). Since no significant seasonal differences were noticed for rainy and dry season (ANOVA statistical testing gives $P \leq 0.05$ in all corresponding sections per season), all the results have been pooled together resulting in Table 4.

Nutrients stock (NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$) and their spatial distribution within the *Rhizophora* and *Ceriops* study plots

In order to investigate on the nutrient (NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$) stock in our study plots, five 1m x 1m subplots were established within the two study plots. Six core samples (plexiglass cores I.D. 3.6 cm, height 25 cm) were taken randomly from each subplot. Immediately after sampling, one core from each plot was used for Redox potential determination using platinum electrode with calomel reference. This was done within two hours of sample collection. The remaining twenty five cores from the five subplots were rushed to the laboratory (two hours drive) where they were sectioned into 0-1, 1-2, 2-4, 4-6, 6-8, 8-10 and 10-12 cm sections. Corresponding sections of one core from each subplot were pooled together and mixed thoroughly. This mixed sediment was used for porosity and density determination. All the other segments were extracted individually with corresponding volumes of potassium chloride (40 ml 1N KCl:10g sediment) under nitrogen gas as explained earlier. The ammonium pool obtained represents total ammonium (free plus ionically-bound) concentrations.

Ammonium stock and its spatial distribution within the *Rhizophora* plots

Total ammonium concentrations in the sediment for the upper 12 cm section were found to vary between 100 and 200 μM . Cores from subplots A and D in the plot were taken from an area with a dense network of fine roots as compared to cores from subplots B, C and E. Based on this and the nitrate profiles, results from these cores were averaged together to form two groups; namely A and D group and the B, C, E group. Fig. 13 shows the average NH_4^+ profiles from subplot A and D and those obtained from the average of subplot B, C and E (excluding standard deviation). These two profiles were not only similar but almost coinciding. The average NH_4^+ concentration profile (including standard deviation) of all the cores sampled (20 cores) was found to fit well between the first two profiles. One clear observation noticed from these profiles is that the NH_4^+ concentrations in the upper 12 cm depth of *Rhizophora* sediment varies between 100 and 200 μM with the maximum always observed between 1 and 2 cm depth followed by a gradual decrease with depth. One other characteristic noticed with the NH_4^+ profile is the high standard deviation which lies between 10 to 30% of the observed concentration. This stresses on the fact that even within a one by one meter subplot standard deviation on sampled cores could be as high as 30% of the concentration measured. On the average, the results obtained indicates that cores taken from any

Table 4a : A table showing various physico-chemical parameters at Rhizophora sediment as observed during the dry and rainy season of 1992/3/4. TOC , TON and C/N atom ratio are for the samples of 1992. n= number of observations.

Section (cm)	Density (g cm ³) (n=24)	Porosity cm ³ cm ³ (n=24)	Organic Matter LOI (%) (n=24)	TOC (%) (n=4)	TON (%) (n=4)	C:N (n=4)	$\delta^{13}\text{C}$ (n=4)
0-1	1.35±0.05	0.92 ± 0.04	21.08 ± 0.93	9.27 ± 0.93	0.47 ± 0.05	23.01 ± 0.84	-25.52 ± 0.42
1-2	1.33±0.07	0.85 ± 0.05	19.16 ± 1.58	9.59 ± 1.16	0.44 ± 0.05	25.43 ± 0.42	-25.97 ± 0.25
2-4	1.36±0.05	0.82 ± 0.03	17.48 ± 1.05	9.32 ± 2.25	0.41 ± 0.11	26.52 ± 1.67	-26.36 ± 0.14
4-6	1.42±0.03	0.78 ± 0.02	17.36 ± 1.72	8.22 ± 0.75	0.35 ± 0.05	27.40 ± 1.24	-26.45 ± 0.10
6-8	1.49±0.03	0.78 ± 0.01	15.55 ± 1.69	8.06 ± 0.59	0.32 ± 0.03	29.39 ± 0.85	-26.36 ± 0.13
8-10	1.48±0.01	0.78 ± 0.02	14.16 ± 1.50	7.84 ± 0.91	0.29 ± 0.03	31.54 ± 0.60	-26.46 ± 0.06
10-12	1.48±0.03	0.74 ± 0.02	13.21 ± 1.63	6.78 ± 0.60	0.26 ± 0.04	30.42 ± 0.76	-26.46 ± 0.04

Table 4b : A table showing various physico-chemical parameters at Ceriop sediment as observed during the dry and rainy seasons of 1992/3/4. TOC , TON and C/N atom ratio are for the samples of 1992. n = number of observations.

Section (cm)	Density (g cm ³) (n=24)	Porosity cm ³ cm ³ (n=24)	Organic Matter LOI (%) (n=24)	TOC (%) (n=4)	TON (%) (n=4)	C:N (n=4)	$\delta^{13}\text{C}$ (n=4)
0-1	1.91 ± 0.14	0.46 ± 0.05	2.40 ± 0.50	0.81 ± 0.22	0.05 ± 0.01	18.90 ± 0.91	- 22.94 ± 0.53
1-2	1.80 ± 0.12	0.50 ± 0.04	3.07 ± 0.50	1.06 ± 0.31	0.05 ± 0.01	24.73 ± 2.81	- 23.49 ± 0.44
2-4	1.74 ± 0.16	0.55 ± 0.05	5.46 ± 1.31	1.77 ± 0.31	0.08 ± 0.02	25.81 ± 2.50	- 23.59 ± 0.36
4-6	1.63 ± 0.16	0.57 ± 0.07	7.34 ± 1.85	2.87 ± 0.27	0.11 ± 0.01	30.44 ± 1.70	- 24.13 ± 0.37
6-8	1.62 ± 0.05	0.66 ± 0.04	9.23 ± 1.61	3.51 ± 0.35	0.13 ± 0.01	31.50 ± 2.01	- 24.49 ± 0.40
8-10	1.57 ± 0.05	0.66 ± 0.02	10.64 ± 1.21	4.12 ± 0.44	0.13 ± 0.01	36.97 ± 1.90	- 24.37 ± 0.21
10-12	1.48 ± 0.07	0.65 ± 0.02	10.46 ± 1.20	4.66 ± 0.24	0.14 ± 0.01	38.83 ± 1.78	- 24.51 ± 0.28

part of the plot would give representative NH_4^+ profile of the general area. Experiments on adsorption capacities of *Rhizophora* sediments (results not included) indicates that upto about 55 % of this total ammonium concentration (free and ionically bound NH_4^+) is adsorbed and only about 45 % is free within the interstitial water.

Nitrate stock and its spatial distribution within the *Rhizophora* plots

Unlike the ammonium profiles, nitrate profiles exhibited two distinct patterns. All cores taken from subplots A and D displayed a maximum at between 2 and 5 cm depth. Cores taken from subplots B, C and E were found to have a different type of profiles with high concentrations found at the top section and decreased sharply with depth. As explained earlier, samples from sub-areas A and D were characterized by the presence of a dense root network as compared to sub areas B, C and E. Nitrate profiles from subplot D indicated that even within a one by one square meter plot, nitrate concentration might be very different despite having the same profile pattern. Core D3 indicated a maximum peak value of ca. $7.50 \mu\text{M}$ while core D1 has a maximum concentration of ca. $2.0 \mu\text{M}$ at similar depth. This stresses on the fact that even on an area with roots, the biomass of the live roots or proximity of the sampling spot to the roots may result in having different concentrations within a closeby vicinity. Figure 19 gives profiles for mean nitrate values for subplots B, C and E and A and D where apart from the surface section whose concentrations are statistically not different ($p=0.051$; $n=20$), the other concentrations below are different. The lack of statistical difference in the nitrate concentrations at the surface implies that while the nitrate concentrations below the surface may depend on the presence or absence of roots to transport O_2 to the anaerobic sediment, the surface nitrate mostly depends on molecular diffusion of oxygen from the water column into the sediment. The figure also displays the average nitrate profile (including standard deviation) obtained from all the twenty cores. The difference in profile patterns obtained between the cores from subplots A and D and those from B, C and E and the high standard deviation (almost 100% between 3 and 5 cm depth) observed when pooling all the results together confirm that unlike the ammonium stock, a few cores taken randomly from a mangrove sediment biotope can not be used to give a general nitrate profile of the area. Since the two different profiles obtained for nitrate did not affect the general profile of ammonium pool (Fig.13), this suggests that nitrification due to oxygen supply by roots is also of less magnitude and does not affect the ammonium profile significantly. Any effect on the ammonium pool could easily be masked by the high standard deviation noticed on ammonium concentrations.

Redox potential profiles

The redox potential profiles (Eh) obtained in subplots A, B, C, D and E within the *Rhizophora* plot in all five cases showed that redox potential within the water column (1 cm above sediment surface) was between + 250 and + 300 mV indicating relatively higher oxygen concentrations. However at 0-1 cm depth, the redox potential dropped to about + 150. In all the profiles we notice a steady decrease of redox potential up to 6.5 cm depth (for profiles B, C and E) and 7.5 depth (for A and D Profiles) where it then remains at -50 mV down to 12 cm depth. Note that core C displayed higher redox potential between the 1 and 4 cm depth than all the other cores despite being in the subplots considered to be roots-free as the others. McKee et al. (1988), investigating on physico-chemical parameters of sediment colonised by mangrove vegetation observed a positive correlation between soil redox potentials and the presence of the aerial roots of mangrove trees. Soil redox potentials near the aerial roots were always found to be higher than in the adjacent sediment. The increase of redox potential between the 1 and 4 depth in core C is also most likely due to fine roots since nitrate profiles from subplot C were also slightly higher than those from subplots B and E (figs. 16 & 17). From figure 20, we find that below 1cm depth redox potential values for cores A and D starts being more positive than those of cores B and E (disregard core C profile). This increase of redox potential is most probably due to the supply of oxygen by the roots hence the higher nitrate concentrations at 2-5 cm depth noticed for nitrate profiles from subplots A and D. Note that while the widest difference in redox potential was found between 5 and 7 cm depth, the nitrate maxima in subplots A and D were found at a slightly upper depth (2-5 cm depth). Potential nitrification experiments in *Rhizophora* sediment (discussed latter) indicates significant reduction of nitrifiers bacterial biomass below 4 cm depth.

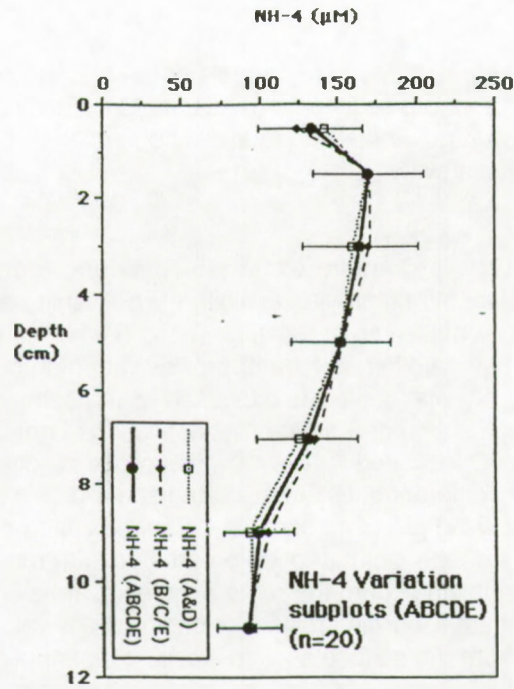


Fig. 13: Ammonium profiles as observed for subplots A & D and B, C and E in Rhizophora sediments. A profile giving average values (including S.D.) for all the 20 cores analysed is also shown.

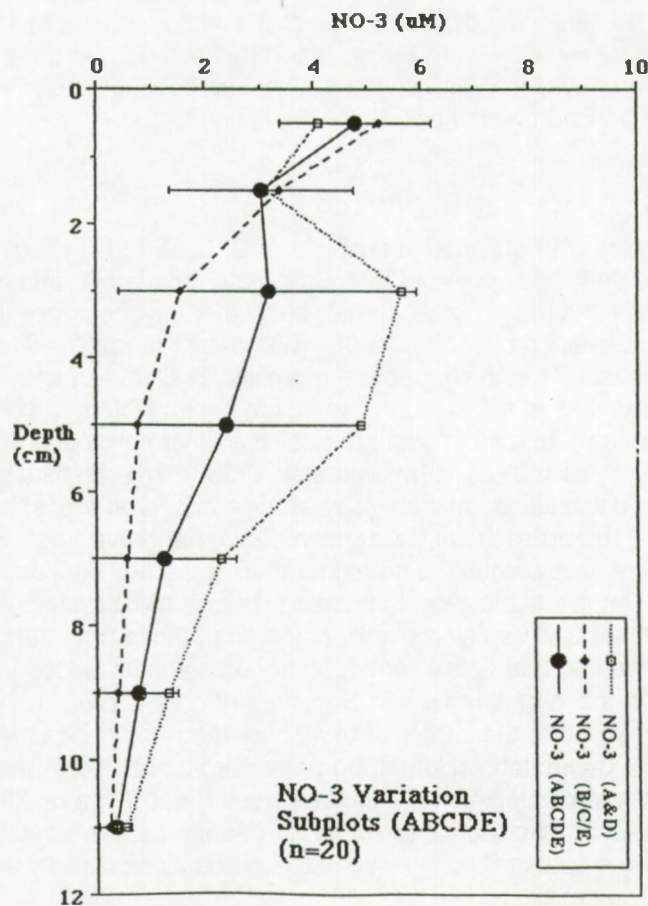


Fig. 19: Average nitrate profiles from subplots A&D and B, C and E. The average nitrate profile (\pm S.D.) for all the five subplots (ABCDE) is also displayed.

Ammonium stock and its spatial distribution within the *Ceriops tagal* study plots.

Ammonium variations in the five individual subplots within the *Ceriops* biotope were more-or - less the same as those displayed for the *Rhizophora* sediment. The mean vertical NH_4^+ profile (Fig. 21) was similar to that of *Rhizophora* sediment except that ammonium concentrations were higher (varying mostly between 100 and 300 μM) with an average maximum of about $260 \pm 55 \mu\text{M}$ at about 2 cm depth. Adsorption capacity of *Ceriops* sediments (results not shown) indicated that unlike the *Rhizophora* sediments about 80 % of this total ammonium pool is free within the interstitial pool while only ca. 20 % is adsorbed.

Nitrate stock and its spatial distribution within the *Ceriops* study plot

The nitrate profiles from the *Ceriops* plot displayed slightly higher concentrations with sub-surface peaks (Fig. 23). Values as high as 30 μM nitrate concentrations were observed for *Ceriops* sediments.

Redox potential profiles

In all the twenty cores analyzed, none had maximum concentration at the surface (0-1 cm) as displayed for some cores in *Rhizophora* sediment. This implies that the oxygen made available by the *Ceriops tagal* root system plays a major part in maintaining the high sub-surface nitrate concentrations in *Ceriops tagal* sediment. Fig. 23 gives nitrate profile (including S.D) for all the twenty cores sampled. Maximum concentrations are found to lie between 1 to 4 cm depth. The high standard deviations noticed are also most probably due to differences in a core's proximity to a root system.

Redox potential (Eh) for the five sub plots were also found to be higher than those found in *Rhizophora* sediment indicating that the *Ceriops* sediments are more oxidizing than the *Rhizophora* sediment. In fact none of the cores indicated a redox potential of ≤ 0 mV for the upper 12 cm depth. Fig. 24 displays the average redox potential values for the two sediment biotopes where the *Ceriops* sediments are clearly seen to be more oxidizing. Though slight differences have been observed for the two sediment biotopes (*Rhizophora* and *Ceriops*) these dissolved Inorganic nutrient (DIN) concentrations are generally low as it is in other tropical marine sediments (Alongi et al. 1992). The concentrations are typically within the μM range and composed mostly of ammonia with lesser amounts of nitrate and nitrite. DIN in other types of sediments e.g the salt marshes in temperate regions are usually higher and sometimes by even more than one order of magnitude (Klump and Martens, 1981; Kemp et al. 1990).

N-Transformational processes in *Rhizophora* and *Ceriops* sediment

Ammonification, a process of transforming organic nitrogen to ammonium is the first very important process of introducing inorganic nitrogen into our sediment system. However, part of this produced NH_4^+ can be assimilated back by the bacteria responsible for the ammonification process. Regeneration rate minus assimilation rate therefore gives the net ammonification rate. $^{15}\text{NH}_4^+$ isotope dilution technique has been used by several scientists (Blackburn, 1979; Bowden, 1984; Caffrey & Kemp, 1990) for studies of regeneration and assimilation processes in sediments. In this study, we used two different methods for studying ammonification process in *Rhizophora* and *Ceriops* sediment. The first method which involved incubating 10 g of wet sediment in 30 ml of distilled water on a shaker table gave us potential net ammonification value. Ammonification values obtained from this technique were always found to be higher than rates determined by other methods. Values obtained from this technique were therefore used for comparison of the ammonification process in the two mangrove sediment types and also monitor seasonal variations if any. The second technique used for establishing regeneration and assimilation rates involved the use of labeled N-15 compound ($^{15}\text{NH}_4\text{Cl}$), as discussed by Blackburn, 1979. This technique gave regeneration rate, assimilation rate and the net ammonium production. These values were then used for calculation of the nitrogen - budget in the mangrove sediments. Since most mangrove sediments have different porosities, we decided to present ammonification rates in units per gram dry weight instead of units per liter for comparisons. We have therefore expressed our rates in $\text{nmoles N g}^{-1} (\text{D.W}) \text{ d}^{-1}$. These units can easily be converted into $\text{mmoles N m}^{-2} \text{ d}^{-1}$ using the average density and porosity values (tables 4a and 4b).

For *Rhizophora* sediments the average potential ammonification rates (PAR) for dry season

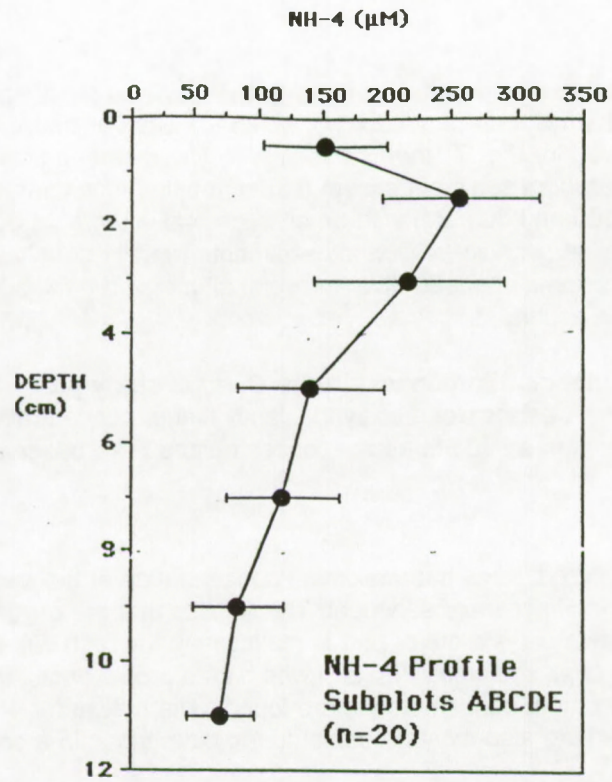


Fig. 21: Average (\pm S.D.) ammonium profile for all the 20 cores sampled at *Cerriopstagal* plot.

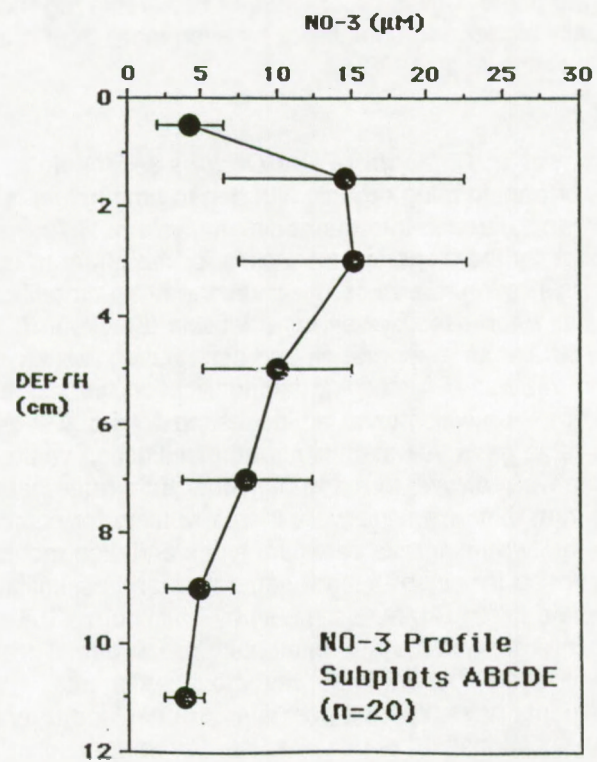


Fig. 23: Average nitrate profile (including S.D.) for all the 20 cores sampled at *Cerriopstagal* plot.

were found not be significantly (at all corresponding depths, $p < 0.05$) different from those observed in rainy season. In the dry season, PAR at the surface was 585 ± 71 and decreased gradually to 211 ± 28 nmoles N g⁻¹(D.W) d⁻¹ at 12 cm depth while in rainy season it decreased from 627 ± 55 at the surface to 207 ± 11 nmoles N g⁻¹ (D.W) d⁻¹ at 12cm depth.

Despite having relatively lower organic nitrogen content, potential ammonification (PAR) rates for *Ceriops* sediment were found to be similar to those of *Rhizophora* sediment. The average PAR during dry season at *Ceriops* sediment was found to be 578 ± 58 nmoles N g⁻¹ (D.W) d⁻¹ at the surface and decreased to 221 ± 31 nmoles N g⁻¹(D.W) g⁻¹ at 12 cm depth while for the rainy season it was 612 ± 57 nmol N g⁻¹(D.W) g⁻¹ at the surface decreasing to 234 ± 31 nmol N g⁻¹(D.W) g⁻¹ at 12cm depth. Ammonification rate measured in anaerobic mangrove sediment of Hinchinbrook Island (Izumi, 1986) displayed rates ranging from 30 to 130 nmol N g⁻¹(D.W) d⁻¹ while Rosenfield (1979), reported net ammonium release of 76 nmol N g⁻¹(D.W) g⁻¹ for Florida mangrove sediments. Average values of 600 nmol N g⁻¹(D.W) g⁻¹ are therefore quite high and are only comparable to those found in Malaysian mangrove sediments (Shaiful et al., 1986) which ranged between 450 and 750 nmol N g⁻¹(D.W) d⁻¹. As noticed earlier organic matter content also did not display seasonal change. Table 7 shows the mean potential ammonification rates of *Rhizophora* and *Ceriops* sediment (pooled data of dry and rainy seasons) of 1992 to 1994. The rates are also expressed in mmol N m⁻²d⁻¹ for comparison with other rates.

Ammonification rates as measured by ¹⁵NH₄⁺ isotope dilution technique

Regeneration and assimilation rates are mostly reported in units of mmol N m⁻² d⁻¹. We have therefore transformed our rates into these units for easy comparison with other reported work. Regeneration (r) and assimilation rates (u) for the two study biotopes again indicated no significant variation with seasons. All observed rates for each biotope were therefore pooled together in Tables 8 and 9 for *Rhizophora* and *Ceriops* sediment. The 0-1 cm sections were incubated aerobically while for the 1-6 cm section the sediments were incubated under anaerobic conditions (N₂ gas).

Potential nitrification in *Rhizophora* sediment

The results are presented in Table 10 and 11. To check possible seasonal variation on potential nitrification (PN) in the *Rhizophora* sediment, PNR determination was done once a month between February, 1993 and July 1994. At each time 10 cores were taken randomly at the study plot, sectioned into 0-1, 1-2 and 2-6 cm sections and all corresponding sections pooled together and mixed thoroughly. Subsamples were then taken from these mixed slurries and used for PNR determination as outlined earlier. No significant difference is noticed on the Potential Nitrification rate. Henriksen et al. (1981) investigating on actual and potential nitrification rates in Danish sediments observed no seasonal variations while Alongi (1989) pointed out that bacterial distributions in mangroves and adjacent sandflats in dry tropics, exhibit little or no seasonality over weekly or monthly intervals.

Potential nitrification rates in *Ceriops tagal* sediments

Ceriops tagal sediment displayed very different potential nitrification rate (PNR) levels (Table 12) as compared to *Rhizophora mucronata* sediments. Surface PNR rates did not exceed 20 nmol N g⁻¹ (D.W) d⁻¹ for any of the subplots randomly selected though a gradual decrease of PNR with depth was also noticed. Redox potential profiles for the four subplots indicated slightly higher values than those found in *Rhizophora* sediment. This would imply more oxidizing environment. The low PNR in *Ceriops tagal* sediment imply low numbers of nitrifying bacteria as compared to the numbers that would be found in *Rhizophora* sediments.

Actual nitrification (ANR)

A direct method of measurement was also used to assess actual nitrification rates within Gazi mangrove sediments:

One of the main steps for the nitrification to occur is bacterial conversion of NH₄⁺ to NO₂⁻:



Table 7 : Average potential ammonification rates of *Rhizophora* and *Ceriops* sediments. The rates are given in both $\text{nmol N g}^{-1}(\text{D.W.})_{\text{sediment}} \text{d}^{-1}$ and $\text{mmol N m}^{-2} \text{d}^{-1}$.

Depth (cm)	Rhizophora Mucronata sediment		Ceriops tagal sediments	
	$\text{nmol N g}^{-1} \text{d}^{-1}$	$\text{mmol N m}^{-2} \text{d}^{-1}$	$\text{nmol N g}^{-1} \text{d}^{-1}$	$\text{mmol N m}^{-2} \text{d}^{-1}$
0-1	606.0	2.61	595.0	8.63
1-2	504.5	2.42	574.0	7.46
2-4	395.0	4.27	421.5	10.03
4-6	313.0	4.01	379.5	8.05
6-8	244.0	3.46	349.0	6.70
8-10	221.0	3.09	280.5	5.11
10-12	209.0	2.93	227.5	3.78

Table 8 : Regeneration (r) and assimilation (u) rates ($\text{mmol N m}^{-2} \text{d}^{-1}$) of *Rhizophora mucronata* sediment as observed between 1992 and 1994. n= number of observations .

Depth (cm)	r (n = 14)	u (n = 14)	r-u (n = 14)	u/r (%)
0-1	3.99 ± 1.12	2.42 ± 0.94	1.51 ± 0.39	60.65
1-6	11.60 ± 3.56	6.96 ± 3.00	4.64 ± 1.58	60.00
0-6 (integrated)	15.59 ± 3.73	9.38 ± 3.14	6.21 ± 1.62	60.17

Table 9: Regeneration (r) and Assimilation (u) rate ($\text{mmol N m}^{-2} \text{d}^{-1}$) of *Ceriops tagal* sediments as observed between 1992 and 1994. n = number of observations.

Depth (cm)	r (n = 12)	u (n = 12)	r-u (n = 12)	u/r (%)
0-1	9.61 ± 2.16	3.72 ± 1.95	5.89 ± 1.48	38.71
1-6	25.42 ± 5.83	10.83 ± 5.97	14.59 ± 3.04	42.60
0-6 (integrated)	35.03 ± 6.63	14.55 ± 6.28	20.48 ± 3.38	41.54

Table 10 : Average rates (without S.D.) of potential nitrification (PN) of subplots A, B, C and D in Rhizophora sediments in January 1993. The rates are also expressed in $\text{mmol N m}^{-2} \text{d}^{-1}$ for easy comparison with actual nitrification rates.

Section (cm)	PN ($\text{nmol N g}^{-1} \text{(D.W.) d}^{-1}$)	PN ($\text{mmol N m}^{-2} \text{d}^{-1}$)
0-1	249.39	1.07
1-2	224.67	1.08
2-4	165.28	1.79
4-6	42.87	0.59
6-8	4.77	0.07
8-10	0.77	0.00
10-12	0.26	0.00

Table 11; Potential nitrification rates ($\text{nmol N g}^{-1} \text{(D.W.) d}^{-1}$) in the upper 6 cm of the Rhizophora sediment for dry and rainy season of 1993 and 1994.
Means \pm S.D. (n = number of observations).

Section (cm)	Dry Season (n = 4)	Rainy Season (n = 5)
0-1	264.40 \pm 35.0	253.14 \pm 25.05
1-2	227.50 \pm 24.50	203.63 \pm 30.19
2-6	128.83 \pm 33.60	116.24 \pm 35.49

Table 12 : Potential nitrification rates ($\text{nmol N g}^{-1} \text{(D.W.) d}^{-1}$) for Ceriops sediment in January 1993. Subplots A, B, C and D were randomly selected within the Ceriops plot. Mean \pm S.D. (of duplicate samples).

Section (cm)	Subplot A (PNR)	Subplot B (PNR)	Subplot C (PNR)	Subplot D (PNR)
0-1	17.22 \pm 2.14	16.85 \pm 1.66	18.32 \pm 2.07	12.21 \pm 1.47
1-2	11.70 \pm 2.11	13.13 \pm 1.36	22.14 \pm 1.99	12.71 \pm 0.84
2-4	10.43 \pm 1.35	6.46 \pm 1.14	14.14 \pm 1.56	12.22 \pm 1.18
4-6	6.50 \pm 0.72	7.58 \pm 0.69	8.31 \pm 1.42	8.31 \pm 1.23
6-8	6.50 \pm 0.43	4.60 \pm 0.32	8.56 \pm 0.73	5.71 \pm 0.26
8-10	1.90 \pm 0.44	2.85 \pm 0.33	1.58 \pm 0.29	0.79 \pm 0.32

It is possible to block this process by adding nitrification inhibitors which are capable of blocking the reaction (Henriksen et al. 1993). Differences in accumulation of ammonium between inhibited and uninhibited samples allow estimates of nitrifying activity (actual nitrification rate) to be determined (Hall, 1984). Two of the most commonly used nitrification inhibitors are Nitrapyrin and Allythiourea (ATU). In this study, we used ATU and followed the method described by Hall, 1984. One of the most important requirement for the nitrification blocking method is to have sediments with relatively low variation in ammonium pool concentrations (Henriksen et al., 1993). As discussed earlier, one of the main characteristics of the mangrove sediment in Gazi bay is the high (10-30%) standard deviations noticed for NH_4^+ profiles even for cores taken within an area of 1x1 metre square. Due to this, differences in NH_4^+ concentrations between inhibited and uninhibited cores were always found to lie within the standard deviation of the subsamples (implying no significant difference for the means). The actual nitrification results presented here are therefore only for those experiments whose difference in NH_4^+ concentration between inhibited and uninhibited samples (especially for the 0-1 cm section) was larger than the sample's standard deviation. These rates should therefore only be considered as maximum possible rates. Table 14 gives a summary of all the results obtained from the five experiments conducted between September and October 1994. The table shows

that nitrification rate is only observable at the surface (0-1 cm). Below this, the rate is undetectable. The average surface (0-1 cm) nitrification rate from the five observations is therefore $0.43 \pm 0.12 \text{ mmol N m}^{-2} \text{ d}^{-1}$. This should however be considered as the maximum possible rate since all experiments in which the difference in NH_4^+ concentration between inhibited and uninhibited samples was not bigger than the sample's standard deviation were ignored and the results not recorded. Ideally these experiments should be considered to have given undetectable nitrification rates. Relatively lower values of actual nitrification rates (averagely $0.16 \pm 0.10 \text{ mmol N m}^{-2} \text{ d}^{-1}$) were detected for *Cerriops* tagal sediments implying that the relatively high nitrate levels noticed earlier for *Cerriops* sediment may be as a result of accumulation. The O_2 supplied by the roots in *Cerriops* sediments (as observed from the relatively high redox potential values) comparatively makes the system less prone to denitrification hence the possibility of nitrate accumulation.

Nitrogen fixation

The results calculated using the theoretical factor of three acetylene molecules equivalent to one nitrogen molecule (Turner and Gibson, 1980), are expressed in $\mu\text{mol N m}^{-1} \text{ h}^{-1}$ (Fig. 28). At any tide and any season, nitrogen fixation activity was higher in *Cerriops* sediments and lower in *Rhizophora* one. Values of nitrogen fixation rates in seagrass meadow sediments lay in between the values of *Cerriops* and *Rhizophora*. In both sediments of *Cerriops* and *Rhizophora*, the nitrogen fixation activity was higher at low tide compared to high tide, during the long rains (June-August 1994) and the short rains (November 1994). During the dry season (March 1994), measurements were done with one core only, at high tide. If we assume to have lower activity at high tide during the dry season, as it was observed during the rainy seasons, nitrogen fixation activity of mangrove and seagrass sediments should be higher during the dry season compared to the rainy one.

Table 15 shows the input of allochthonous nitrogen to the mangrove lagoon, as calculated from: (1) litterfall data (Slim & Gwada, 1993); (2) initial nitrogen content of leaves; (3) nitrogen fixation associated with decaying mangrove leaves (Woitchik et al. 1995) and (4) nitrogen fixation associated with sediments.

Denitrification

Rates of denitrification of $^{15}\text{NO}_3^-$ (D_{15}) and $^{14}\text{NO}_3^-$ (D_{14}) were calculated from the productions of ^{29}N and ^{30}N (Nielsen, 1992).

$D_{15} = ^{29}\text{N} + (2 \cdot ^{30}\text{N}) = \text{denitrification from labelled nitrates}$

D_{14} is calculated from D_{15} :

$D_{14} = \{^{29}\text{N} / (2 \cdot ^{30}\text{N})\} \cdot D_{15} = \text{coupled denitrification-nitrification}$

Total denitrification (D_{total}) = $D_{14} + D_{15}$

The results of June - July 1994 are summarized in Table 16. Denitrification rates of *Rhizophora* sediment are higher than those of *Cerriops* sediment. Denitrification rates are lower than nitrogen fixation rates in *Cerriops* sediment while in *Rhizophora* sediment, rates of denitrification are found to

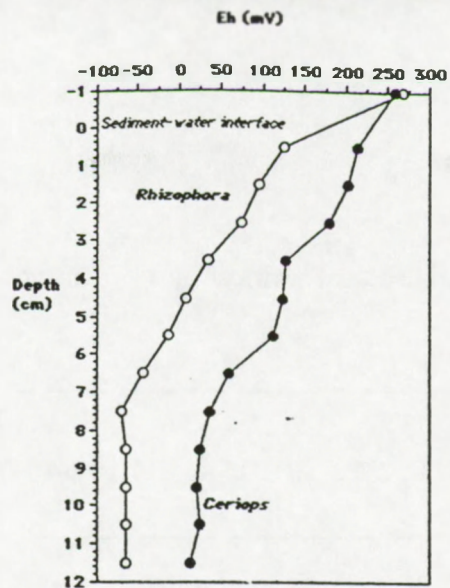


Fig. 24 : Average redox potential values (mV) for the *Rhizophora* and *Ceriops* sediments of Gazi Bay.

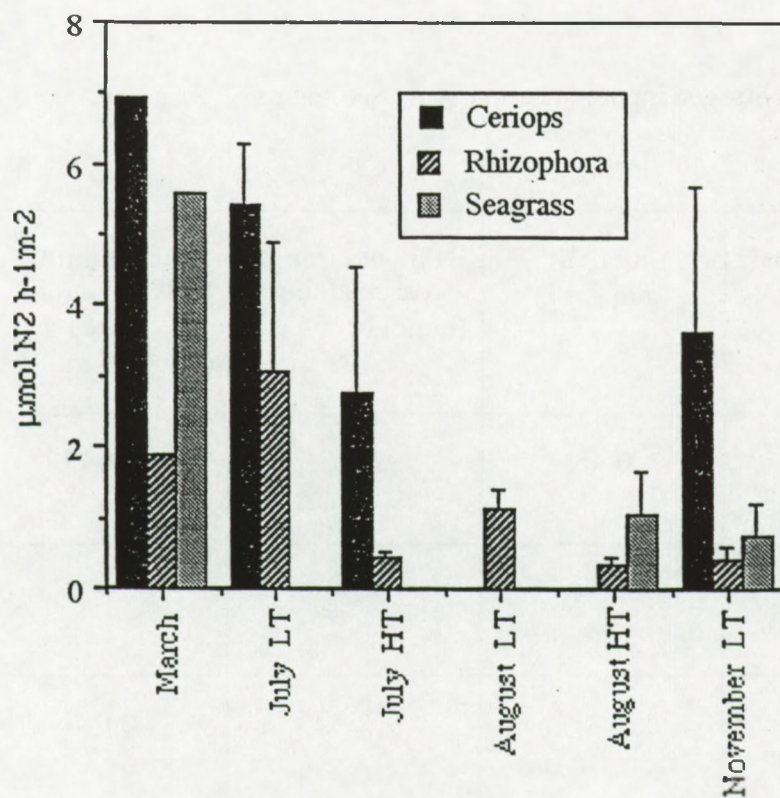


Fig. 28 : Nitrogen fixation in sediments of Gazi bay, LT = low tide; HT = high tide

Table 14 : Maximum possible actual nitrification rates ($\text{mmol N m}^{-2} \text{d}^{-1}$) in *Rhizophora* sediment

Depth (cm)	07.09.94	23.09.94	12.10.94	24.10.94	28.10.94	Average \pm S.D.
0-1	0.64	0.45	0.36	0.32	0.40	0.43 \pm 0.12
1-2	0.03	0.00	0.00	0.00	0.00	0.06 \pm 0.13
2-3	0.00	0.00	0.00	0.00	0.00	0.00
3-4	0.00	0.00	0.00	0.00	0.00	0.00

Table 15 : Nitrogen input to the mangrove sediments of Gazi bay.

experimental plot and season	Litterfall * ($\text{g m}^{-2} \text{d}^{-1}$)	N input through leaf shedding ($\text{mmol N m}^{-2} \text{d}^{-1}$)	N input through N_2 fixation (leaf) ($\text{mmol N m}^{-2} \text{d}^{-1}$)	N input through N_2 fixation (sediment) ($\text{mmol N m}^{-2} \text{d}^{-1}$)
Ceriops dry season	0.43	0.062	0.049	0.332
Ceriops rainy season	1.34	0.249	0.020	0.188
Rhizophora dry season	3.22	0.552	0.087	0.092
Rhizophora rainy season	4.66	0.999	0.296	0.066

(1) data from Slim & Gwada, 1993

(2) data from Woitchik et al. 1995

be similar to nitrogen fixation .

Epibenthic fluxes (sediment/water fluxes)

Once produced from decaying organic matter, part of the ammonium is incorporated back by the bacteria while at the oxic layer part of it can be nitrified. The produced nitrate and the balance of the produced ammonium can either be taken up by trees or diffuse by molecular diffusion out into the water column. In principle, the ammonium and nitrate concentration found in sediments are usually orders of magnitude higher than those found in the water column so the fluxes are always expected to be upward. However, research conducted in different marine sediments indicate that this may not always be the case. Blackburn and Henriksen (1983), looking into nitrogen cycling in different types of Danish marine sediments observed no significant correlation between ammonium flux and ammonium pore water gradient. These authors concluded that the ion exchange capacity may be more important in controlling ammonium flux from sediment to the overlying water. Henriksen et al. (1983) also observed no correlation between concentration gradient of NO_3^- across the sediment/water interface and the measured NO_3^- flux. They suggested that the NO_3^- flux is more correlated to the nitrification rate than to the concentration gradient.

Intact core incubations

In order to calculate the outflux from the sediments, a number of incubations were done as described earlier, applying increasing times of incubations. The concentration of the DIN at the end of the incubation was measured and plotted versus incubation time. The flux rate was calculated from the linear regression obtained. Table 17 gives the overall results for epibenthic fluxes obtained by this method for the period October - November 1994.

One-time incubation experiments were carried out on routine basis in 1992, 1993 and part of 1994 and all the results obtained from each core were used in plotting frequency distribution charts (figs. 30a & b and 31a & b). Figure 30a gives the frequency distribution chart of NH_4^+ flux in *Rhizophora* sediment. While the sediment/water column NH_4^+ flux rate is shown to vary between -1.0 to +1.4 $\text{mmol N m}^{-2} \text{d}^{-1}$, the highest frequency is seen to fall at around 0.4 $\text{mmol N m}^{-2} \text{d}^{-1}$. For nitrate (fig. 30b) the values are much lower. The nitrate flux rate is seen to vary between -0.06 to +0.75 $\text{mmol N m}^{-2} \text{d}^{-1}$. However the highest frequency is at about +0.02 to +0.06 $\text{mmol N m}^{-2} \text{d}^{-1}$. The flux of dissolved inorganic nitrogen ($\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$) from the *Rhizophora* mangrove sediments into the water column is therefore about 0.46 $\text{mmol N m}^{-2} \text{d}^{-1}$ if we only consider rates with the highest frequency occurrence. These obtained values should also be considered as highest possible values since our experimental observation was that however careful one was in adding the filtered sea water into the cores, there was always an element of disturbing the thin sediment surface layer. The highest recorded fluxes of ammonium and nitrate (1.4 and 0.75 $\text{mmol N m}^{-2} \text{d}^{-1}$ respectively) could therefore have been as a result of this disturbance. Fig. 31 a and b gives the frequency chart for NH_4^+ and $\text{NO}_3^- + \text{NO}_2^-$ fluxes respectively, across the *Cerriops* sediment-water interface. The highest occurrence for NH_4^+ flux is found to lie between 0.5 and 0.7 $\text{mmol N m}^{-2} \text{d}^{-1}$ while that of $\text{NO}_3^- + \text{NO}_2^-$ lies between 0.02 and 0.05 $\text{mmol N m}^{-2} \text{d}^{-1}$. The flux of dissolved inorganic nitrogen ($\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$) from the *Cerriops* sediment into the water column is therefore 0.75 $\text{mmol N m}^{-2} \text{d}^{-1}$. *Cerriops tagal* sediment is therefore found to contribute slightly more DIN into the overlying water than the contribution made by *Rhizophora* sediments. In either case, more than 98% of this contribution is in the form of ammonium while $\text{NO}_3^- + \text{NO}_2^-$ contribution is very minimal.

calculated fluxes

An attempt was also made to calculate the ammonium flux using Fick's first law equation as expressed by Lerman, 1978;

$$J = \Phi D_s dC/dx$$

In this equation :

J = diffusive flux across the sediment water interface

Φ = sediment porosity

D_s = corrected diffusion coefficient = $D_o \Phi^2$

Table 16 : Denitrification rates ($\text{mmol N d}^{-1} \text{ m}^{-2}$) in sediments of Gazi bay

sampling site	^{29}N production	^{30}N production	D_{14}	D_{15}	D_{total}
Ceriops	0.0072	0.0197	0.0086	0.0466	0.0552
Rhizophora	0.0103	0.0439	0.0115	0.0982	0.1010

Table 17 : benthic ammonium fluxes ($\text{mmol d}^{-1} \text{ m}^{-2}$) measured by the incubation core system in Gazi bay (n = number of cores).

sediments	NH_4^+ flux $\pm \sigma$
Ceriops 19/10/94 ($n=3$)	0.288 ± 0.17
Ceriops 21/11/94 ($n=4$)	0.432 ± 0.22
Rhizophora 19/10/94 ($n=6$)	1.128 ± 0.43
Rhizophora 25/10/94 ($n=4$)	0.264 ± 0.10
Rhizophora 11/11/94 ($n=5$)	0.336 ± 0.14

Table 18 : calculated benthic ammonium fluxes in Gazi bay

sampling site	Φ	D_s ($\text{cm}^{-2} \text{ h}^{-1}$)	NH_4^+ (0-1 cm) ($\mu\text{mol cm}^{-3}$)	J ($\text{mmol m}^{-2} \text{ d}^{-1}$)
Ceriops	0.46	0.0151	0.190	0.31
Rhizophora	0.92	0.0603	0.060	0.79

Table 19: Calculated organic nitrogen stocks, regeneration and turnover rates for the upper 6 cm of *Rhizophora* and *Ceriops* sediments.

Item	Rhizophora	Ceriops
Depth (cm)	6.0	6.0
TON stock (mmol N m^{-2})	9337.14	3996.4
r (reminer. - $\text{mmol N m}^{-2} \text{ d}^{-1}$)	15.59	35.03
Turnover rate (yrs)	1.6	0.31
Average C/N ratio (approx.)	26.0	26.0

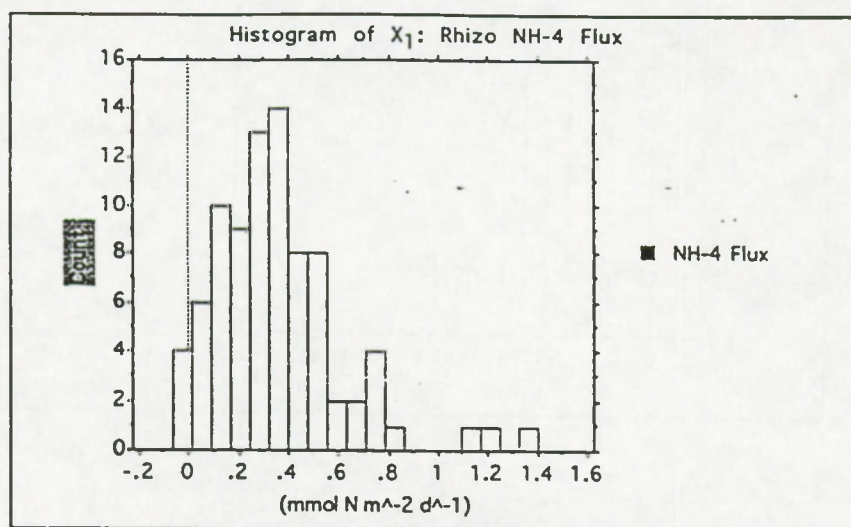


Fig. 30a: Histogram of ammonium sediment-water interface flux rate ($\text{mmol N m}^{-2} \text{d}^{-1}$) as observed on *Rhizophora mucronata* plot between 1992 and 1994.

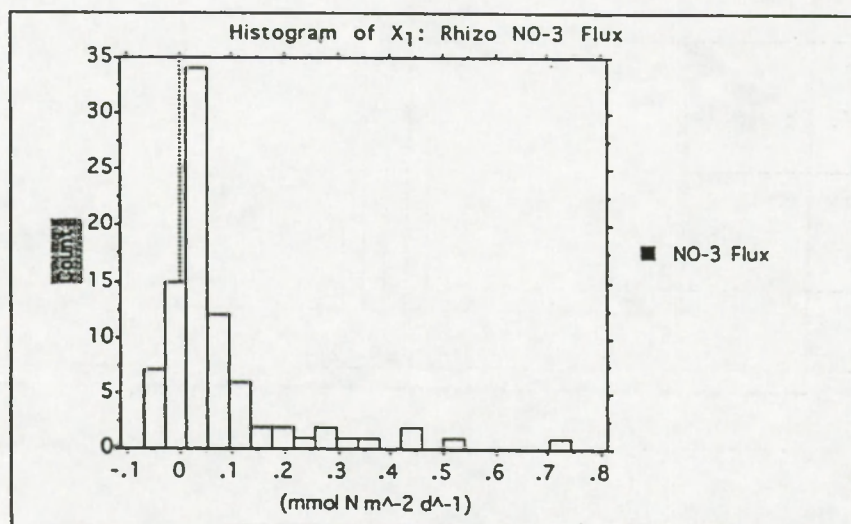


Fig. 30b: Histogram of nitrate sediment-water interface flux rate ($\text{mmol N m}^{-2} \text{d}^{-1}$) as observed on *Rhizophora mucronata* plot between 1992 and 1994.

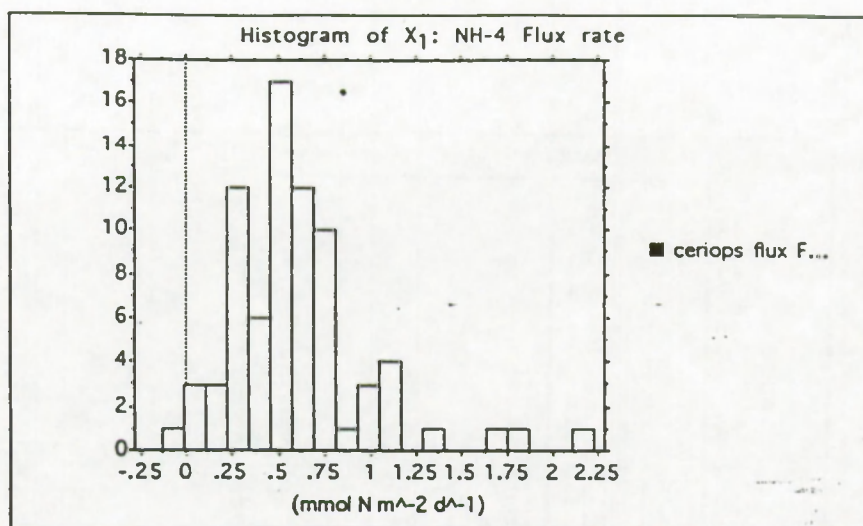


Fig. 31a: Histogram of ammonium sediment-water interface flux rate ($\text{mmol N m}^{-2} \text{ d}^{-1}$) as observed on *ceriops tagal* plot between 1992 and 1994.

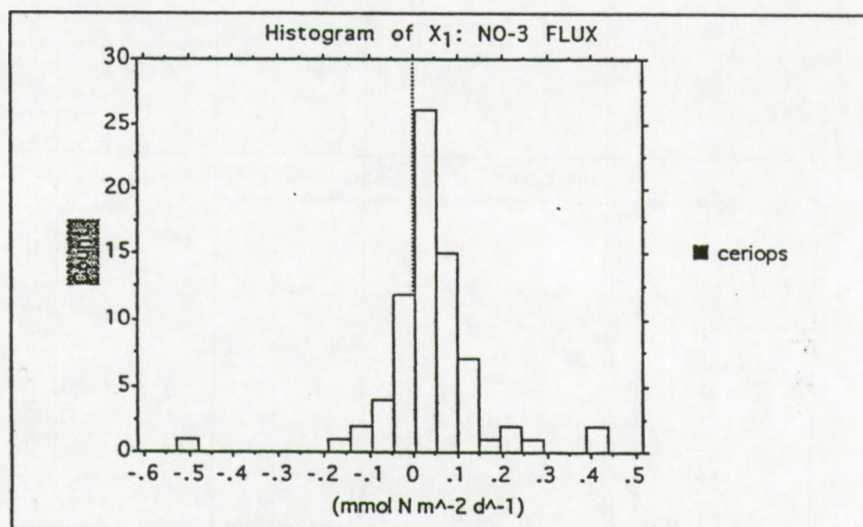


Fig. 31b: Histogram of nitrate sediment-water interface flux rate ($\text{mmol N m}^{-2} \text{ d}^{-1}$) as observed on *ceriops tagal* plot between 1992 and 1994.

$D_0 = 19.8 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ (Li & Gregory, 1974)

dC/dx = concentration gradient at the sediment water interface

We took : $dx = 1 \text{ cm}$

C (water column) = $0.0003 \mu\text{mol N cm}^{-3}$

Table 18 below gives the results of the calculations. The obtained values fall within the flux range observed from the frequency graphs of one (fixed) time incubations.

DISCUSSION

Early diagenetic reactions particularly those directly or indirectly involving the decomposition of organic matter are most intense and rapid in the upper 1 m and especially in the upper 10 cm of marine sediment (Aller, 1980). It is this zone where most benthic organisms live and interact with sediments and where exchange rates of dissolved and particulate material between sediment and overlying water are largely determined. Knowledge of the processes taking place in this zone are therefore essential for understanding the chemistry of the sediments and the water overlying the sediments. Sediment mineralization and bacterial synthesis occur in zones dominated by different electron acceptors. As carbon is oxidized in these different zones, organic nitrogen is also mineralised to ammonium ion. However, once produced, part of this ammonium can again be incorporated (assimilated) back into bacterial cells by the bacteria responsible for mineralization process. Net production of ammonium hence depends very much on the quality and quantity of the organic substrate (Aller, 1980; Middelburg et al. 1993).

The quantity can be determined by the stock of organic matter while the quality can be assessed from the C:N ratio of the organic matter. Blackburn (1986), demonstrated that organic matter with a C:N ratio of ≤ 20 favours net mineralization while those of C:N ratio ≥ 20 would favour immobilization.

The C:N values obtained for the *Rhizophora mucronata* (23 ± 1 to 30 ± 1) and *Cerriops tagal* (19 ± 1 to 39 ± 2) sediments suggest that the sediments should favour immobilization with no significant net mineralization observed. However, ammonification rates observed for the two sediment biotopes indicates very active mineralization process which favours net production of ammonium. Though the two sediment types displayed different organic matter content ($21 \pm 1\%$ and 2.1 for surface *Rhizophora* and *Cerriops* sediments respectively) they both gave more or less same potential ammonification rates per unit gram dry weight ($600 \text{ nmol N g}^{-1}(\text{D.W.}) \text{ d}^{-1}$). This implies that ammonification rates in the two sediment types is independent of the organic matter content within the two plots. It was also noticed that this ammonification process is not affected by seasonal climatic changes. Results obtained from regeneration and assimilation experiment indicates that the regeneration rate of NH_4^+ in *Rhizophora* sediment is about $15.59 \pm 3.73 \text{ mmol N m}^{-2} \text{ d}^{-1}$ for the upper 6 cm depth. However, about 60% of this is assimilated back giving a net production of $6.21 \pm 1.63 \text{ mmol N m}^{-2} \text{ d}^{-1}$ available for nitrification or plant uptake. For *Cerriops* sediment, the regeneration rate was 35.03 ± 6.63 while the uptake rate was $14.55 \pm 6.23 \text{ mmol N m}^{-2} \text{ d}^{-1}$ giving a net production of $20.48 \pm 3.38 \text{ mmol N m}^{-2} \text{ d}^{-1}$ available for plant uptake or other nitrogen processes. These results seem to be similar to the rates reported in other mangrove sediments. Nedwell et al. 1994 estimated $10 \text{ mmol N m}^{-2} \text{ d}^{-1}$ to be the net ammonium produced for plant uptake in a Jamaican mangrove forest. It is important to note that while comparing rates in $\text{mmol N m}^{-2} \text{ d}^{-1}$ we should take note of the depth and porosities of the sediments since these could create a difference even if the rates are the same as calculated per gram dry weight. Before looking into other processes, it's important to compare these rates with the standing stocks in order to get an idea about the turnover rates. From the total organic nitrogen (TON) contents and porosity values given in Tables 4a and 4b it is possible to calculate the organic nitrogen stock for the 0-6 cm depth. Table 19 below, gives the stocks, regeneration and turnover rates for the upper 6 cm depth for both *Cerriops* and *Rhizophora* sediment.

Remineralization rate of 15.59 and $35.03 \text{ mmol N m}^{-2} \text{ d}^{-1}$ would imply a carbon mineralization rate of 405.3 and $910.78 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for the *Rhizophora* and *Cerriops* sediment plots respectively at an average observed C/N ratio of 26. However, direct measurements of carbon dioxide flux from the *Rhizophora* sediment gave a carbon remineralization rate of $60.5 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (Middelburg, et al., submitted) implying that the organic matter responsible for this production does not have a C/N of 26 but of about 3.8. If this is so, then the actual carbon dioxide

flux rate at our *Cerriops tagal* sediment should be $240 \text{ mmol C m}^{-2} \text{ d}^{-1}$ which also falls within the range found by Middelburg, et al (submitted), for the *Cerriops* sediment (30 to $450 \text{ mmol C m}^{-2} \text{ d}^{-1}$) of Gazi Bay. Since C/N ratios of marine bacteria range from 3 to 7 (Nagata, 1986; Lee and Fuhrman, 1987), the calculated C/N ratio of 3.8 as being responsible for the CO_2 flux (sediment / water interface) and organic nitrogen remineralization rate in *Rhizophora* and *Cerriops tagal* sediments of Gazi Bay would imply active involvement of benthic bacterial biomass. Recent studies in mangrove sediments of tropical Australia (Alongi, 1989) have demonstrated very high bacterial densities and productivities in these sediments with bacterial productions sometimes being 10 times higher than those reported for other marine sediments.

$\delta^{13}\text{C}$ isotope signature for the mangrove sediments in Gazi bay are found to be very close to those of the mangrove leaves (Rao et al. 1994; Hemminga et al. 1994). This has led to the conclusion that organic carbon from the mangroves forms the major part of the organic carbon in sediments. However, the observed sediment's C/N atom ratio of 26 (for the upper 6 cm) is too-low compared to that of senescent leaves of the mangroves (*Rhizophora*: 193 ± 45 ; *Cerriops*: 218 ± 26 ; Rao et al. 1994). A number of explanations have been given for this nitrogen enrichment in sediments which has resulted in reduction of the C/N ratio to about 26. These explanations include nitrogen fixation (Woitchik et al. 1994) and import and degradation of seagrass (Hemminga et al. 1994). While nitrogen fixation could be an important source, Capone (1983), concluded that N_2 fixation in mangrove forests are generally low. As observed in *Rhizophora* and *Cerriops tagal* sediments, the highest input of N through N_2 fixation was only about 0.1 and $0.33 \text{ mmol N m}^{-2} \text{ d}^{-1}$ respectively (Table 15). $\delta^{13}\text{C}$ isotope signature for seagrass in Gazi Bay were found to lie between -10‰ (near the open sea) and -20‰ (next to the mangrove zone) while the C/N ratio of the same were found to be about 20 uniformly across the transect (Hemminga et al. 1994). If we assume that this seagrass with a C/N ratio of about 20 is responsible for the enrichment of nitrogen and hence decrease of C/N from the expected (200) to 26, then a very big quantity would have been needed. This would then have shifted the $\delta^{13}\text{C}$ isotope of the mangrove sediment quite significantly to less negative values. As it is, the difference between the sediment $\delta^{13}\text{C}$ and the mangrove leaves for *Rhizophora* and *Cerriops* biotopes is only 2.9 % and 1.4 % respectively (Hemminga et al. 1994). While we appreciate that this drop could have been brought up by import of seagrass into the mangrove zone, the fact that the main organic matter that undergoes remineralization in the mangrove sediments is found to have a C/N ratio of about 4 could also imply the presence of another (perhaps more important) different source of organic material within the mangrove sediment.

Though the C/N atom ratio of senescent mangroves leaves were found to be very high, dissolved organic material e.g (amino acids) leached, could have very low C/N value. Valiela et al. (1985) found that dissolved organic material released as leachate from several particulate organic material is potentially nutritious as it is high in soluble proteins, carbohydrates and lipids which have low C/N values. Marinucci, 1982 also found that leached dissolved organic material could have a lower C/N value than the initial POM. The DOM leached is also biologically labile and rapidly taken up by microbes (Benner et al. 1986; Biddanda, 1985). The microbes taking up this DOM tend to have similar $\delta^{13}\text{C}$ isotope signature as the initial POM. Boto et al. 1989 demonstrated that in mangrove sediments, about 35% of this produced dissolved organic matter is used to support benthic bacterial productivity. Despite having a higher concentration gradient of DOC between porewaters and overlying tidal water, no significant efflux of DOC was observed in Australian mangrove forest (Boto et al. 1989). If about half of the produced DOM is used to support benthic bacterial productivity and no significant net efflux into the water column is noticed, then what is the fate of the other half? One of the fates of dissolved organic material (DOM) released by decomposing macrophytes is aggregation into amorphous particles called organic aggregates (Albert and Valiela, 1994a). Though this process has only been demonstrated in seawater within the water column (Albert and Valiela, 1994a) we are not aware of any reason as to why it can not happen in sediment's interstitial water. This process of aggregation is largely driven by bacteria and the aggregate composition does not vary with species neither does it reflect the composition of either the macrophyte or the DOM from which it is derived (Albert and Valiela, 1994b). Instead, these aggregates are similar in quality to bacteria. Due to the high bacterial biomass and productivity in mangrove sediment, formation of these aggregates of amorphous organic material whose quality is similar to bacteria is possible and could be the reason why we have a high stock of organic matter in Gazi mangrove sediments. Organic matter remineralization in the mangrove

sediments could then imply turnover rates of these formed aggregates (hence the low turnover rates observed in *Rhizophora* and *Cerriops* sediments) whose C/N ratio is likely to be similar to that of bacteria. The increase of C/N atom ratio with depth as seen for the *Rhizophora* and *ceriops* sediment could also imply decrease of the aggregates quantity with depth. This is highly likely since aggregation is bacterial driven and bacterial biomass is found to be very high at the upper 1 cm of the mangrove sediments (Boto et al. 1989) and decreases with depth (Alongi, 1989). A similar increase of C/N atom ratio with depth has been observed for most mangrove sediments, e.g. the south-east Asian mangrove swamp (Kristensen et al. 1988). Though there is a possible decrease of the quantity of these aggregates with depth which may result in the observed increase of the C/N ratio (table 4a & 4b), $\delta^{13}\text{C}$ isotope signature is not expected to change significantly with depth since the formed aggregates and bacteria are expected to display $\delta^{13}\text{C}$ signature similar to the main source of the supply. The less negative $\delta^{13}\text{C}$ values found at the surface (table 4a & 4b) could therefore also reflect an external addition from either the marine open waters or seagrass (Hemminga et al., 1994). Both these sources have POM whose $\delta^{13}\text{C}$ is less than that of mangrove vegetation (-10 to -20 ‰ for seagrass and ca. -20 ‰ for marine POC; Hemminga et al., 1994; Rezende, et al. 1992).

From the regeneration and assimilation experiments for the *Rhizophora* and *Cerriops* sediment, about $6 \text{ mmol N m}^{-2} \text{ d}^{-1}$ and $20 \text{ mmol N m}^{-2} \text{ d}^{-1}$ respectively are made available for either tree uptake or nitrification process.

Potential nitrification rates are found to be relatively higher in *Rhizophora* than in *Cerriops* sediment. The low PNR in *cerriops* tagal sediment imply low biomass (or activity) of nitrifying bacteria as compared to the biomass (activity) that would be found in *Rhizophora* sediments. It is not very clear as to why we have very big difference in the nitrifiers biomass (assuming PN rate is proportional to biomass of nitrifying bacteria; Henriksen et al. 1981) in the two biotopes. However, Chen et al. (1976) studying salinity effect on nitrification, concluded that nitrification rate was inversely proportional to salinity. This would imply that the higher the salinity the lower the nitrification rate. Billen (1975) also made similar observations while studying nitrification process in Scheldt estuary. Salinity at the *Cerriops* sediment were found to be relatively higher (ca. 42 - 58 ppt for the upper 12 cm depth) than in *Rhizophora* sediment (34-40 ppt). During neap tide, the salinity in the upper cm of *Cerriops* tagal sediment could rise upto ca. 58 ± 3 ppt (personal observations) due to infrequent flooding and evapotranspiration of the surface pore water. The maximum difference in salinity between the two sediments could therefore be about 20 ppt. This difference is likely to affect the biomass of the nitrifying bacteria in *cerriops* tagal sediment. Another possible reason for the big difference in biomass of nitrifying bacteria could be excessive heat. Mangrove trees of *Rhizophora mucronata* species are usually quite big with big leaves which always covers the sediment from direct sun light while *Cerriops* tagal species have short trees with small leaves which are not densely packed (Slim and Gwada, 1993). Since the *Cerriops* sediments are only inundated during spring tides, the prolonged absence of water during neap tide coupled by direct sun light would raise the sediment's (especially the upper few centimeters) temperature. Carlucci and strictland (1968) found that the optimum temperature for several nitrifiers from the northern Pacific ocean was about 28°C while Waterson and Waterburg (1971), noted that the nitrate oxidisers, nitrospina and nitrococcus both grew optimally at $25 - 30^\circ\text{C}$. The higher temperatures ($35 - 39^\circ\text{C}$; personal observations) sometimes found in the *cerriops* upper (1 cm) sediments (during neap tide) could therefore also contribute to the relatively low biomass of nitrifying bacteria in *Cerriops* tagal sediments.

While ammonification rate for the 0-1 cm *Rhizophora* sediment depth indicates net production rate of ca. $1.57 \text{ mmol N m}^{-2} \text{ d}^{-1}$ (table 8) potential nitrification value for the same depth (table 10b) indicates that almost 70% of the produced ammonium can be oxidized into nitrate. However actual nitrification rates determined from the same sediments indicates low nitrification process (table 14). Only about 25 % (ca. $0.43 \text{ mmol N m}^{-2} \text{ d}^{-1}$) of the produced ammonium is nitrified at the upper 1 cm section while below

1 cm depth hardly any actual nitrification is noticed. For *Cerriops* tagal sediments, actual nitrification rates for the surface (0-1 cm) were averagely about $0.16 \pm 0.10 \text{ mmol N m}^{-2} \text{ d}^{-1}$ (results not shown). Henriksen et al. (1993) observed that most marine sediments had nitrification rates ranging between 0.7 and $1.8 \text{ mmol N m}^{-2} \text{ d}^{-1}$. Though our maximum possible nitrification rate in *Rhizophora* is found to be (ca. $0.55 \text{ mmol N m}^{-2} \text{ d}^{-1}$) the same order of magnitude as the values mentioned by Henriksen et al. (1993), our values are much lower since our range is essentially 0 -

0.55 mmol N m⁻² d⁻¹ when we also consider the experiments which had undetectable nitrification rates. Since ammonium stocks at the surface are relatively high and determination of potential nitrification has indicated possible active nitrification process above 4 cm depth, the low actual nitrification rate observed in *Rhizophora* sediment is most likely due to low oxygen availability.

Organic matter content found in the *Rhizophora* sediment is very high compared to that found in most mangrove sediments. The LOI organic matter content at the sediment surface was found to be about 20 % (dry wt.), while POC and PON were found to be about 9 % and 0.4 % respectively (table 4a). In comparison, LOI organic matter content found in a south-east Asian mangrove swamp was only about 8 % while the POC and PON were 2 % and 0.09 % respectively (Kristensen et al. 1988). In a mangrove swamp of Indus delta, Pakistan, Kristensen et al., 1992 found LOI organic matter content of 5 % (dry wet). Kristensen et al. (1988) demonstrated that up to 73 % of the available oxygen could be used to support decay of algal cells in a mangrove swamp. The low actual nitrification process in *Rhizophora* sediment could thus be due to high use of oxygen to support decomposition of the observed high organic matter stock hence lowering the concentration of diffused oxygen available for nitrification. For *Ceriops* tagal sediments, the low actual nitrification process could be due to low biomass of nitrifiers as a result of high salinities and temperatures of the *Ceriops* sediments.

Despite having higher nitrification rate, the *Rhizophora* sediments are found to have lower subsurface nitrate stock compared to the *Ceriops* sediments. *Ceriops* sediments being more oxidized than the *Rhizophora* sediments may be having a lower denitrification rate hence a possible accumulation of nitrate. Indeed, higher denitrification rates in the *Rhizophora* than in the *Ceriops* sediments were observed in this study. However, despite having relatively higher NO₃⁻ stocks, the *Ceriops* sediment displays more-or-less same flux rates (0.02 to 0.06 mmol N m⁻² d⁻¹) as those observed in *Rhizophora* sediments. The sediment / water interface NH₄⁺ flux rates appear to be slightly higher with highest frequency for *Ceriops* sediment occurring between 0.5 and 0.7 mmol N m⁻² d⁻¹ while for *Rhizophora* it ranges between 0.3 and 0.4 mmol N m⁻² d⁻¹. The maximum possible flux rate of dissolved inorganic nitrogen from the *Rhizophora* and *Ceriops* sediments is therefore 0.46 and 0.76 mmol N m⁻² d⁻¹ respectively. Though flux rates from sediments may be calculated from porewater concentration gradients and diffusion coefficients using diagenetic models, bioturbation in mangrove sediments may require more complex modelling to compute the fluxes mathematically (Alongi et al., 1992). However, as a first approximation, our calculated flux values seem to fit within our ban of high occurring frequency in our 'one time' incubation results as well as with the results from the repeated incubations.

To assess the contribution of dissolved inorganic nitrogen by mangrove sediments to the overlying water system, a number of assumptions have been made : At Gazi Bay the area covered by mangrove vegetation is about 6.61 km² (Hemminga et al. 1994). During spring high tide, water level at the *Rhizophora* plot is about 2 meters while at *Ceriops* plot it is about 1 m decreasing progressively up into the basin shrub type *Avicennia* vegetation. If for the sake of argument, the level of water covering the entire vegetation at high spring tide is assumed to be about 1 metre throughout the entire area covered by the mangrove vegetation, then we have a total water volume of about 6.61 x 10⁹ litres above the Gazi mangrove sediments. The average maximum DIN flux from the *Ceriops* and *Rhizophora* sediment is observed to be 0.61 mmol N m⁻² d⁻¹. For an area of 6.61 km², this would give an output of about 4032 mol N d⁻¹ into a water volume of about 6.61 x 10⁹ litres. This would increase the water column concentration by 0.61 µmol N l⁻¹ d⁻¹. This would imply an addition of about 0.025 µmol N l⁻¹ h⁻¹. However, in spring high tide, the *Rhizophora* is covered by water only for about 4 hrs while *Ceriops* is covered only for about 2.5 hrs. To work on maximum possible input into the water column we can assume that during high tide the sediment is covered by water for about 4 hours hence a total increase of 0.1 µmol N l⁻¹ during the high tide duration. The rate of primary production within the Gazi mangrove creek during dry season was found to be 377.67 ± 159.7 mg C m⁻³ d⁻¹ (Kitheka et al., this issue). Using Redfield ratio of 6 for Carbon to Nitrogen, this production would require 0.20 µmol N l⁻¹ h⁻¹. This nitrogen demand is eight times higher than the supply through sediment - water fluxes. In order to sustain this demand, there must be another more important source of nitrogen within the water column.

Two possibilities exist for this additional nitrogen requirements - either through seepage or leaching of nutrients from surface sediments during outgoing ebbtide water flow (Boto, 1982). Time series studies conducted at the entrance of Kidogoweni creek (Kitheka et al, this issue) indicates no significant difference in nutrients concentrations between incoming and outgoing water during dry season. This implies that any additional dissolved inorganic nitrogen which may be added to the

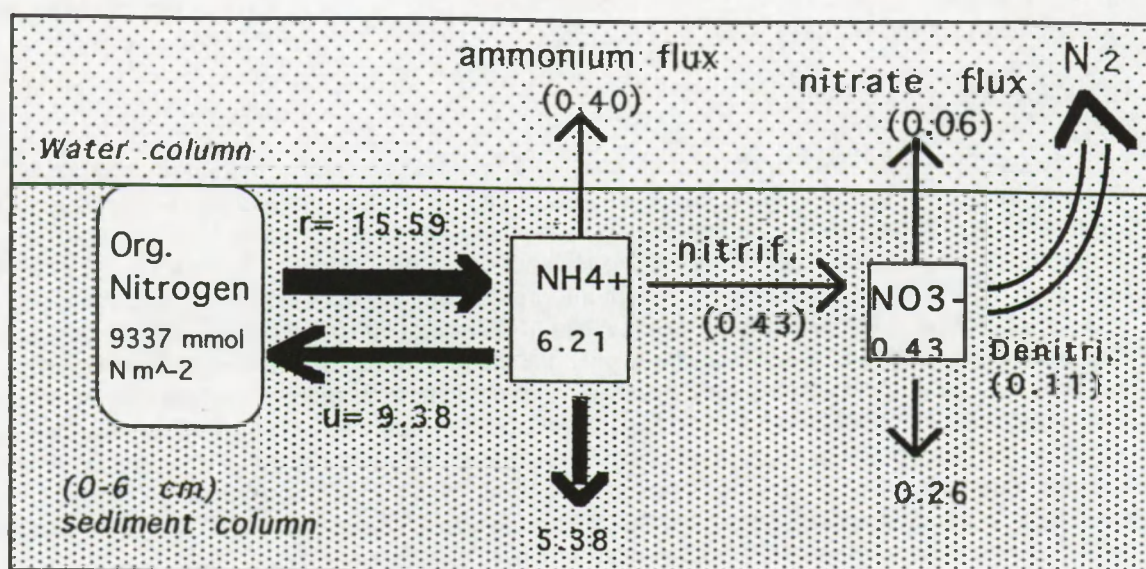


Fig. 32 : Schematic representation of nitrogen transformational processes in *Rhizophora mucronata* sediments (0-6 cm depth) of Gazi Bay. All rates are in mmol N m⁻² d⁻¹.

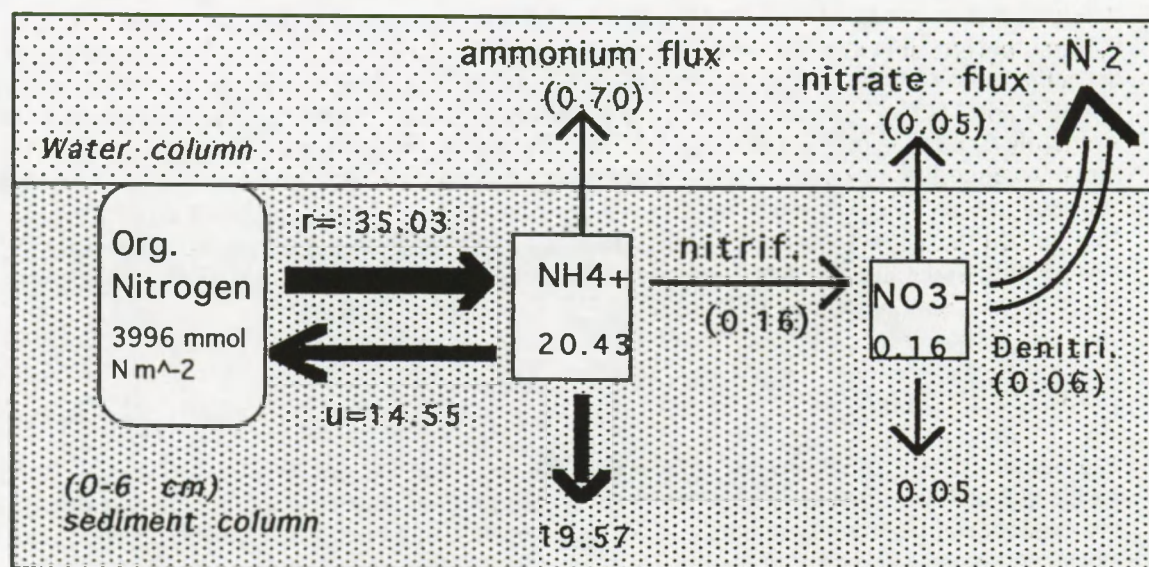


Fig. 33 : Schematic representation of nitrogen transformational processes in *Ceriops tagal* sediments (0-6 cm depth) of Gazi Bay. All rates are in mmol N m⁻² d⁻¹.

mangrove creeks by either seepage or nutrient leaching of top sediment soil is immediately taken up resulting in the slightly higher observed primary production in the creeks as compared to the closeby open waters (Kitheka et al., this final report).

CONCLUSION

Despite having organic matter whose C:N atomic ratio is ≥ 20 , the Gazi mangrove sediments are found to favour net ammonium production instead of immobilization as expected (Blackburn, 1988). Figures 32 and 33 below gives a schematic presentation of the rates for some of the nitrogen transformational processes and fluxes in the Rhizophora and Ceriops sediments, respectively of Gazi Bay. The total organic nitrogen content integrated over the upper 6 cm of Rhizophora sediment is found to be $9337 \text{ mmol N m}^{-2}$. While $15.77 \text{ mmol N m}^{-2}$ is found to be regenerated per day, about 60% of this is assimilated back giving a balance of about $6.13 \text{ mmol N m}^{-2} \text{ d}^{-1}$ of ammonium. Out of this balance, only about $0.40 \text{ mmol N m}^{-2} \text{ d}^{-1}$ diffuses out into the water column while another $0.43 \text{ mmol N m}^{-2} \text{ d}^{-1}$ is nitrified. About $5.38 \text{ mmol N m}^{-2} \text{ d}^{-1}$ of NH_4^+ is therefore available for tree uptake in Rhizophora plot. Since about $0.06 \text{ mmol N m}^{-2} \text{ d}^{-1}$ of nitrate is fluxed out into the water column everyday and another $0.11 \text{ mmol N m}^{-2} \text{ d}^{-1}$ of the produced nitrate is denitrified a balance of $0.26 \text{ mmol N m}^{-2} \text{ d}^{-1}$ becomes available for tree uptake. Nitrogen fixation and denitrification rates were seen to be balanced in Rhizophora sediment.

For Ceriops sediments (Fig. 33) about 19.60 and $0.07 \text{ mmol N m}^{-2} \text{ d}^{-1}$ of NH_4^+ and NO_3^- becomes available for tree uptake everyday. Rates of nitrogen fixation were found to be twice those of denitrification in these sediments. Incubation for determination of actual nitrification in the sediments, eliminates the constant supply of O_2 by roots. Due to this the actual produced NO_3^- in these sediments is underestimated- especially for Ceriops sediments which are more oxidizing. The higher NO_3^- concentrations at sub-surface levels of Ceriops sediments are therefore due to constant oxidation of NH_4^+ by the roots supplied O_2 .

Rhizophora sediments are found to have a higher biomass of nitrifying bacteria as compared to Ceriops sediment. The low biomass of nitrifying bacteria in Ceriops sediment is attributed to both higher salinities and temperatures observed in the sediments..

From the overall results obtained, very little dissolved inorganic nitrogen is supplied into the overlying water through the sediment water boundary. Rhizophora sediment is seen to supply ca. $0.46 \text{ mmol N m}^{-2} \text{ d}^{-1}$ while the Ceriops sediment supplies $0.76 \text{ mmol N m}^{-2} \text{ d}^{-1}$. If we assume that the overall volume of water above the mangrove vegetation is 6.61×10^9 litres we estimate an increase of $0.025 \text{ } \mu\text{mol N l}^{-1} \text{ h}^{-1}$. However primary productivity within the mangrove creeks is found to be averagely $377 \text{ mg C m}^3 \text{ d}^{-1}$ (Kitheka, et al., this issue). This would require $0.21 \text{ } \mu\text{mol N m}^{-2} \text{ d}^{-1}$. It is therefore seen that epibenthic fluxes of dissolved Inorganic nitrogen across the sediment - water interface is not enough to meet the high nitrogen demand within the mangrove creeks. Boto, 1982 suggested that nutrient from the mangrove soil could be leached out during ebb flow. This together with seepage could be the other sources of the extra nitrogen to support the relatively high primary production in Gazi mangrove swamp.

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LEAF-LITTER REMOVAL BY *TEREBRALIA PALUSTRIS* (GASTROPODA) AND *SESARMA GUTTATUM* (DECAPODA) IN THE MANGROVE OF GAZI BAY (KENYA)

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INTRODUCTION

Mangroves are open systems, coupled to coastal waters by tidal currents. To what extent the organic matter produced is exported to adjacent ecosystems is determined by physical and biological factors (Woodroffe, 1992). Several studies show that large proportions of the leaf litter reaching the forest floor are consumed or buried by crabs (e.g., Robertson, 1986; Micheli et al., 1991). This consumption and retention of litter within the mangrove forest by the benthos will have profound effects on the pathways of energy and matter flow within forests and their exchange with nearby systems. Robertson and Daniel (1989), for instance, showed that Sesarmid crabs removed between 20 and 80 % of the litter fall in different forest types in northeastern Australia. Beside studies on the mangrove litter processing activity of crabs, some studies have focussed on litter processing snails (Soemodihardjo & Kastoro, 1977; Nishihira, 1983).

In the present study quantitative measurements of the rates of leaf litter fall removal by the benthos in monospecies stands of *Rhizophora mucronata* and *Ceriops tagal* in Gazi Bay (Kenya) were carried out. The *Rhizophora* stand is flooded every high tide and Sesarmid crabs are the main feature of the macrobenthos. In the *Ceriops* stand, which is situated higher in the intertidal zone, the mollusc *Terebralia palustris* and fiddler crabs are dominating the macrobenthos. The litter removal rates determined were combined with data on litter fall and inundation frequencies to calculate the tide-mediated efflux of leaf litter from both types of mangrove stands.

STUDY AREA

The present research was carried out in the mangrove forest of Gazi bay (Kenya). The mangrove vegetation in the bay covers a total area of 6.61 km². A total of 8 mangrove species are found in the mangrove forest. Field experiments on litter fall removal by the benthos were conducted in study plots of 20 x 20 meter in monospecies stands of *R. mucronata* and *C. tagal*. The *R. mucronata* plot was the nearest to the low water line and was inundated at each high water, whereas the *C. tagal* plot was situated at a higher elevation and was only inundated around spring tides. The biomass and litter fall in these plots have been determined earlier (Slim et al., submitted). The site characteristics relevant to the present study are shown in Table 1.

MATERIALS AND METHODS

Leaf removal experiments

Field experiments were carried out to assess the influence of time of day and lunar cycle (i.e. inundation frequency) on the rate of leaf removal by the benthos. To this aim, tagged senescent leaves of *Ceriops* and *Rhizophora* were laid out on the forest floor of the respective stands during ebb tide, and leaf removal was measured. The leaves that were used in these experiments were yellow, senescent leaves, picked from the trees less than 24 hours before the start of the experiment. The outline of each leaf was traced on a transparency, allowing the use of a video camera and digital image analysing software to estimate its surface area. Each leaf was sewed at the

Table 1: Characteristics of the *C. tagal* and *R. mucronata* study sites (data from Slim et al., submitted).

	unit	<i>Cerriops</i>	<i>Rhizophora</i>
stem density	n/100 m ²	164 ± 64	198 ± 67
biomass	DW kg m ⁻²	4.01 ± 0.34	24.9 ± 4.01
litter fall	DW g m ⁻² day ⁻¹	1.05 ± 0.49	2.51 ± 1.15
litter fall	n leaves m ⁻² day ⁻¹	2.92 ± 1.37	1.97 ± 0.98
litter stock	n leaves m ⁻²	5.3 ± 1.9	2.7 ± 1.1
flooding			
-time	min. day ⁻¹	116	575
-time	%	8.1	39.9
-frequency	% of HW occurrence	35	100

petiole to a thin (ϕ 0.3 mm) nylon line of approximate 1.5 metre. This line had a tag for identification of the leaf. At the beginning of low water the lines with the leaves were attached to the trunk or stilt root of a tree. Four sites, of approximate 15 m² and at 10 metre from each other, were used in each vegetation, to account for spatial variance. At each site 10 tagged leaves were set out. The number of leaves set out in the experiment accounted only for a small fraction of the natural leaf litter density. So we assumed that our experiment did not change the normal density of litter and that the observed fate of the leaves set out in the experiment is the same as for natural litter. At the end of the low water period the leaves were recovered and their outline was traced over the initial drawing on the transparency, to quantify the leaf area removed. Repeated experiments were carried out at spring, neap and intermediate tides at low water periods during day and night time. The experiments were set up in such a way that each experiment was either completely in the dark period (i.e. "night"; between 18:30 - 05:00) or in the light period (i.e. "day"; between 05:00 - 18:30).

Observations on *Terebralia palustris*.

The snail *T. palustris* was a conspicuous feature of the benthos in the *C. tagal* stand and was studied in more detail. Density of the snail was assessed by counting all the snails present in 2.5 x 2.5 m plots (n=13). Twice the water content of *T. palustris* was assessed. Once under "wet" conditions, when the plot had been flooded by 8 successive high tides and once, under "dry" conditions, after 4 successive high tides which did not reach the stand. Fresh weights (FW) of the snails were measured after rinsing the snails and removing the adherent water with a tissue. Dry weights (DW) were measured after drying until constant weight at 70 °C. In both measurements the shell was included. Size distribution was assessed by measuring the shell length of all snails present in 3 squares of 2.5 x 2.5 m. To confirm the observation that the snails gathered near the trunks of the trees when the plot was not flooded during successive high tides, the number of snails in concentric circles around 5 different trees at neap and spring tide were counted.

RESULTS

Litter removal in the *C. tagal* stand.

Overall analysis of covariance showed that the association between "day" and "night" was strikingly different for the "dry" and "wet" condition. Therefore it was decided to analyze the litter removal under these conditions separately. If the plot was not flooded by the high water prior to the experiment (i.e. condition "dry" in Table 2), the median litter removal was in all cases less than 2 % and no significant differences were found between "day" and "night" (Table 2, Fig. 1). However, if the plot was flooded by the high water prior to the experiment (i.e. condition "wet"), the litter removal much more leaf material was removed. Furthermore, in the "wet" condition litter removal differed significantly between "day" and "night" ($P < 0.002$; ANCOVA) and nearly for high tide level ($P = 0.056$; ANCOVA; Fig. 1). After a high water level prior to the experiment of 330 cm above datum (i.e. 50 cm above plot level in *C. tagal* stand), the estimated median percentage litter removal is about 1.5 times higher at night than by day: 41.6 % (95% CI: 35.3 - 48.1%) and 25.2 (95% CI: 19.8 - 31.1%) respectively. These results suggests that the snails eat more during night time.

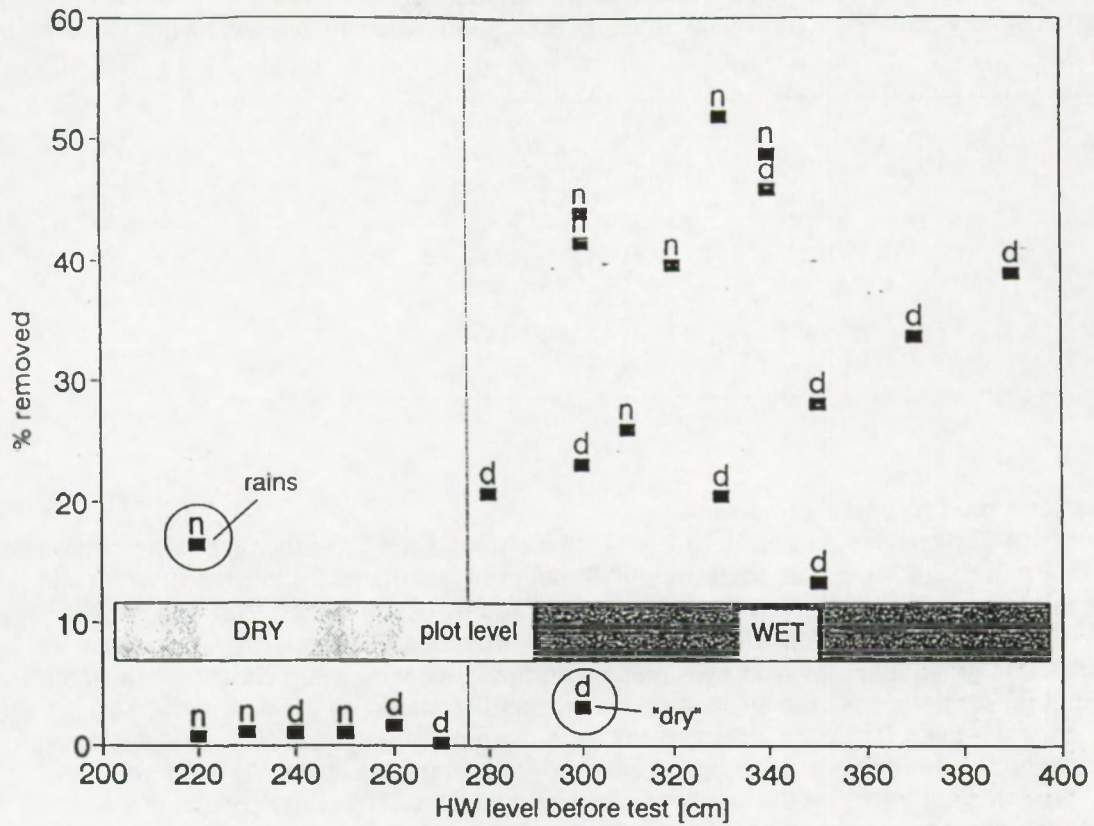


Fig. 1. Percentage of litter fall removed by *Terebralia palustris* at different high water levels, prior to the observations (d=day, n=night) in the *C. tagal* stand. Encircled data were excluded from statistical analysis (see text).

During one experiment, where the plot was not flooded previous to the test, a high percentage of litter removal was observed, most likely as result from wet conditions due to rainfall. In an other experiment, a low percentage was observed, presumable caused by the fact that the wet conditions were minimal due to a relative short flooding time and a previous long dry period of over 20 hours; moreover this the experiment took place during the warmest period of the day. The results of these two experiments were therefor excluded from the statistical analysis (Fig. 1).

Table 2: Median and 95% confidence intervals of percentage leaf litter fall removed in the *C. tagal* stand. (P value on test for difference between day and night; ANCOVA).

condition	period	median	CI	P	n
dry	day	0.81	0.37-1.42	0.777	3
	night	0.71	0.30-1.28		3
wet	day	25.22	19.78-31.08	< 0.01	8
	night	41.60	35.26-48.08		6

Table 3: Counts of *T. palustris* in concentric circles (with radii: of 20, 40 and 60 cm) around trees of *C. tagal* under "dry" and "wet" conditions. (mean \pm S.D. (n=5); calculated densities (n m⁻²) between brackets).

CIRCLE	DRY	WET
0 - 20	47.8 \pm 35.9 (380)	17.8 \pm 15.2 (28)
20 - 40	15.4 \pm 17.1 (41)	16.2 \pm 16.1 (26)
40 - 60	6.4 \pm 5.0 (10)	28.0 \pm 9.4 (45)
0 - 60	69.6 \pm 48.9 (61)	62.0 \pm 37.3 (55)

Observations on *Terebralia palustris*

The density of *T. palustris* was 33.0 ± 10.2 (n = 13) individuals m⁻². Average size of the snails was 44.9 ± 15.5 mm (n = 828). Snails smaller than 20 mm or bigger than 85 mm were hardly found. The food niche of litter in the *C. tagal* stand was only exploited by bigger (> 5cm shell length) individuals of the mollusc. This snail was observed eating not only from our tethered leaves, but also propagules and green leaves, which were present on the forest floor, were consumed. It was observed that during neap tides the snails were inactive and clustered on the floor around trunks and knee roots of the trees (Table 3). These places were more moist and shaded from direct sunlight. Small individuals were often found dugged in the soil. At spring tides the snails were actively moving, leaving clear tracks on the wet floor and eating the litter. The water content of the snails (including the shell) around neap tide was 15.5 ± 4.7 % (n = 52) which was significant lower than the water content at spring tide 18.1 ± 2.4 % (n = 40) (T-test; P < 0.01).

Litter removal in the *R. mucronata* stand

The decapod crab *Sesarma guttatum* was observed eating and digging in the leaves. Looking from the perspective of the amount of litter removed, dug in leaves were considered 100 % removed, i.e. not available for tidal transport. Therefore our litter removal percentages do not refer to food intake of the crabs.

The estimated median percentage litter removed in the *R. mucronata* stand during the day-time was significantly higher than during the night-time: 40.3% (95% CI: 33.1 - 47%) and 21.7% (95% CI: 15.6 - 28.6%), respectively (Table 4). In contrast with the pattern of litter removal in the *C. tagal* stand, no significant differences were found between the flooding level and the percentage litter removed.

Table 4: Median and 95% confidence intervals of percentage leaf litter fall removed in the *R. mucronata* stand. (P value on test for difference between day and night; ANCOVA).

period	median	CI	P	n
day	40.30	33.06-47.75	< 0.0111	12
night	21.73	15.59-28.57		

DISCUSSION

It is evident that the availability of water in the *C. tagal* stand is a determining factor in the amount of litter being removed by the benthos. Flooding by high waters, prolonged flooding around spring tide, rains and night conditions (lower temperature, reduced evaporation) coincide with higher litter removal percentages. The snail *T. palustris* was observed to be the exclusive consumer of the litter in this mangrove stand. The relation between moisture and litter removal is a direct consequence of the behaviour of this snail to reduce desiccation. The inactivity of the snails, when high waters do not reach the stand, will conserve the use of water, as the mucous trail, produced by active snails (Barnes, 1974), leads to water losses. The snails also avoid exposure of the soft body tissue to direct sun irradiance. The observed clustering of snails around trees and knee roots, i.e. shaded areas, and the hiding of small snails in the soil are examples of cool and moist refugia available for species living in the intertidal environment and suffering from the danger of desiccation and thermal stress (McMahon and Britton, 1983 and references therein).

Leaves falling when the stand is inundated, i.e. 8% of the time (Table 1), are considered to be exported from the stand by the tidal waters. This implicates that up to 92% of the litter fall in the *C. tagal* stand is available, for some time, for the snails to feed on. Favourable "wet" conditions for litter removal are only caused by 35 % of the high waters occurring, which are equally distributed over the time of day. Combining the data on litter removal at different conditions, we can arrive at an approximation of the average fraction of the total litter fall removed by the snails from the *C. tagal* vegetation; i.e. [fraction of leaf litter fall available] * [(fraction removed under dry condition) + (fraction removed under wet condition at day time) + (fraction removed under wet condition at night time)]. In values: $[100 * 0.92] * [(0.65 * 0.008) + (0.35 * 0.5 * 0.252) + (0.35 * 0.5 * 0.416)] = 0.112$. Thus 11.2 % of the total leaf litter fall is consumed by the *T. palustris* community in our *C. tagal* stand, which is low compared other studies. Robertson (1986) found that up to 28 % of the produced litter was removed by *Sesarmid* crabs in mid-intertidal forests. In high-intertidal forests, such as our *C. tagal* stand, over 70% of the litter fall can be removed by crabs (Robertson and Daniel, 1989; Michelli et al., 1991; Emmerson and McGwynne, 1992). The difference in litter removal between our study and the mentioned literature can be explained from the inactive period of the snail during neap tides to avoid the danger of dehydration. Crabs can forage at neap and spring tide thanks to their capability of digging holes by which they can reach the underground water table of the intertidal area and avoid problems of dehydration (MacNae, 1968).

The low percentages of leaf litter removed at neap tide, due to the inactive period of the snails, will allow a gradual build-up of litter on the forest floor. With the first high water reaching the plot the build up litter stock will be flushed away. The overall result is a pulsating efflux of litter from the *Cerriops* stand with highest litter transports at the beginning of spring tide. The high litter removal activity we observed during a rainy day suggests that the seasonal rains will also cause a seasonal activity pattern of the snail *T. palustris*. With the supply of water by the rains, their activity will increase. Combined with the reduced litter fall for the same season (Slim et al, submitted), the litter removed by tidal export from the *C. tagal* stand will fluctuate over the year, with lowest values during spring tide in the rainy seasons.

In the *R. mucronata* stand several leaf eating *Sesarma* species were present. *Sesarma guttatum* is the most common one in this low lying mangrove forest (J. Schrijvers, pers. comm.) and was observed eating from the litter present on the forest floor. Other species present were *Sesarma smithii* and *Sesarma leptosoma* (J. Schrijvers, pers. comm.). *Sesarma leptosoma* is known to feed on fresh leaves, it obtains these by climbing into the trees (Vannini and Ruwa, 1994). According to these authors *Sesarma leptosoma* cannot be responsible for the litter removal as this species does not venture onto the free mud surface at low tide. *Sesarma smithii* is a nocturnal species, known from northeastern Australia to feed on fallen litter. The litter removal data show higher activity at day time than at night time in our *R. mucronata* stand, suggesting that *Sesarma guttatum* is more important for the process of leaf litter removal than *Sesarma smithii*.

Following the same line of calculations as for the *C. tagal* stand, the estimated litter removal averaged over time, as a fraction of total litter fall, in the *R. mucronata* stand is; $[(100 * 0.60)] * [(0.5 * 40.3) + (0.5 * 21.7)] = 0.186$. Compared with other authors (Robertson and Daniel, 1989; Michelli et al., 1991; Emmerson and McGwynne, 1992) the figure of 18.6‰ of the litter removed is rather low. Robertson (1986) presents 22‰ as the lowest seasonal value for a mixed *Rhizophora* forest in Australia. But in absolute figures our level of litter removal is larger than the one determined by Robertson, i.e. 170 g DW m⁻²y⁻¹ and 154 g DW m⁻²y⁻¹ respectively.

Although the *C. tagal* stand is less frequently flushed by the tidal waters, the loss of litter due to tidal flushing is of similar order as from the twice a day flooded *R. mucronata* stand. From the *C. tagal* stand 89 % (i.e. 0.93 g DW m⁻²d⁻¹) of the litter fall is subject to tidal transport and for the *R. mucronata* stand this value is 81 % (i.e. 2.04 g DW m⁻² day⁻¹). Due to the higher amount of litter fall in the *Rhizophora* stand the absolute losses are bigger from this mangrove forest. Retention of litter by local decomposition will be of minor importance in both stands. In the *Rhizophora* stand the residence time of litter is restricted to a single low water period, i.e. maximum 6 hours. In the *Ceriops* stand the residence time can be longer especially around neap tides when the stand is not inundated by high water. But these dry conditions are not favourable for the decomposition process (Robertson, 1988; Hemminga and Nieuwenhuize, 1991).

The litter processing in the *C. tagal* stand by snails differs from the general description of litter processing in literature where *Sesarmid* crabs play an important role. Consumption and burial of the litter by crabs will cause retention within the forest of the litter (Robertson, 1986; Robertson and Daniel, 1989; Michelli et al., 1991; Emmerson and McGwynne, 1992). In the *C. tagal* stand only consumption, but no burial of litter occurred. The consumed litter will only return to the system after digestion by the snail as faeces. As *T. palustris* is a mud dweller its faeces will be deposited on the top of the soil and become available for detritus feeders, i.e. young individuals of *T. palustris*, fiddler crabs (*Uca lactea* and *Uca inversa* are abundantly present) and other small benthos. Due to tidal flushing inevitable loss of the faeces and its nutrient contents will occur, as the snails are only active when high waters reach the stand. Our results clearly show that processing of the litter in an intertidal mangrove forest is not a unique feature of a benthic community dominated by crabs, but that the activities of the snail *T. palustris* should be included in the models of energy flow in mangrove forests.

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OUTWELLING AND TRAPPING OF MANGROVE CARBON IN GAZI BAY

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INTRODUCTION

Mangroves are open systems, coupled to the coastal waters by tidal currents. Several studies indicate that export of particulate organic matter from mangrove forests may be a general feature of these systems (Boto & Bunt 1981; Twilley, 1985; Robertson, 1986; Flores-Verdugo et al., 1987). The factors that determine the magnitude of this transport and the spreading of the material in the adjacent coastal zone are poorly known, but they will include geomorphological and hydrodynamic factors (Twilley, 1985; Woodroffe, 1992; Wolanski et al., 1992). Mangroves occur in a number of different environmental settings. An intriguing situation is the co-occurrence of mangroves, seagrass meadows and coral reefs. These can be found as adjacent systems in tropical coastal zones. It is known that the level of nutrient availability in both seagrass and reef systems may have profound effects on their structure and function (e.g. Harlin & Thorne-Miller, 1981; Smith et al., 1981; Brock & Smith, 1983; Birkeland, 1987; Short, 1983, 1987; Hallock, 1988; Fourqurean et al., 1992). Thus, if particulate organic carbon and associated nutrients such as nitrogen and phosphorus are exported from the mangrove forest and enter the adjacent seagrass and reef systems, an influence on the structure and functioning of these systems is not unlikely.

During the project, we investigated the fluxes of particulate carbon between the mangrove in Gazi Bay (Kenya) and the adjacent seagrass meadows and reef zones, as part of the first objective of the project to assess the nutrient sink or source function of mangroves.

STUDY AREA

Gazi Bay is situated 50 km south of Mombasa on the Kenyan coast (4° 25'S, 39° 30' E). On the landward side a mangrove of 6.61 km² covers much of the Bay (Fig. 1). There are two major tidal creeks penetrating the mangrove forest. The western creek is the mouth of the river Kidogoweni, a seasonal river. The eastern creek, called Kinondo creek, is a tidal creek. The present investigation focussed on the outflow of this creek. A total of 8 mangrove species are found in Gazi Bay. Directly adjacent to the mangroves on the seaward side are intertidal flats intersected by some channels, and shallow, subtidal areas. Both the intertidal and subtidal areas are to a large extent covered by various species of seagrasses and, to a lesser extent, by macro-algae. Particularly relevant to this study was the subtidally growing seagrass *Thalassodendron ciliatum*. *Thalassodendron* forms dense beds in Kinondo creek and in the channels between the tidal flats. In subtidal area of the bay, the species is present in monospecific meadows which spread to the reef zone. *Thalassodendron* is a stem-forming species, giving the plant a total height of up to 80 cm. The reef zone in front of the bay is part of the fringing reef that forms a nearly uninterrupted belt along the Kenyan coast. The distance between the mouth of Kinondo creek and the reef zone is approximately 4 km.

MATERIALS AND METHODS

Various types of samples (see below) were taken on 4 subtidal transects, positioned in the channel

forming the continuation of Kinondo creek and in the shallow bay waters more closely to the reefs. Thalassodendron ciliatum was the only, or the dominant, seagrass species on these transects. On each transect, 4 sediment cores were taken using a sediment corer with an internal diameter of 7 cm. The distance between sampling sites on a transect was approximately 20 m. The upper 7 cm of

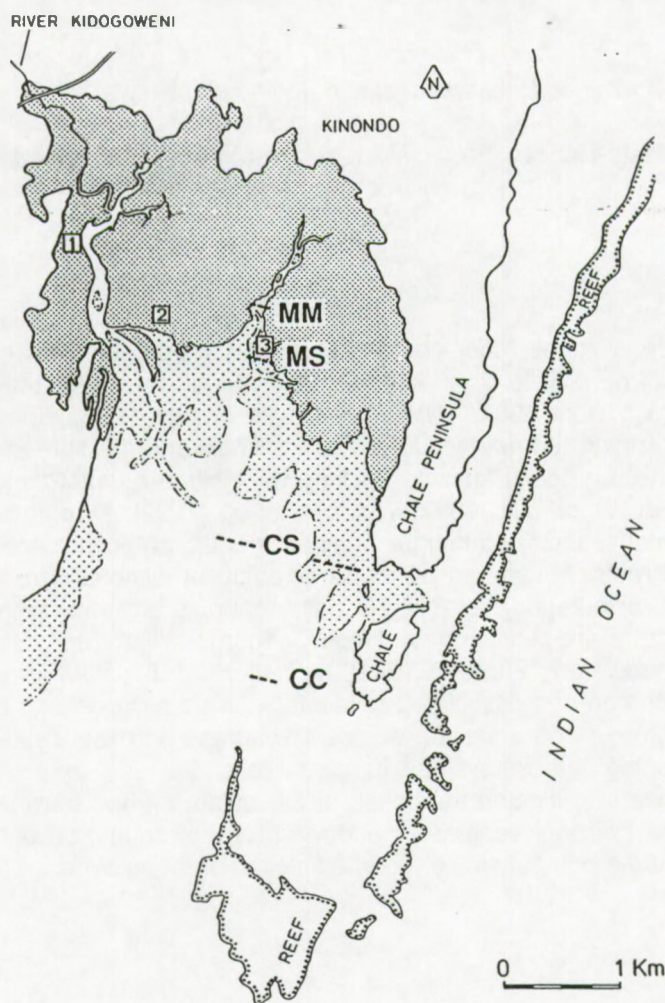


Fig.1. Map of Gazi Bay. The mangrove area is indicated in dark grey. The seagrass zone is south of the mangrove; the intertidal part of it is indicated in light grey. Sampling transects in the seagrass zone are indicated with a two-letter code. 1: Cerriops tagal sampling site; 2: Rhizophora mucronata sampling site; 3: location of work platform.

each core was immediately transferred to a sample container. At each sampling site, the above-ground biomass of Thalassodendron was clipped from 3 plots of 25 X 25 cm. Sediment and seagrass samples were lyophilized. The lyophilized sediments were sieved over a 2-mm mesh sieve to remove coarse material (mainly seagrass roots and mollusc shells). The three seagrass samples collected at each sampling site were pooled, yielding a total of 4 samples per transect. To decrease the variability which might arise from analyzing seagrass leaves of different developmental stage, only the third youngest leaves of each Thalassodendron shoot in a sample were collected and used for further chemical analyses (stable carbon isotope signature, nutrient contents). These third-youngest leaves are nearly full-grown, but they lack the crust of epiphytes complicating the analysis of older leaves. Analyses were carried out after drying of the leaf material at 70°C.

Sediment traps were used to obtain particulate matter depositing in the seagrass zone. 4 Traps were positioned on each transect, in the plots which had been cleared of Thalassodendron. They were made of PVC tube with a internal diameter of 7.6 cm, and a length of 33 cm, closed on one side by a PVC disc. A steel pin connected to the disc was used to anchor the tube in an upright position in the sediment. The opening of the traps was positioned at the level of the canopy of the Thalassodendron vegetation. After 10-17 days of deployment, the sediment traps were closed underwater with rubber stoppers and returned to the field laboratory. The contents were filtered through a 1-mm sieve, and the coarse matter retained on the filter was discarded. Subsequently, 200-400 ml of the filtrate was filtered over Whatmann GF/C filters. The particulate material retained on the filters was lyophilized prior to further chemical analyses.

To investigate changes in seston characteristics in the tidal water when it passed the seagrass zone, seston samples were collected during one ebb tide (June 24) and two flood tides (June 30 and July 1). Ebb water flowing from the mangrove forest in seaward direction was collected on the MM and the CS transect. Incoming flood water was collected on the CC and MM transect. Water samples were collected over the full duration of each tide (approximately 1 sample per hour on each transect). Water samples (25-l each) were collected with a hand diaphragm pump, 1 m above the subtidal sediment surface. The samples were filtered over Whatmann GF/C filters. The filters were dried by lyophilization.

Additional sediment samples (upper 7 cm) were collected from the intertidal flats adjacent to the subtidal MS and CS transects, from stands of Rhizophora mucronata and Ceriops tagal, and from Chale lagoon, directly east of Gazi Bay (Fig 1.). This lagoon is separated from Gazi Bay by Chale Peninsula and Chale Island by a broad sill of fossil coral inbetween both formations, restricting direct water exchange between Gazi Bay and the lagoon. Thalassodendron is abundant in the lagoon, and samples of this seagrass were also collected here. Processing of the sediment and seagrass samples was carried out as described above. Finally, green, fully-grown leaves of all mangrove species present in Gazi Bay were collected and dried (70°C) for chemical analyses.

RESULTS

Leaves form the major category of organic material produced by the mangrove trees in Gazi Bay (F.J. Slim, unpublished data). Table 1 shows the $\delta^{13}\text{C}$ values the leaves of the various mangrove species occurring in Gazi Bay, ranging from -28.25‰ in Rhizophora mucronata to -24.12‰ in Ceriops tagal.

Table 1. Carbon isotope signature ($\delta^{13}\text{C}$) of mangrove leaves occurring in Gazi Bay. Means of two samples of pooled (10-20) leaves.

Species	$\delta^{13}\text{C}$ (‰)
<u>Rhizophora mucronata</u>	-28.25
<u>Ceriops tagal</u>	-24.12
<u>Sonneratia alba</u>	-27.15
<u>Avicennia marina</u>	-26.84
<u>Bruguiera gymnorrhiza</u>	-27.30
<u>Xylocarpus granatum</u>	-24.86
<u>Lumnitzera racemosa</u>	-26.99
<u>Heritiera littoralis</u>	-27.73

$\delta^{13}\text{C}$ values of organic matter in the sediments of Rhizophora and Ceriops stands (-25.31 and 22.69‰ , respectively, see Table 2), are less depleted than those of the leaves. The $\delta^{13}\text{C}$ value of the sediment of the Kinondo creek (MM transect) falls in the range of the mangrove sediments. However, as Table 2 shows, there is a conspicuous enrichment in ^{13}C in the seagrass zone away from the mangrove. At the CC transect the $\delta^{13}\text{C}$ value of the sediment (-15.14‰) is not significantly different from that of the Chale lagoon sediment (-14.75‰), the sample location outside Gazi Bay.

The data of the two intertidal locations show a similar trend.

Table 2. Carbon isotope signature ($\delta^{13}\text{C}$), and carbon and carbonate content (% weight) of sediment samples in Gazi Bay and Chale lagoon. Means and S.D. Data in a column sharing a common superscript letter are not significantly different ($\alpha=0.05$).

Location	$\delta^{13}\text{C}$ (‰)	% carbon	%carbonate	Nr. of obs.
Mangrove (Rhizophora)	-25.31±0.33 ^a	15.37±5.02	1.20±0.66	3
Mangrove (Ceriops)	-22.69±0.57 ^b	1.71±0.24	0.60±0.26	3
subtidal MM	-22.94±0.26 ^b	3.78±0.95 ^a	38.77±4.86 ^a	4
subtidal MS	-20.61±1.46 ^c	2.22±0.88 ^b	43.30±6.11 ^a	4
subtidal CS	-18.48±0.31 ^d	0.68±0.16 ^c	27.65±7.85 ^b	4
subtidal CC	-15.14±0.77 ^e	0.67±0.45 ^c	80.30±2.01 ^c	4
Chale lagoon	-14.75±0.52 ^e	0.63±0.19 ^c	88.03±0.83 ^c	3
intertidal MS	-20.99±1.02 ^c	5.13±2.86	55.42±5.87	4
intertidal CS	-17.13±0.76 ^f	0.67±0.53	59.70±33.30	4

The organic carbon content of sediment at the MM transect is relatively high. However, coinciding with the enrichment in ^{13}C in seaward direction, the organic carbon content of the subtidal sediments decreases significantly. These data suggest outwelling of mangrove-derived POM, but also suggest that this POM is trapped in the seagrass zone, close to the mangrove.

Enrichment in ^{13}C with increasing distance from the mangrove, is also very clearly found in the *Thalassodendron* growing on these sites (Table 3). Seagrass at any of the four subtidal transects, however, is always more enriched in ^{13}C than sediment of the same site.

$\delta^{13}\text{C}$ values of seston were determined to investigate if shifts in organic composition of the seston occurred during the flow of the tidal water mass over the seagrass zone. During ebb tide, the seston was less depleted in ^{13}C than at the CS transect (at a distance of 2.5 km from the mangroves) than at the MM transect. The difference is statistically significant ($p < 0.01$). No difference was found in salinity of the water between these locations. These results exclude the possibility that mixing of water ebbing from the eastern part of the mangroves with water from the river Kidogweni caused the shift in carbon isotope signature. The increase

Table 3. Carbon isotope signature ($\delta^{13}\text{C}$) of *Thalassodendron ciliatum* growing at increasing distance from the mouth of Kinondo creek, Gazi Bay, and in Chale lagoon. Means and S.D. of 4 (pooled leaf) samples.

Data sharing a common superscript letter are not significantly different ($\alpha=0.05$).

Location	$\delta^{13}\text{C}$ (‰)
subtidal MM	-19.65±0.39 ^a
subtidal MS	-18.30±0.45 ^b
subtidal CS	-15.77±0.47 ^c
subtidal CC	-10.70±0.23 ^d
Chale Lagoon	-10.72±0.36 ^d

Table 4. Seston and POC levels in tidal water crossing the seagrass zone.

Means and S.D. of samples taken at approximately hourly intervals over the duration of the tide. Differences between transect seston and POC data were statistically analysed for each tide separately. Data sharing a common superscript letter are not significantly different ($\alpha=0.05$).

<u>Tide</u>	<u>Date</u>	<u>Transect</u>	<u>Seston (mq/l)</u>	<u>POC (mq/l)</u>	<u>Nr. of obs.</u>
ebb	24/6	MM	1.99 \pm 1.63 ^a	0.32 \pm 0.06 ^a	5
		CS	3.30 \pm 1.53 ^a	0.46 \pm 0.16 ^a	5
flood	30/6	CC	3.45 \pm 1.71 ^a	0.28 \pm 0.13 ^a	5
		MM	6.23 \pm 2.56 ^a	1.12 \pm 0.39 ^b	5
flood	1/7	CC	2.78 \pm 0.95 ^a	0.35 \pm 0.07 ^a	6
		MM	8.65 \pm 6.61 ^a	1.76 \pm 1.27 ^b	5

in the $\delta^{13}\text{C}$ value of the seston is consistent with the above-mentioned process of sedimentation of mangrove-POM in the seagrass zone. However, uptake of particulate material from the seagrass zone could contribute to the shift in $\delta^{13}\text{C}$ values: there was a moderate increase in average seston and seston-POC content going from the MM to the CS transect (Table 4), but the differences were not significant. Clearly, more data are needed before any conclusion can be made regarding this point.

The seston of the ocean water that enters the bay during flood tide (1 July), sampled at the CC transect, has $\delta^{13}\text{C}$ values ranging between -17.27 and -19.04‰ (mean value -18.10‰). However, when the water has crossed the seagrass zone and is about to enter the mangroves, the $\delta^{13}\text{C}$ values are consistently shifted to more negative values, ranging from -22.04 to -23.70‰ (mean value: -22.88‰). For the flood tide of June 30th (not shown) identical results were obtained (mean $\delta^{13}\text{C}$ value at CC transect -18.22‰ ; at MM transect -23.43‰ ; means of 5 observations). These highly significant shifts ($p<0.001$) most probably are due to resuspension and uptake of organic material in the seagrass zone, not to sedimentation processes: the ocean water that enters the bay has a relatively low POC content (CC transect, Table 4), but on reaching the MM transect the POC content has increased significantly. Thus it appears that, besides outwelling of mangrove carbon, there is also a reversed transport of POC from the seagrass zone to the mangroves, achieved by the incoming flood tides.

Most of the sediment traps deployed in the seagrass zone contained some detached leaves or large leaf fragments of *Thalassodendron*. This coarse material was not included in the chemical analyses of the trap contents, as the contents of the traps were filtered over a 1-mm sieve prior to analysis. The remaining material consisted of very fine, dark brown to black coloured, unrecognizable particles. $\delta^{13}\text{C}$ values of this material increased from a strongly negative value of -23.30‰ at the MM transect to a value of -13.96‰ at the CC transect (Table 5). The C:N ratios of the material collected in the sediment traps (Table 6), show values between 8.5 and 11.2. The C:N ratio of the seston filtered from the water were on average between 6.5 and 10, and are thus of the same order of magnitude. There is a remarkable contrast between these values and the C:N ratios of mangrove leaves, particularly senescent leaves, which can have C:N ratios of more than 200.

Table 5. Carbon isotope signature ($\delta^{13}\text{C}$) of particulate organic material collected with sediment traps in the seagrass zone of Gazi Bay. Means and S.D. Data sharing a common superscript letter a not significantly different ($\alpha=0.05$).

<u>Location</u>	<u>$\delta^{13}\text{C}$ (‰)</u>	<u>No. of obs.</u>
subtidal MM	-23.30 ± 0.40^a	4
subtidal MS	-22.47 ± 0.21^a	3
subtidal CS	-19.15 ± 0.85^b	3
subtidal CC	-13.96 ± 0.63^c	4

Table 6. C:N ratios of seston collected at subtidal transects during 1 ebb and 2 flood tides (data of the 2 flood tides were pooled), and of sediment trap contents. Seston data were statistically analysed per row. Data sharing a common superscript letter are not significantly different ($\alpha=0.05$). For comparison, C:N ratios of the dominant seagrass and mangrove species in the study area are also given. The data of *Thalassodendron* are from the 3 samples of pooled third-youngest leaves collected at the MM transect. Data of mangrove leaves are based on two samples of pooled leaves (10-20 leaves).

Means and S.D. Number of observations given in brackets.

<u>Location</u>	<u>sedim. traps</u>	<u>seston ebb water</u>	<u>seston flood water</u>
subtidal MM	10.0 ± 1.0^{ab} (4)	7.0 ± 1.7^b (5)	10.0 ± 1.6^a (10)
subtidal MS	11.2 ± 0.5^b (3)		
subtidal CS	9.1 ± 1.5^a (3)	6.8 ± 1.2^b (6)	
subtidal CC	8.5 ± 0.7^a (4)		6.5 ± 0.9^b (11)

<u>seagrass and mangrove leaves</u>			
	<u>fresh leaves</u>		<u>senescent leaves</u>
<i>Thalassodendron ciliatum</i>	19.3 ± 0.4	(3)	
<i>Rhizophora mucronata</i>	43.0	(2)	193 (*)
<i>Ceriops tagal</i>	59.2	(2)	218 (*)
<i>Bruguiera gymnorhiza</i>	44.5	(2)	187 (*)
<i>Sonneratia alba</i>	25.1	(2)	72 (*)
<i>Avicennia marina</i>	31.8	(2)	88 (*)

(*) data from Rao et al., (1993)

DISCUSSION

The carbon isotope signatures of leaves and sediments collected in the mangrove forest show that the organic matter in the mangrove is characterized by strongly negative $\delta^{13}\text{C}$ values. Only the $\delta^{13}\text{C}$ value of the sediment of the seagrass zone in direct proximity of the mangrove (MM transect) falls in the range of the mangrove sediment values. Further away, the mangrove signal fades out rapidly, and our data indicate that already at a distance of 2 km from the mouth of Kinondo creek the input of mangrove carbon is of marginal influence in determining the $\delta^{13}\text{C}$ value of the sediment. Thus it appears that during ebb flow, carbon depleted in ^{13}C is exported from the mangrove, but that all or part of this outwelling carbon is trapped in the seagrass zone before it reaches the coral reefs.

Remarkably, the carbon isotope signature of *Thalassodendron* shows a trend similar to that of

the sediment values with increasing distance from the mangrove. It is known that the isotope signature of seagrasses is highly variable (McMillan et al., 1980). Probably, these values are a reflection of the amount of mangrove carbon that is available for assimilation by the seagrasses. CO_2 resulting from the mineralization of mangrove-POM trapped in the seagrass zone will supply T. ciliatum with inorganic carbon relatively depleted in ^{13}C ; moreover, it cannot be excluded that dissolved respiratory CO_2 , directly exported from the mangrove forest, is a source of carbon for the seagrass.

There appears to be not only a simple unidirectional efflux of carbon from the mangroves, but also a reversed flux from the seagrass zone back to the mangroves. During both flood tides which were studied, highly significant decreases in the $\delta^{13}\text{C}$ values of the seston from the CC to the MM transects were found ($\pm 5\text{‰}$), coinciding with significant increases in the POC content of the seston. The $\delta^{13}\text{C}$ values of the flood seston at the MM transect (circa -23‰) are clearly more negative than the $\delta^{13}\text{C}$ value of the seagrass vegetation at this transect (-19.65‰). These strongly negative values suggest that at least part of the carbon taken up in the seagrass zone by the flood tides originally comes from the mangrove forest. Presumably, both autochthonous seagrass particles and allochthonous particles from the mangroves, deposited in the seagrass zone at earlier ebb tides, will be taken up by the incoming water and transported into the forest. Circumstantial evidence for this process, moreover, is found in the carbon isotope signature of the mangrove sediment. The $\delta^{13}\text{C}$ sediment value of the Rhizophora mucronata sample site, a low-lying site that is inundated each flood tide, is conspicuously less negative (2.9‰) than the $\delta^{13}\text{C}$ values of the R. mucronata leaves. Such a decrease would not be expected if litter from the tree was the only source of the organic matter in the sediment, the more so as the carbon isotope signature of leaves of R. mucronata in Gazi bay shows more pronounced ^{13}C depletion in senescent leaves prior to leaf fall (Rao et al., in press). Sedimentation of particulate material from the seagrass zone in the R. mucronata zone would result in less depleted sediment $\delta^{13}\text{C}$ values. Using the $\delta^{13}\text{C}$ values of the flood seston and of those the R. mucronata leaves as end members, a simple calculation indicates that to arrive at the $\delta^{13}\text{C}$ sediment value, R. mucronata carbon and flood seston carbon would have to be mixed in a proportion of 1: 1.33. At the Cerriops tagal site the difference between carbon isotope signature of sediment and leaf material is small (1.4‰ lower in the sediment). This site is only inundated at spring tides, and the external input of tidally born particulate matter probably is more restricted.

The material captured by the sediment traps in the seagrass zone will be a mixture of locally derived resuspended particles and allochthonous material. It is remarkable that the C:N ratio of the seston collected in the sediment traps is low, varying between 8.5 and 11.2. Neither these values, nor the C:N ratios of the seston obtained by filtering the tidal water above the seagrass zone (C:N ratios 6.5 to 10), are close to the C:N ratios of either mangroves or seagrasses (Table 4). Possibly, the seston contains an important fraction of organic particles derived from the mangroves and seagrass vegetation that has already gone through a phase of intensive processing; this has resulted in shifts in the chemical characteristics of these particles. We have suggested above that the organic particles from the mangroves (together with seagrass particles) may go through repeated efflux-reflux cycles. These transport cycles enhance the proportion of older, more processed organic material in the seston and may therefore be a crucial element in explaining the low C:N ratios of seston and seston trap material.

A progressive change in C:N ratios may be caused by several processes. Increases in nitrogen levels during decomposition have been observed in many types of vascular plant detritus (Swift et al., 1979). Robertson (1988) observed this phenomenon also during decomposition in mangrove leaves. The C:N ratio in decomposing leaves of Rhizophora stylosa, Avicennia marina and Cerriops tagal was approximately halved after 160 days of decomposition. Secondly, nitrogen fixation may enrich the litter. Nitrogen fixation activity is widespread in the mangrove forest (Alongi et al, 1992), and is also found in association with decaying leaf litter (Goto and Taylor, 1976; van der Valk and Attiwill, 1984). Nitrogen fixation has been found both in the mangroves and in Thalassodendron meadows in Gazi bay (A.F. Woitchik, this cruise report). Thirdly, several studies have shown that planktonic bacteria have a low carbon conversion efficiency on detrital substrates (Newell et al., 1981; Linley and Newell, 1984; Bauerfeind, 1985; Bjornsen, 1986). We may speculate that a decrease in C:N ratio of detritus-bacteria aggregates is furthered by such a low conversion efficiency of the heterotrophic bacteria associated with the particles. In summary, the key features of POM fluxes in Gazi Bay which emerge from this study as follows: (1) spatially restricted outwelling of mangrove carbon; (2) reversed fluxes of POM from the seagrass zone to the

mangroves; (3) transported POM characterized by low C:N ratios.

In Gazi Bay, the seagrass zone appears to function as a buffer in between the mangroves and the coral reefs, trapping outwelling POM at close distance from the mangroves. This spatially restricted outwelling of mangrove-POM implies that effects of the exported mangrove-POM primarily must be sought in the adjacent seagrass zone.

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TIDAL EXCHANGE OF LEAF LITTER BETWEEN MANGROVE FORESTS AND ADJACENT SEAGRASS BEDS: A PRELIMINARY BUDGET APPROACH

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INTRODUCTION

One of the central questions in the present STD-3 research project is whether the mangrove ecosystem can be considered as a source or a sink. In this part of the project, the quality and quantity of the transported coarse Particulate Organic Matter (cPOM: mangrove and seagrass leaves, and seaweed) was determined. From catches of cPOM at a number of tides at different sites in the intertidal and subtidal parts of Gazi Bay (Kenya), the nature of the transported material (leaves of which species, nutrient content) and quantity (does export exceed import?) was derived. Research on the transport of macro material has been carried out in a number of mangrove ecosystems. As far as we know, however, there has not been a study on this subject that included the suspended macrolitter, using large nets that sampled the entire water column. In this study the portion of litter that is of mangrove origin will be divided into a floating fraction and a "sinking" fraction, since the whole water column is sampled.

Since the nets used to collect the cPOM were positioned on the edges of the intertidal flat it was possible to gain information about the exchange of material between the mangrove forest and the intertidal flat, and between the intertidal flat and the subtidal flat and coral reefs. These three compartments (mangrove forest, intertidal flat, subtidal flat and coral reefs) will be considered as units, from which litter is exported or imported.

METHODS

Study area

The research was carried out in Gazi Bay (Kenya). The mangrove forest on the seaward side is dominated largely by *Rhizophora mucronata* (>75%). Also, stands of *Bruguiera gymnorhiza*, *Ceriops tagal*, *Sonneratia alba* and *Avicennia marina* are found. The mangrove forest in Gazi Bay can be classified as a *Rhizophora* dominated littoral fringe inundated by daily tides. The average difference between low and high tide is about 3 meters. Between the mangrove forests and the coral reef, in the intertidal and subtidal zone, dense populations of seagrass species can be found.

Litter transport

In order to trap tidally transported macrolitter, large wooden frames were built that consisted of two tripods made from mangrove poles. In these frames, nets were attached to the poles with hooks and rings. A set of lines (thin nylon ropes) that were put through the rings enabled the nettings to be closed and opened before actually being taken out. One net was positioned in the mouth of the Kinondo creek (Fig.1). Two other nets were placed on the intertidal flat close to the mangroves. These three nets were 2.5 meters high, 6 meters long and 1.5 meters wide. Towards the ocean, at the edge of the intertidal flat, a fourth and fifth net were placed. These two nets had a height of 6 meters. With these nets it was possible to catch macrolitter present over the entire height of the water column. All nets had a mesh size of 2 mm.

The nets were opened at high water (ebb catch) or at low water (flood catch) and closed at the moment the tide changed. After the required period, the nets were taken out and the catch was weighed. The catch was sorted according to the categories indicated in Table 1. The mangrove leaves were separated into a floating and a sinking fraction by making use of a sea water tank. The mangrove catch was dispersed in the water. After three to five minutes the mangrove leaves that

were clearly floating were taken from the surface, sorted and weighed and categorized as "floating". The mangrove leaves that were found on the bottom of the water tank or were suspended in the water column were collected, sorted and weighed and categorized as the "sinking" fraction. The seagrass leaves and seaweeds were not categorized into a floating and sinking fraction. From each catch category dry weight samples were taken (total floating mangrove leaves, total sinking mangrove leaves, total seagrass and total seaweed). Of these dry weight samples the carbon and nitrogen contents (with a Carlo Erba NA1500 CN analyzer) and phosphorous contents (with a spectrophotometer Milton Roy type 301) were determined.

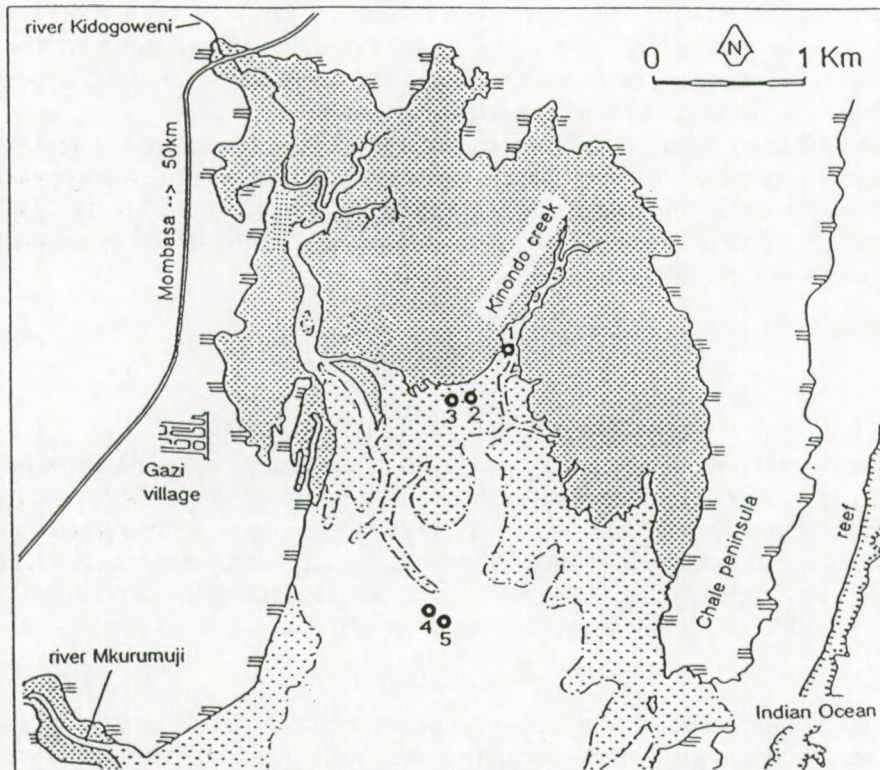


Fig.1; Map of the study area Gazi Bay. Dotted area is mangrove forest. Numbers indicate the positions of the nets.

Table 1; categories according to which the catch was sorted. Categories with "" were sorted, categories with "-" were not sorted.

Category	floating	sinking	total
<i>Sonneratia alba</i>	*	*	-
<i>Rhizophora mucronata</i>	*	*	-
<i>Brugiera gymnorhiza</i>	*	*	-
<i>Ceriops tagal</i>	*	*	-
<i>Avicennia marina</i>	*	*	-
rest mangrove leaves	*	*	-
Seagrass	-	-	*
Seaweed	-	-	*

Statistical methods. All data were submitted to a variance test in order to investigate the differences at neap and spring tide, at ebb and flood and between different nettings (sites). The test used was the Tukey-Kramer method for multiple comparisons among pairs of means. Calculations were carried out by a computer model SYSTAT version 5.0 (SYSTAT inc.). Values discussed will be "comparison probabilities", which indicate whether a comparison is statistically significant or not. Probabilities smaller than 0.05 will be considered to indicate a statistically significant difference between the two compared variables. To obtain normally distributed results, fractions were transformed into arcsinus values while other data were transformed into logarithmic values before submitting the data to the Tukey-Kramer test.

RESULTS

Chemical composition

The results on the chemical analyses of samples of the litter catch are summarized in Table 2. There were no sufficient data to determine whether differences between neap and spring tides existed. Statistical analyses showed that there are no differences in sites or tides (ebb/floods) with respect to the nitrogen, carbon and phosphorous contents of mangrove leaves or seagrasses or seaweed. There is a striking difference, however, between the nitrogen and carbon contents of seaweed and mangrove leaves. The seaweed biomatter appears to have a clearly different carbon and nitrogen content. The analyses of data on phosphorous contents showed no significant differences at all.

Mass fluxes. Not all measurements planned could be carried out. Sometimes the frame of the nettings broke down due to strong spring tide currents. On some occasions strong wind blowing in the direction opposite to the actual tidal current blew the nettings empty. On the whole, however, a considerable amount of data was obtained. A number of times the catch was too much to sort all of it within the short available time span. In those cases a sample was taken after which its biological composition was extrapolated onto the total catch.

It appeared that mangrove leaves in the category "sinking" may constitute 11-83% of the total dry weight catch of mangrove leaves, indicating that the fraction of exported mangrove leaves that is suspended in the water column represents a significant part of the total. *Rhizophora mucronata* was by far the most abundant species in the catch of mangrove leaves in all nets. A good second was *Sonneratia alba*. Mangrove leaves were also trapped in the nets set out at flood

tides, suggesting that some of the mangrove leaves were captured by the seagrass meadows in the bay. Fig. 2 shows that the largest portion of the dry weight of the samples consists of seagrass material (on average 57.1%) The mangrove leaves that were classified as "floating" constituted only some 3-48% (average 18.8%) of the dry weight of the total catch.

Table 2. Average chemical composition of litter catch.

Biomass	%C	%N	%C/%N	%P	C:N:P (atomic ratio)
M.floating	41.8	0.3	128.2	0.02	5406:39:1
M.sinking	46.2	0.4	125	0.02	5973:43:1
Seagrass	27.3	1.2	23.3	0.09	784:30:1
Seaweed	23.5	1.6	14.9	0.10	606:37:1

Table 3. Average catches (\pm standard deviations, sd) of tidally transported macrolitter in Gazi Bay (g, D.W.) at neap tides (N), spring tides (S) and tides in between neap and spring (NS).

Averages and standard deviations at ebb								
	Seagrass+seaweed		Mangrove total		Mangrove floating		Mangrove sinking	
tide	avg	\pm sd	avg	\pm sd	avg	\pm sd	avg	\pm sd
N	348	283	41	57	37	51	4	7
NS	341	355	128	157	62	68	62	104
S	128	100	218	117	144	116	74	72
Averages and standard deviations at flood								
N	84	151	14	23	10	16	4	7
NS	321	333	73	77	68	78	5	5
S	437	488	238	437	73	144	165	296

Fig.3 shows the results when the average flood catch is subtracted from the average ebb catch. Thus, values above zero imply a net export from the mangrove forest while values below zero mean a net import. For the mangrove leaves (both floating and sinking) it is clear that they are exported to the intertidal flat. The nets four and five, positioned at the edge of the intertidal flat, show a net import of mangrove leaves. Apparently these sites trap leaves that are transported back from the subtidal part of the bay with the flood currents. The results depicted in Fig. 3 also show that there is a clear import of seagrass and macroalgae into the mangrove forest on the sites 1 and 2. Landward transport also dominates transport of these categories of macrolitter on site 5, but not

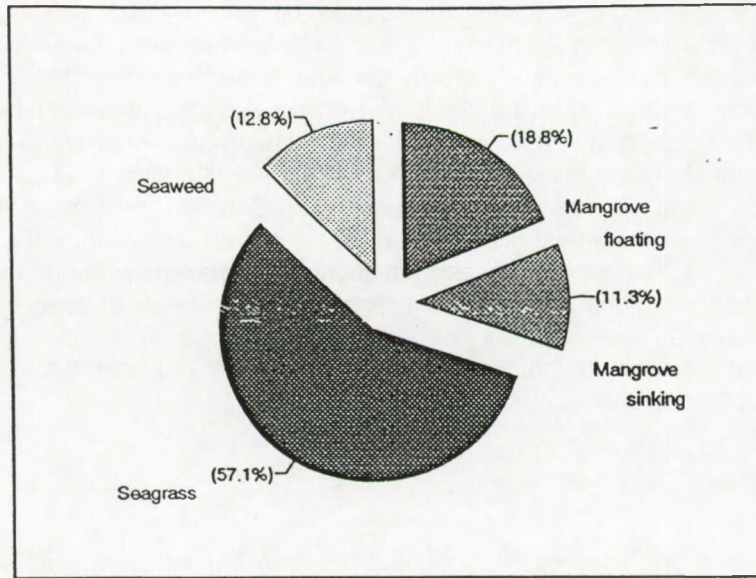


Fig. 2. Tidally transported macrolitter in Gazi Bay, specified as percentage of total catch.

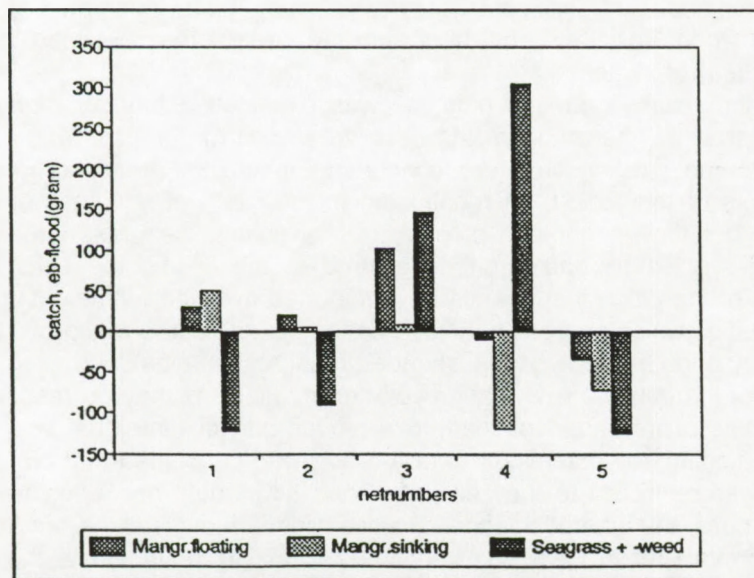


Fig.3 Macrolitter fluxes in Gazi Bay, calculated by subtracting average flood catches from average ebb catches. The numbers on the horizontal axis indicate the net position (see Fig. 1). Values above zero imply a net export in seaward direction.

on the nearby site 4. The data show that the mass flow of seagrass and macroalgae may be substantial and must be taken into account when describing direct fluxes between mangrove forests and seagrass beds. However, calculating of accurate budgets will be difficult due to the site variation which emerges from the present results. For the interpretation of the results it is important to determine which factors produce the variability between the individual catches. The major factor obviously is difference between ebb and flood. A second possibly important factor may be the difference between the catches at neap tide and those at spring tide. Analysis of the data (summarized in Table 2) do not show a consistent relation between the quantity of the catch and the phase of the tidal cycle, i.e. whether it was neap tide, spring tide, or a tide in between the two, when we consider all categories of macromaterial. The data, however, show that the quantity of the mangrove litter transported clearly increases with increasing maximum water height. This is the case both with ebb and with flood tides. The average dry weight catch of seagrass plus macroalgae, in contrast, showed an inverse trend at ebb that is difficult to explain. These differences nonetheless imply that it is recommendable to do experiments both at neap tide and at spring tide if one is interested in correct quantities of transported macro litter.

DISCUSSION

In this study the flux of macro litter was investigated between the mangrove forest and the intertidal mud flat, and between the intertidal mud flat and the subtidal flat and coral reefs. To investigate the interlinkages between coastal ecosystems in Gazi Bay, the mangrove forest (1), the intertidal flat (2), and the subtidal flat and coral reefs (3) were distinguished as individual systems or compartments. The direct flux approach as a quantification method is difficult for a number of reasons (Hopkinson, 1988). Reliable data on water current velocities are difficult to obtain, since they vary with tides and within the water column's cross section. Furthermore, the diurnal inequality of tidal cycles leads to large differences in the net fluxes over a cycle. However, in the present study the total tidal flux over a specific phase of the tidal cycle (ebb or flood) at several sites was measured by standing nets. By this procedure, some of the disadvantages associated with taking samples at time intervals are avoided. By positioning nets in this study it was attempted to gain insight in the transport of macrolitter in Gazi Bay, and, hence, in the interlinkages between the mangrove forest and the adjacent seagrass systems.

Based on the results from the nets, as was expected, export of mangrove leaves takes place from the forest, while there appears to be a net import of seagrass and macroalgae into the mangrove forest. In the existing literature concerning macrolitter transport in a mangrove area, known to the authors of this report, no mentioning of the catch of seagrass or seaweed is made. This is remarkable, for the phenomena of packages of floating seagrass leaves is well known. If only floating mangrove leaves had been considered in this study, the catch would have been restricted to 3-48% of the catch that is actually transported over the full height of the water column. This means that studies which address only the floating flux of coarse mangrove litter underestimate reality with 52-97% (seagrass+seaweed+suspended mangrove leaves).

The effect of the outwelling of mangrove litter in Gazi Bay may be restricted to the intertidal area, since there was a net import of mangrove leaves into the intertidal seagrass zone. This is consistent with the findings of Hemminga et al. (1994), who concluded that outwelling of mangrove litter in Gazi Bay was restricted to the seagrass zone and would not reach the coral reefs. Their transects did not pass the intertidal zone. So, considering our results we may speculate that outwelling of mangrove litter in Gazi Bay very likely is mainly restricted to the intertidal seagrass zone and will not reach the coral reefs. Moreover, the net carbon outwelling from the mangrove forest may nullified by the import of seagrass and macroalgal biomass into the mangrove forest. It is certainly not unthinkable that the mangrove forest actually is a net sink of particulate organic matter due to the extent of the latter process. As seagrass and macroalgal material has a higher nutrient (nitrogen and phosphorus) content than mangrove leaf material, trapping of the former material could coincide with a considerable nutrient input into the mangrove system.

The importance of import of seagrass material is suggested also by direct observations of seagrass litter in the mangrove. Seagrass leaves are always present on the mangrove floor in Gazi Bay in large quantities. The available quantity of seagrass leaves on the mangrove floor may constitute some 7-60% of the total dry weight of coarse organic material lying on the sediment (Slim, unpublished data). Our observations suggest that the dry weight quantity of transported seagrass may exceed the dry weight quantity of transported mangrove leaves. Consequently, dependence of seagrasses on the mangrove forest for nutrient input seems unlikely since the intertidal seagrass area may export more than it imports. This conclusion is in line with a study on primary production and nutrient levels in Thalassodendron ciliatum (described elsewhere in this final report) which showed that seagrass functioning seemed not to be influenced by the mangrove outwelling (Hemminga et al., 1995).

The present study was carried out in a restricted period of two months, and the results in terms of general conclusions therefore have a preliminary character. Some of the observations may have been connected to the specific conditions of the year. Seasonal factors which may be relevant for the outcome of flux studies are (among others) input of fresh water (rainfall, river water), direction of winds, and the number of storms. In what way the import of seagrass and the export of mangrove litter may balance each other on an annual basis should be elucidated by further research in this area.

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LEAF LITTER PRODUCTION AND DEGRADATION IN MANGROVE COMMUNITIES OF UNGUJA ISLAND (ZANZIBAR), TANZANIA.

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INTRODUCTION

The incidence of maximum production of mangrove litter has been attributed to a number of factors including precipitation, temperature, wind and decreased salinity (Lugo and Snedaker 1974; Pool et al. 1985; Sesakumar and Loi 1983; Steinke and Ward 1990), and on several occasions more litter fall has been observed during the dry season or summer months. Some studies, however, e.g. Woodroffe and Moss (1984) have found no pronounced seasonality. This makes it difficult for any generalisation regarding when to expect maximal litter fall in mangroves. Quantitative information on litter fall in East African mangroves is lacking such that there is reason for studies on this aspect in order to understand the role of detritus in the nutrient dynamics of these intertidal forests. Studies carried out on rates of litter degradation show that the decomposition of plant litter depends on mechanical fragmentation through weathering, leaching of water soluble substances, breakdown by macro-invertebrates, microbial colonisation and utilization of particulate or dissolved organic matter (Camilleri and Ribí 1986). Fast initial weight losses have been shown for leaves of terrestrial plants when incubated in water, followed by more gradual decreases (Douce and Crossley 1982; Killingbeck et al. 1982). Similar observations have been recorded for some swamp forests (Boomruang 1978 and Boto 1982).

It has been suggested that decomposition dynamics in mangrove environments are primarily controlled by temperature, humidity, soil pH, aeration, microbial populations, soil fauna and the chemical nature of the plant material (Lugo and Snedaker 1974). Consistently low decomposition rates for example of *Rhizophora* leaves have been attributed to among other things their relatively higher tannin content (Boomruang 1978, Cundel et al. 1979). The presence of tannin in mangrove leaves probably delays their colonisation by fungi and bacteria (Benoit and Starkey 1968) thereby retarding decomposition. Decomposition of marine macrophytes and mangroves is characterised by an initial leaching of soluble organic and inorganic compounds, with subsequent colonisation by bacteria, fungi and protozoans which utilize labile substances and initiate the breakdown resulting in physical and biological fragmentation (Tam et al. 1990). The ease with which mangrove leaf litter decomposes and the amount of nutrient released to the surrounding environment are primarily functions of the chemical composition of the source material and thus are species specific. Plant materials high in crosslinked celluloses and lignins resist decay while those high in soluble ash, organic nitrogen and other hydrolysable components are easily degraded (Twilley et al. 1986). Rice and Tenore (1981) showed that macroalgae, with a high proportion of soluble cell components degrade more readily than seagrasses which are composed of relatively more structural tissues.

One of the important aspects concerning the breakdown of detritus is the nutrient flux and the fate of the nutrients in the ecosystem. An accumulation of nitrogen in leaf detritus during decomposition has frequently been observed (Steinke et al. 1983, Tam et al. 1990) and is believed to enhance the recycling of nitrogen on the forest floor, as well as providing a mechanism to conserve nutrients within the mangrove ecosystem. Various physico-chemical changes take place during the process of decomposition. Such essential studies are lacking in the East African region despite the presence of considerable areas of mangrove forests and their significance to the fishery sector.

METHODS

Litter production

This was studied in five species at the Chwaka Bay swamp, viz: *Sonneratia alba*, *Avicennia marina*, *Ceriops tagal*, *Bruguiera gymnorhiza* and *Rhizophora mucronata*. The latter is infrequent at Maruhubi, consequently only the first four species were studied there. Litter was collected from

randomly selected mature trees of each species using 0.5 x 0.5 m nylon mesh traps. Each trap was made of a square wooden frame with the bottom covered with a flexible nylon netting screen (mesh size 2.5 cm) which was tied in such a way that when the trap was held horizontally, it formed a shallow bag which ensured that any litter trapped was retained. This method is as recommended in Snedaker and Snedaker (1984). Twenty five traps were set at each of the sites. Each was suspended under the mangrove tree by nylon ropes tied to branches in such a way that it was off the ground well above the waterline at high tide, and was unable to tip over and spill the litter which fell off from the tree directly into the trap. The litter collected in the traps was recovered at monthly intervals. The contents of each trap were put in a cloth bag, and labeled with the date of recovery, location of the trap and the identity of the mangrove species. The material was then taken to the laboratory where the contents of each bag were sorted into the different components, viz: leaves, flowers or flower parts, and propagules or fruits. These were then oven dried at 70 °C to constant weight.

Leaf decomposition studies

The method recommended by Snedaker and Snedaker (1984) was applied in this study. Senescent, yellow and just ready to fall leaves of *S. alba*, *R. mucronata*, *B. gymnorrhiza*, *C. tagal* and *A. marina*, from Maruhubi mangrove swamp were used. In the laboratory, the leaves were wiped with a soft cloth to remove surface water and adhering debris. The leaves of each species were then divided into lots of 5-10 leaves and weighed. Each weighed lot was placed in a separate 20x30 cm nylon mesh decomposition bag having a mesh size of 2.5 cm. Each bag had previously been divided into longitudinal compartments by nylon threads. Two to three leaves were placed in each compartment, which was then sealed at the mouth by nylon thread stitching. Seventy bags were prepared in this way for each of the five species. The bags were then tied to a long nylon rope, at a short space from each, making sure that they also did not overlap. The whole preparation was then lowered to the bottom of a tide pool in the mangrove forest. Stone anchors were tied to the rope so that the rope and the bags remained at the bottom of the pond during the entire period of the experiment. Ten bags were recovered from the line at seven day intervals until all were removed. Each time, the contents of each bag was removed and gently cleaned of adhering debris, and oven dried to constant weight at 70 °C. In another set of experiments, the leaves of *B. gymnorrhiza*, *S. alba*, and *R. mucronata* were treated in the same manner except that they were buried in the substrate within the mangrove forest. The same procedure was followed in determining the oven dry weights.

Prior determination of the relationship between fresh and dry weight had been carried out on ca. 100 samples of leaf weights for each species, by oven drying leaf lots of known fresh weight. This provided an average conversion factor of 0.38 for *A. marina*, 0.34 for *C. tagal*, 0.31 for *R. mucronata*, 0.27 for *B. gymnorrhiza*, and 0.15 for *S. alba*. These were then used to calculate the original dry weights of the leaf samples prior to setting them for decomposition. The experiments ran for a maximum of 100 days.

RESULTS

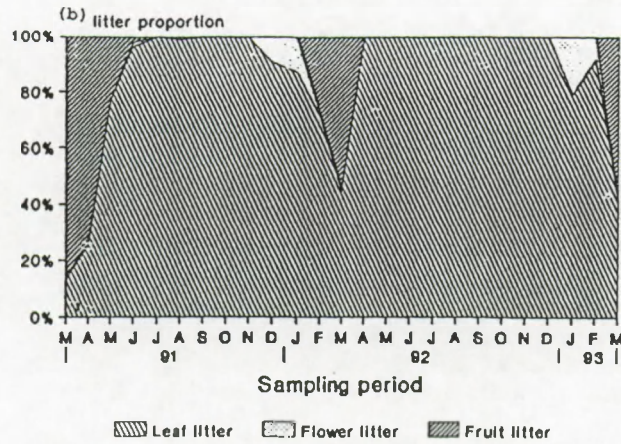
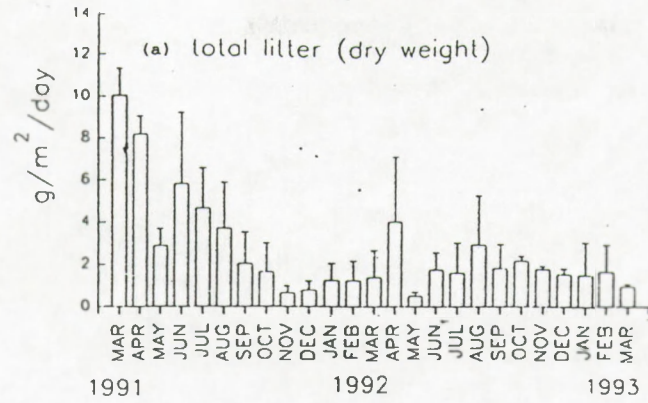
Litter production

The studies on litter fall showed a trend indicating more litter production during the dry season, although the variations were not always statistically significantly different. The results are shown (Fig 1a-r) for each site (means and 95% confidence intervals).

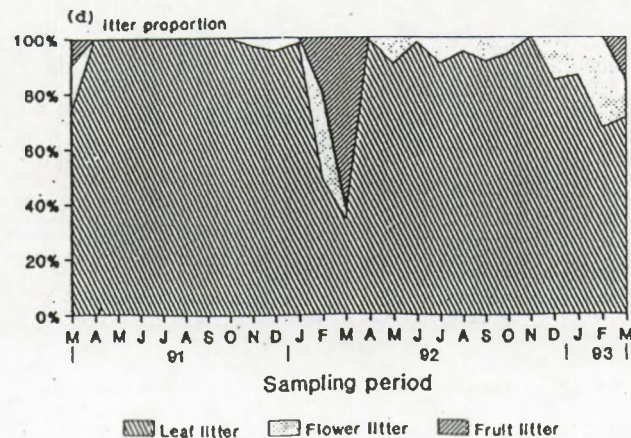
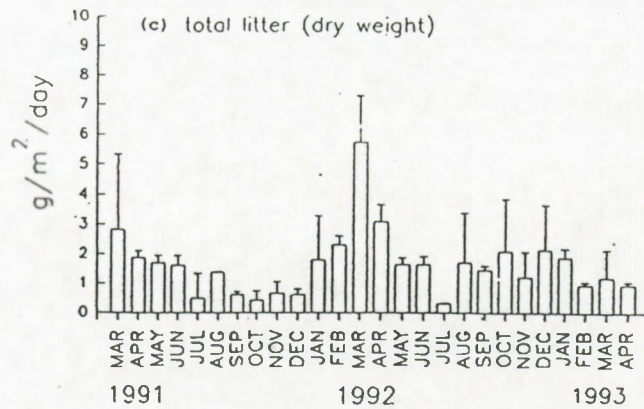
A. marina (Fig. 1a-d) showed distinct trends in which leaf litter production was greater between June and July in 1991, and August-October in 1992 at Maruhubi. At Chwaka, however, production was not so clearly marked.

B. gymnorrhiza (1e-h) showed little seasonal change in litter production at both study sites. At Maruhubi, however, an average of less than 2 g/m/day (dry weight) were produced, while at Chwaka an average of 2.5 g/m/day were shed. *C. tagal* (Fig 1i-l) also showed no obvious significant seasonal variation in leaf litter production at both sites. Again an average of less than 2 g/m/day was produced at Maruhubi compared to more than 2g/m/day at Chwaka. At this site, slightly more litter was produced between November and April and between August and October. Like *C. tagal*, *S. alba*, showed no significant seasonal variations in litter production (Fig 1 m-p), at both sites. While an average of less than 4 g/m/day was shed at Maruhubi, slightly more was produced at Chwaka.

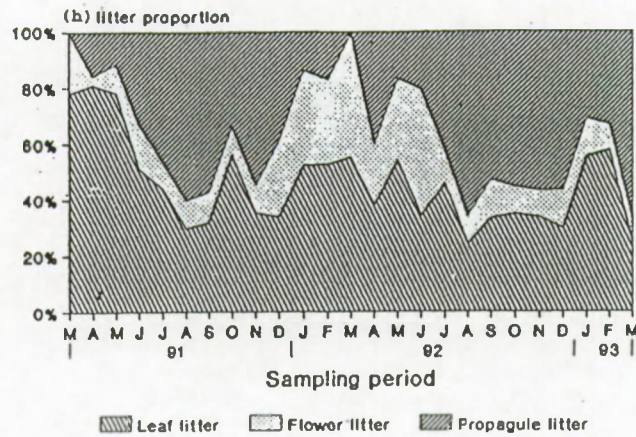
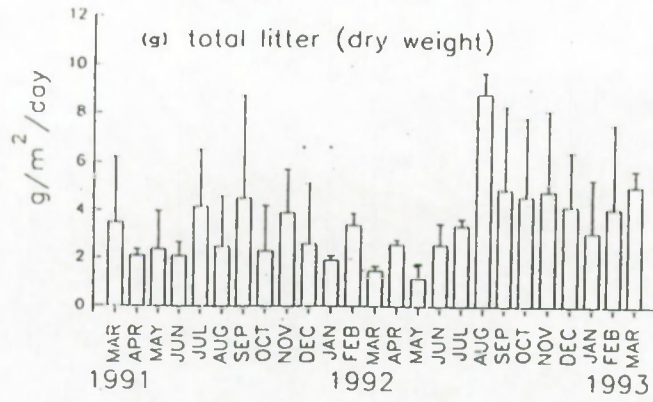
Fig 1. Maruhubi *A. marina*



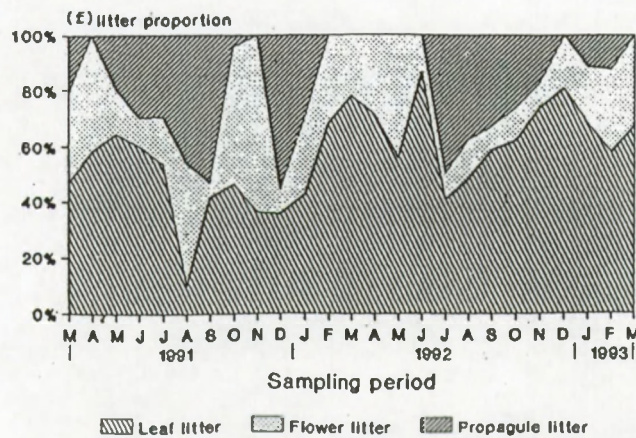
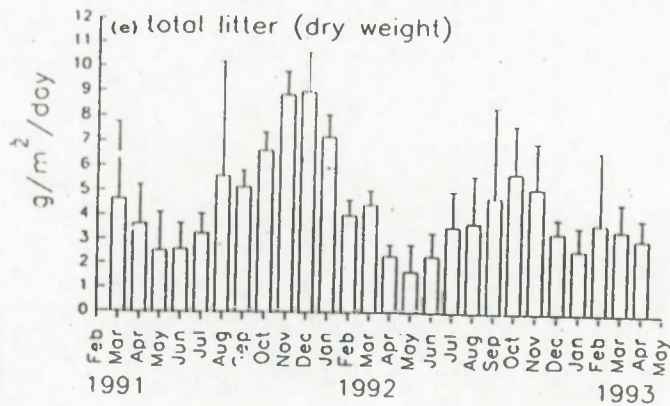
Chwoka Bay: *A. marina*

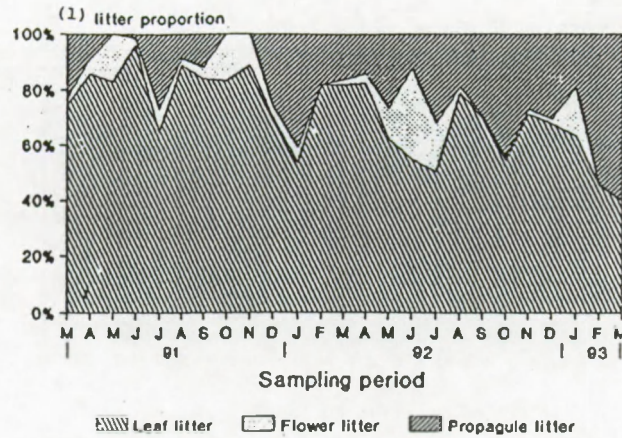
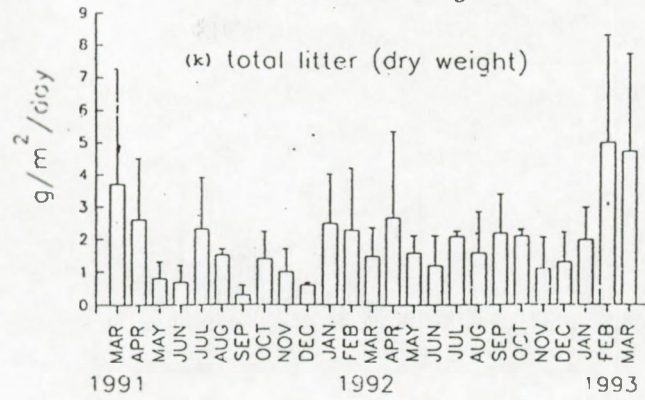
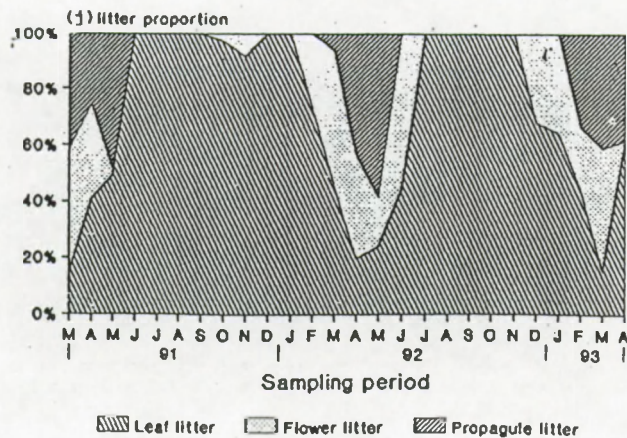
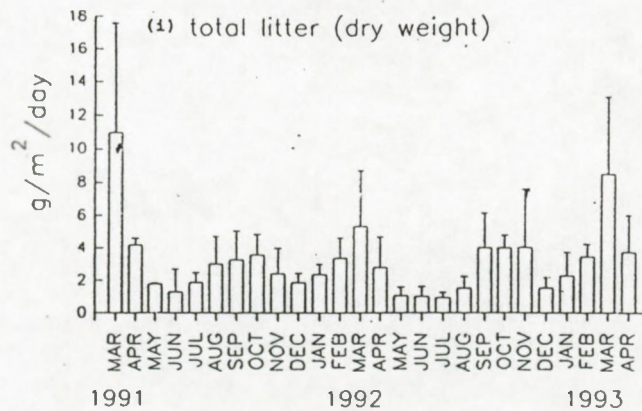


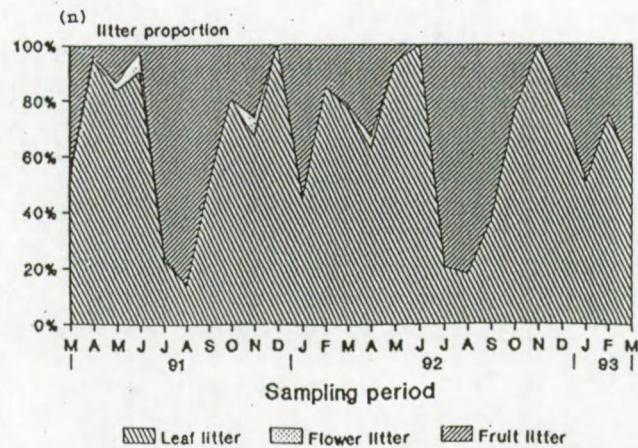
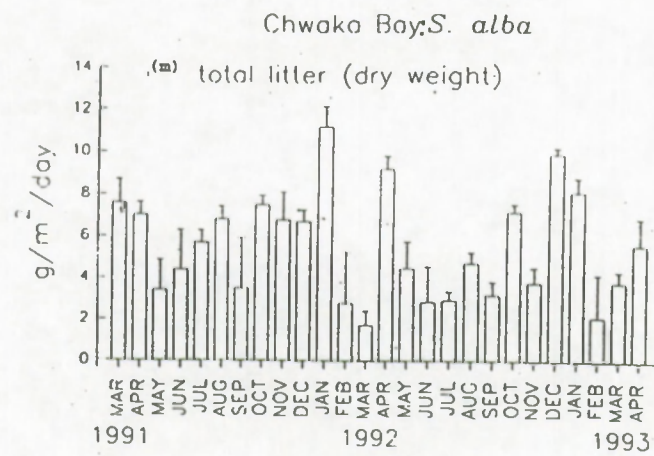
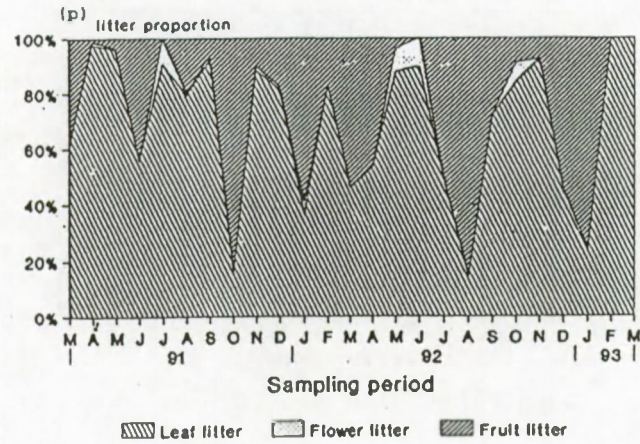
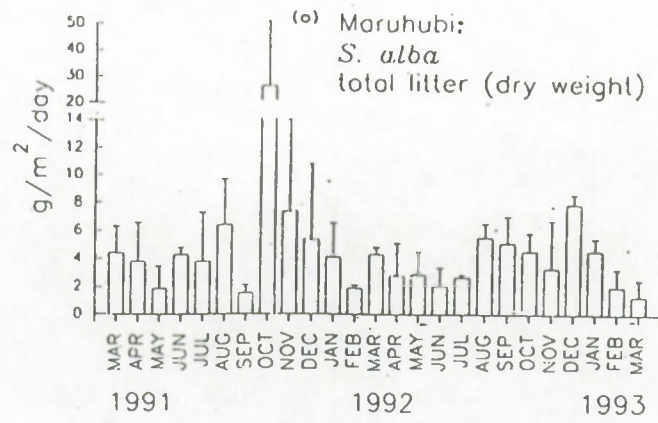
Maruhubi: *B. gymnorrhiza*



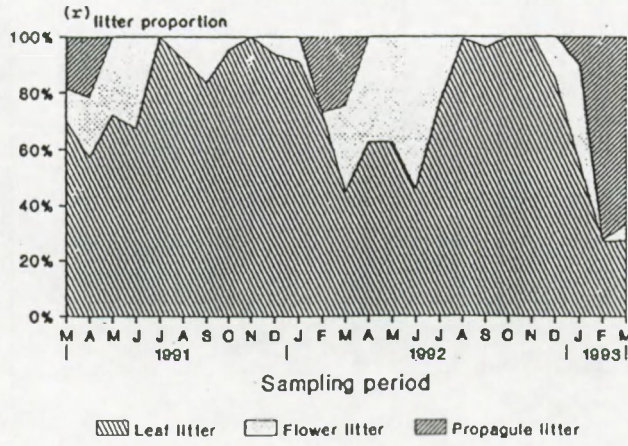
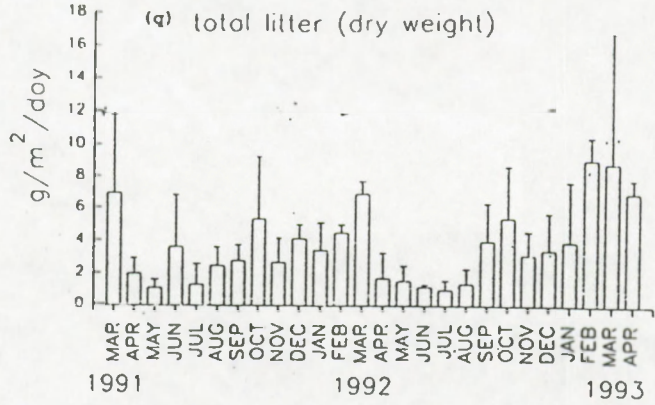
Chwaka Bay: *B. gymnorrhiza*



Chwaka Bay: *C. tagal*



Chwaka Bay: *R. mucronata*



In *R. mucronata* (Fig 1q-r) leaf litter production showed some seasonal trends; lowest production was in April through August of 1992 but this was not so marked in 1991.

Fig.2 Shows the yearly production of leaf litter in tonnes/hectare/year for the various species. It depicts variations between sites and among species.

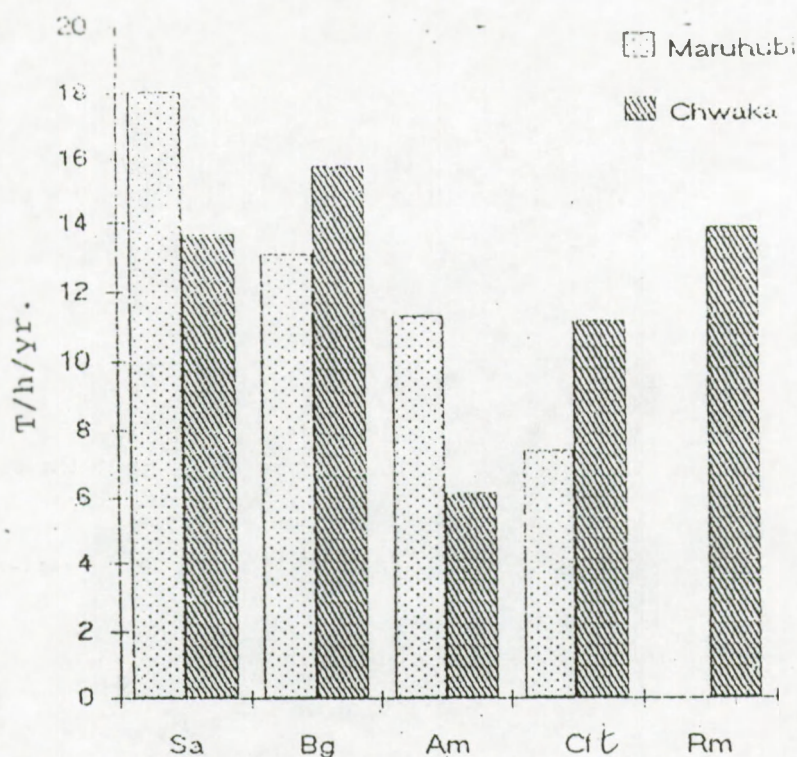


Fig. 2. Total litter production (ton/ha/yr) in Chwaka Bay and Maruhubi mangrove swamps. Sa = *S. alba*, Bg = *B. gymnorrhiza*, Am = *A. marina*, Ct = *C. tagal* and Rm = *R. mucronata*.

Leaf decomposition studies

The results of this study are shown in Figs. 3a - e. The graphs show the decomposition of leaves while submerged in a tide pool as well as buried in the sediment. The species belonging to the family Rhizophoraceae were generally the most refractory. *S. alba* and *A. marina* were the fastest to decompose. Initial loss in weight for *A. marina* was high. Within the first two weeks the leaves lost about 40% of the initial weights and more than 80% in 40 days (Fig. 3a). Decomposition of *C. tagal* leaves (Fig 3b) occurred gradually throughout the experimental period, while in the case of *B. gymnorrhiza* (buried leaves), weight loss was rapid throughout the experiment (Fig 3c). *R. mucronata* leaves (Fig 3d) decomposed at an almost constant rate over the entire experimental period. There was no significant difference in the rate of decomposition between buried and non buried leaves. In the case of *S. alba* (Fig 3e), buried leaf samples decomposed faster than surface samples. Whereas non buried samples lost 50% of initial weight during the first seven days, buried samples lost more than 70%.

DISCUSSION

In the present study, a trend towards peak leaf fall was observed during the dry or summer period as well as during the rainy period. In *A. marina* at both study sites, most of the leaf litter falls during the hot season between June and September, with another minor and irregular peak at the start of the long rains. However, there was no significant difference in litter fall between the seasons, only

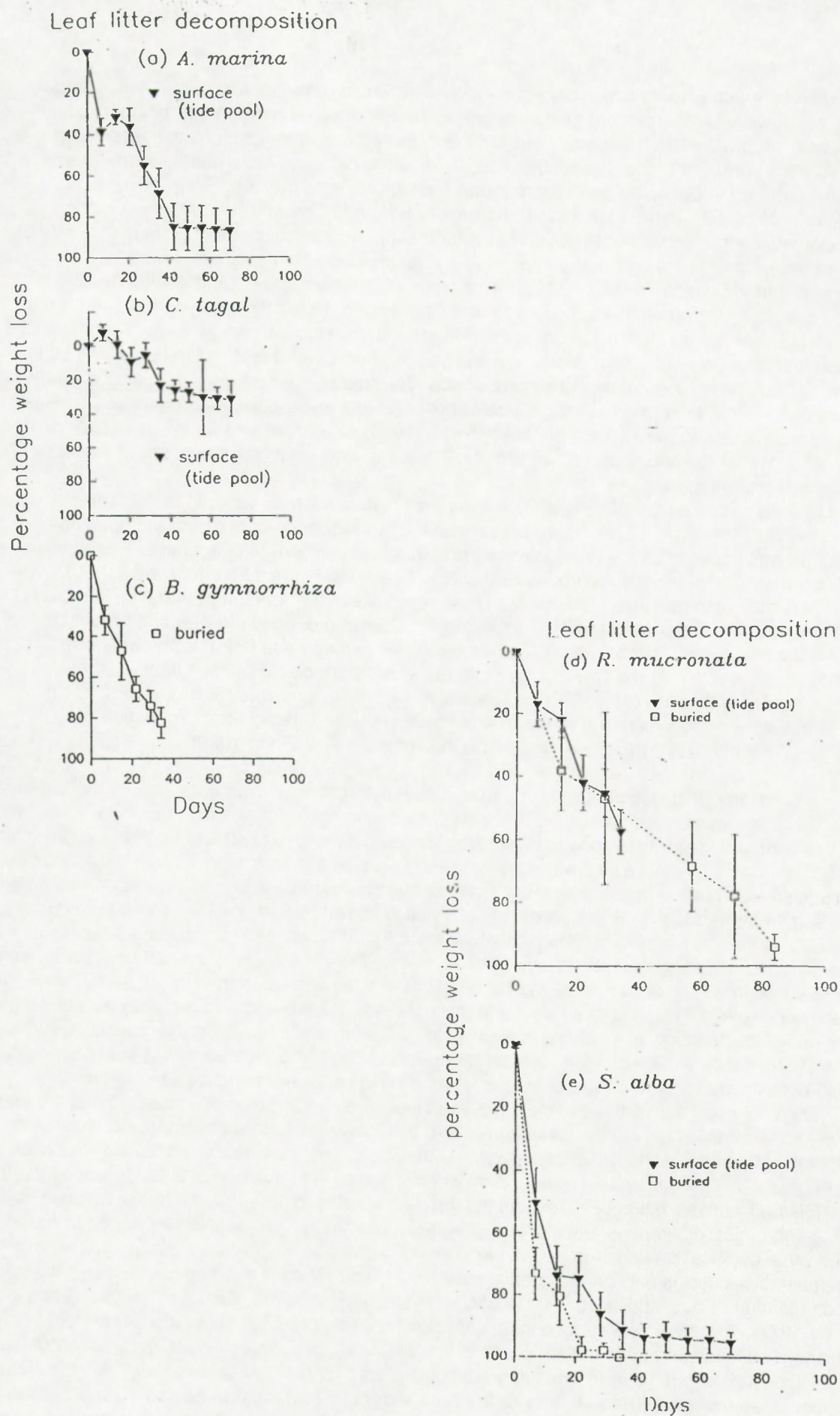


Fig. 3. Decomposition of leaf litter from various mangrove species

a trend was observed. A more statistically accurate result would have been obtained with a larger sample size, however in the present study this was seriously affected by the traps being frequently stolen. It was therefore difficult to control the sample size and in some instances this led to severe departures from normality in the data distribution, reflected in the large error bars in some graphs. Nevertheless the trend observed seems to support findings such as those by Francisco et al. (1987), who noted peak litter fall just before the onset of the rainy season in a Mexican mangrove swamp. Conversely the current observations also lend support to the findings of Robert et al. (1986), who noted peak litter fall during the dry season in a mangrove forest in southwest Florida. It has been argued that increased soil salinity leads to increased leaf senescence and consequently to increased litter fall (Pool et al. 1975, Anderson and Christensen 1978). This may explain the trend towards increased litter fall during the dry season in the current study. It can be argued that litter production increases in response to increased soil salinity, in dry weather conditions, as well as in response to fresh water input during the rainy period. The trend observed here appears, within the limitations of the data, to support the slight peak of litter fall observed during the onset of the rains. This is in agreement with the findings of Twilley et al. (1986) who observed an inverse relationship between annual litter fall and average soil salinity. Thus, reduced salinity at the onset of the rainy season may lead to high litter fall.

Litter fall may also be influenced by mechanical factors such as wind, in addition to stress and senescence (Kozlowski 1973). In the present study, the incidence of rainfall accompanied by strong winds was noted to cause more litter fall, and in all species leaf litter accounted for between 50-80% of total litter, similar to reports by Francisco et al. (1987), Steinke and Ward (1990).

This study also revealed that species show variations in the amount of leaf litter produced even within one site. At the Maruhubi site for example, *S. alba* produced the greatest amount of leaf litter (8.68 tonne/ha/year), followed by *A. marina* (6.50), *B. gymnorhiza* (5.29 tonne/ha/year), *C. tagal* (4.50 tonne/ha/year). At the Chwaka Bay site the various species produced litter in the following sequence: *S. alba* (11.20), *R. mucronata* (9.44), *B. gymnorhiza* (8.35), and *C. tagal* (6.77). These values are within the range of previously reported rates of litter production of between 3 - 17 tonnes/ha/yr, (Duke et al. 1981, Christensen 1978, Gong 1984)

In the current study, leaf decomposition has been found to occur at different rates in the different species. *S. alba* leaves were shown to be the fastest to decompose, followed by those of *A. marina*, *C. tagal*, *B. gymnorhiza* and *R. mucronata*. *S. alba* leaves lost more than 50% of original weight within the first seven days, (Figs. 2a - e), whereas *A. marina* leaves lost less than 40% in the same time. Other species lost much less. *S. alba* and *A. marina* lost 85% and 69% of original weight within five weeks, *B. gymnorhiza* lost 11.6 % in three weeks while *C. tagal* lost 9.46 % in the same period of time and only 23.31 % in five weeks. This indicates some major differences in the biodegradability of the species studied. These observations compare well with those of Steinke and Ward (1987), who observed a loss in weight of 57% in *A. marina* leaf litter in three weeks. In the current study, leaves of the same species lost 41% of original weight in three weeks. Steinke and Ward (1987) also observed a faster rate of degradation in *A. marina* compared to *B. gymnorhiza* under permanent submergency. Mathias (1974) made similar observations on the same species and in the current study, *A. marina* has also been found to degrade faster than *B. gymnorhiza* under permanent submergency.

The ecological significance of the observed differences in decomposition rates is that the most refractory leaves can be moved by ocean currents to distant places before decomposition fully sets in, thus they may be partly responsible for supplying nutrients to ecosystems away from the litter source. Easily degradable leaves may also be important to ecosystems in the vicinity of the mangrove forests.

Several causes have been suggested for the species differences in decomposition rates including anatomical differences. Steinke et al. (1983) showed that *B. gymnorhiza* leaves have surfaces covered by a thick cuticle which impedes the entry of water and degradative organisms. *A. marina* leaves have thick cuticles only on the adaxial surface, the abaxial surface being covered by numerous fine non-glandular hairs and a very thin cuticle, which may even be absent in places (Fahn and Shimony 1977). The lower leaf surface in this species probably provides easy access for degradative organisms. The levels of tannin in the tissues of the different mangrove species may also contribute to the observed differences in the degradation rates. Tannin levels are high in the family Rhizophoraceae, comprising about 40% of the bark weight in *B. gymnorhiza* and *R. mucronata*. *C. tagal* has about 27% (Griffith 1949). Kuthubutheen (1981) and Robertson (1988) have reported 14.6% and 3.5% tannin in the leaves of *B. gymnorhiza* and *A. marina* respectively. Ravi and Kathresan (1990) also found higher levels of tannin compounds in the Rhizophoraceae *R. apiculata*, *R. lamarckii*,

R. mucronata and *Ceriops decandra* compared to *A. marina* of the Avicenniaceae. Benner et al. (1990), found cuticular compounds (aliphatic biopolymers) in *R. mangle* to be very resistant to decomposition and that these substances increased in relative concentration as decomposition progressed. They also noted tannins to have intermediate resistance to decomposition and that these substances remained in fairly constant proportions during decomposition. Species belonging to the family Rhizophoraceae thus contain higher concentrations of tannin and cuticular compounds compared to those in the family Avicenniaceae and Sonneratiaceae. Thus the low rates of decomposition noted in this study in the leaves of the Rhizophoraceae may be partly accounted for by the presence of high levels of these substances.

Investigations on the rate of loss of weight during decomposition of buried leaves of *B. gymnorrhiza* and *S. alba* also showed a faster rate in the latter species compared to the former. *S. alba* leaves lost about 75% of their original weight in seven days, while those of *B. gymnorrhiza* lost about 33% in the same period (Fig. 2c & e). It therefore appears that the least refractory leaves have a higher rate of degradation compared to the most refractory ones, irrespective of whether they are buried or lying on the bottom of a tide pool. However, comparison of the rate of degradation between buried and non-buried leaves of *R. mucronata* alone showed a higher rate for the buried leaves (Fig. 2d). It has been suggested (Lugo and Snedaker 1974) that decomposition dynamics in mangrove environments are primarily controlled by the nature of the plant material, temperature, humidity, soil pH, aeration, and microbial populations and soil fauna. The fairly rapid rate of decomposition of the buried *R. mucronata* leaves can be explained by variations in the above factors. The burying of the leaves may have exposed them to a larger number of various organisms present in the substrate which together might have brought about a faster rate of decomposition. The physical disturbance of the substrate caused by the action of burying the leaves may have also led to improved aeration conditions in the substrate, which could have led to higher aerobic decomposition which is much faster than anaerobic decomposition (Boto 1982).

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Part 2: The functioning of seagrass meadows at varying distance from mangrove forests

MANGROVE OUTWELLING AND THE FUNCTIONING OF ADJACENT SEAGRASS MEADOWS (GAZI BAY, KENYA)

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INTRODUCTION

Mangroves, seagrass meadows and coral reefs may occur as adjacent ecosystems in tropical coastal zones. There has been considerable speculation concerning tide-mediated chemical fluxes between these systems and the effects of these fluxes, but data substantiating these speculations are virtually lacking. Several studies have shown that mangroves export particulate organic matter (Boto & Brunt, 1981; Twilley, 1985; Robertson, 1986; Flores-Verdugo et al., 1987), although specific geomorphological and hydrodynamic conditions in some mangroves may reduce or preclude outwelling (Woodroffe, 1992). Export of mangrove carbon can be traced with the use of stable carbon isotopes, as mangroves are characterized by carbon isotope signatures which show a relatively strong depletion in the heavy isotope ¹³C (Torgeson & Chivas, 1985; Rezende et al., 1990). In a previous section of this final report we presented described evidence indicating that meadows of the seagrass *Thalassodendron ciliatum* (Forsk.) den Hartog positioned between mangroves and coral reefs in Gazi Bay, Kenya, may act as a filter between these systems: the carbon isotope ratio of sediments and seagrass plants outside the mangrove indicated trapping of mangrove-carbon. Moreover, the isotope ratios showed that the mangrove signal completely faded out in the seagrass zone, getting weaker with increasing distance from the mangrove. Thus, the seagrass zone seems to absorb the carbon flux from the mangrove.

Obviously, the mangrove input in the seagrass zone is not necessarily restricted to carbon only: nutrients such as nitrogen and phosphorus will be associated with organic particles exported from the mangrove. Inputs of these nutrients may influence functional and chemical aspects of the seagrass vegetation. Primary production in macrophyte-dominated marine ecosystems is often limited by nutrient availability (Smith, 1984; Howarth, 1988). Enhanced growth after experimental enrichment of seagrass sediments with nitrogen and phosphorus has repeatedly been found, e.g., more recently by Powell et al. (1989), Perez et al. (1991) and Murray et al. (1992). Furthermore, the nitrogen and phosphorus content of seagrasses is dependent on the availability of these nutrients; in situations where the supply is limited, additions of nutrients result in increased tissue contents (Duarte, 1990, and references therein).

In this part of the research we addressed the question whether the trapping of mangrove carbon in the seagrass zone coincides with shifts in primary production and nutrient content of *Thalassodendron ciliatum*, the dominant subtidal seagrass. Primary production and nutrient contents were determined at different distances from the mangrove, i.e., at locations exposed to a variable level of mangrove-carbon input.

METHODS

Study area

The research was carried out in Gazi Bay (Kenya). As described before, directly adjacent to the mangroves in the bay are intertidal flats and shallow, subtidal areas. To a large extent this zone is covered by seagrasses. *T. ciliatum* is the dominant seagrass of the subtidal areas. It occurs in Kinondo creek and in the channels between the tidal flats, and forms monospecific meadows in the southern part of the bay, which stretch down to the reef zone.

Sampling and measurements were carried out by SCUBA divers, primarily on four subtidal sites

positioned in the channel forming the continuation of Kinondo creek and the shallow bay waters more closely to the reefs. These sites were given a two-letter code (MM, MS, CS, CC), which indicates their relative position between mangrove and coral reef. On each of these sites, *T. ciliatum* was the only or the dominant seagrass species.

Additionally, samples were collected in Chale lagoon, directly East of Gazi Bay. This lagoon is separated from Gazi Bay by a broad sill of fossil coral that extends between Chale Peninsula and Chale Island, restricting direct water exchange between Gazi Bay and the lagoon.

Sampling of water and sediment

Water samples for nutrient analyses were collected during two ebb tides and two flood tides. Water samples were collected at the various sites over the full duration of the tide (5-6 samples per tide at a given transect). The samples (25 l each) were collected with a hand diaphragm pump, 1 m above the subtidal sediment surface. Aliquots were filtered (within 1 h after sampling) over Whatman GF/C filters and stored frozen until chemical analyses. Ammonium was measured spectrophotometrically with sodium nitroprusside as colouring reagent. Nitrate was measured after reduction to nitrite in a copper-cadmium reductor column followed by reaction with sulfanilamide and N-naphylethylenediamide; the resulting complex was read colourimetrically. Phosphate was measured colourimetrically after mixing of the sample with ammonium molybdate, ascorbic acid and antimony to yield a phosphomolybdenum blue complex.

Sediment samples at the various sites were obtained with sediment corers with an internal diameter of 7 cm. For analysis of particulate nitrogen content the upper 7 cm of the sediment samples was used. Nitrogen content was measured with a Carlo Erba NA1500 CN analyzer.

Determination of primary production and seagrass nutrient contents

Leaf production of *T. ciliatum* was measured with the plastochrone interval method (Jacobs, 1979). This method has been applied previously by Brouns (1985) for production measurements on *T. ciliatum*. Observations were carried out on the MM, MS and CS site, on 4 plots. The distance between the sampling plots was approximately 20 m. On each plot, the youngest leaf (length > 10 mm above the leaf sheath) of a number of shoots was marked by punching a small hole through the leaf. These shoots were harvested 14-17 days later. The number of new leaves on the shoots were counted to determine the plastochrone interval of the leaves (PIL), i.e., the time interval between the formation of two successive leaves:

$$\text{PIL} = \frac{\text{Number of new leaves since marking}}{\text{Number of days between marking and harvesting}}$$

In addition, 15 shoots of each plot were randomly selected for measurements of length and dry weight (DW) of successive leaves.

Around each of the plots where primary production was measured, 3 samples of above-ground biomass of *T. ciliatum* were collected. Each sample was clipped from an area of 25 X 25 cm. The samples were stored in cooling boxes until return to the field laboratory at the end of the various sampling days. The 3 above-ground seagrass biomass samples collected at each sampling plot were pooled, after the number of shoots in each sample had been counted. The third-youngest leaves of the *T. ciliatum* shoots in each of these pooled samples were collected. Only these were used for chemical analyses, to decrease the variability which might arise from analyzing seagrass leaves of different developmental stage. The third-youngest leaves, as an added advantage, lack the crust of epiphytes complicating the analysis of older leaves. Analyses were carried out after drying the leaf material at 70°C. Additional *T. ciliatum* samples (4) were collected in Chale lagoon. Again, only the third-youngest leaves from these samples were used for chemical analyses.

Carbon and nitrogen contents of the leaf samples were determined with a Carlo Erba NA1500 CN analyzer. Phosphorus content of seagrass leaves was determined spectrophotometrically using ammonium heptamolybdate as colouring reagent.

Results were analysed statistically by one-way analysis of variance, followed by Post-Hoc contrasts to test differences between individual groups. Results were considered significant at the $\alpha=0.05$ level.

Estimation of the production per m² on the various sites involved combination of the data on

production per shoot with the data on shoot density, each parameter having a certain error. A bootstrap procedure was used to calculate averages and confidence intervals for the combined results (Brey, 1990), implying resampling ($n=100$) of the different combinations of shoot production and shoot density.

RESULTS

Environmental parameters

The stable carbon isotope data shown in Table 1 were obtained in the study on carbon outwelling, described earlier in this report. The data show that the MM, MS, CS and CC sites are in decreasing order under the influence of carbon outwelling from the mangrove. The sediment of the MM site has a $\delta^{13}\text{C}$ value close to the level of the mangrove sediment (*Rhizophora mucronata* (Lamarck) site), but there is a conspicuous enrichment in ^{13}C going from the mangrove in seaward direction, indicating decreased input of (^{13}C depleted) mangrove carbon. No evidence was found for trapping of outwelling mangrove carbon at the CC site and in Chale lagoon. The trend in transect $\delta^{13}\text{C}$ sediment values is closely paralleled by the ^{13}C enrichment of *T. ciliatum*. Presumably, this is caused by the uptake of ^{13}C depleted inorganic carbon generated by the mineralization of organic matter from the mangrove.

Table 1 also shows that the nitrogen contents in the sediments are highest close to the mangrove, at the MM and MS sites. The relatively high nitrogen values at these sites coincide with sediment organic carbon levels which are also considerably higher than at the CS and CC sites (Hemminga et al., 1994).

Nitrate, ammonium and phosphate levels in the water are very low, irrespective of the site or the phase of the tidal cycle (ebb or flood). Concentrations of these nutrients are consistently below $1\ \mu\text{M}$. The data indicate that in ebb water the prevailing nitrogen nutrient is ammonium; in flood water, however, ammonium concentrations are even lower than nitrate concentrations.

Table 1. Environmental parameters of study sites. Carbon isotope signature ($\delta^{13}\text{C}$ notation), of sediments and seagrass (*T. ciliatum*) in Gazi Bay and Chale lagoon derived from Hemminga et al. (1994). Data on sediment nitrogen content (N, in % dry weight) are means and S.D. based on 4-7 observations. Data on nutrient contents in water samples are means and S.D of 10-12 observations. Further details: see text.

Site	Sediment	Seagrass	Sediment	-----Ebb water-----			-----Flood water-----		
	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	N (% D W)	NO_3 (μM)	NH_4 (μM)	PO_4 (μM)	NO_3 (μM)	NH_4 (μM)	PO_4 (μM)
Mangrove	-25.31	-	-						
MM	-22.94	-19.65	0.26 ± 0.09	0.3 ± 0.1	0.7 ± 0.2	0.4 ± 0.1	0.6 ± 0.6	0.1 ± 0.1	0.3 ± 0.1
MS	-20.61	-18.30	0.14 ± 0.08	0.2 ± 0.1	0.8 ± 0.2	0.4 ± 0.1	-	-	-
CS	-18.48	-15.77	0.03 ± 0.04	0.1 ± 0.1	0.8 ± 0.3	-	-	-	0.3 ± 0.1
CC	-15.14	-10.70	0.09 ± 0.05	-	-	0.4 ± 0.1	0.3 ± 0.2	0.2 ± 0.2	
Chale	-14.75	-10.72	0.09 ± 0.02	-	-				

Leaf growth and production

T. ciliatum is a stem-forming species. Each living stem carries a cluster of leaves at its apical end. Short secondary stems may develop on the lower part of the stems, which carry leaf clusters with small leaves. These leaf clusters were not included in the study, only the full-grown clusters of the main leaf canopy layer were considered.

The increase in DW of the leaves during growth is shown in Fig. 1. The leaves are numbered according to their position, and hence age, in the leaf cluster. Number 1 represents the youngest

leaf, i.e., the youngest leaf with a minimum leaf length outside the leaf-sheath of 10 mm. Intact sixth leaves were rarely encountered on the MM and CS sites; the same was true for seventh leaves on the MS site. The data show that leaf weights of shoots from the MM site are conspicuously lower than leaves of comparable age sampled from the MS and CS sites. On all three sites, the increases of leaf weight from the fourth to the fifth leaf were small. Leaf lengths of fourth and fifth leaves were similar (data not shown). Thus, full growth of the leaves is attained when they have reached the fourth or the fifth position in the leaf cluster. For calculations of leaf production (see below), we used the data on mean dry weights of the fourth leaves.

Measurement of the PIL reflects the rate of leaf renewal. The values for the plastochrone interval were based on observations of 13-62 marked shoots per plot, with an average of 32 shoots. On the MM site the average leaf rate renewal appeared to be significantly slower (PIL = 10.98 days) than on MS and CS sites (PIL = 8.46 and 8.17 days, respectively; Table 2). To calculate leaf production per shoot per day, we multiplied the PIL of each plot with the mean dry weight of fourth leaves at that plot. The results (Table 2) show that there is a highly significant difference between the groups ($p < 0.001$). Post-Hoc contrasts indicate that significant differences exist between the MM site, which has the lowest production per shoot ($3.08 \text{ mg DW shoot}^{-1} \text{ day}^{-1}$) and the MS and the CS sites, which have higher production rates (7.69 and $9.51 \text{ mg DW shoot}^{-1} \text{ day}^{-1}$, respectively). The difference between the MS and CS site is only just significant ($p = 0.04$). Leaf production per m^2 was calculated by taking the shoot density on the various sampling plots into account. Mean shoot density was 1556 per m^2 on the MM site, and 1137 and 809 per m^2 on the MS and CS site, respectively. Production per m^2 is lowest on the MM site. There is, again, a clear difference between the MM site on the one hand and the considerably higher production rates on the MS and CS sites on the other hand. Production per m^2 was highest on the MS site.

Table 2. Production characteristics of *T. ciliatum* meadows on the MM, MS and CS sites in Gazi Bay. Means and S.D. of observations on 4 plots per site. PIL: plastochrone interval of the leaves. Data in columns sharing a common superscript letter are not significantly different. Data on production/area obtained using bootstrap procedure (means and 95% confidence limits).

Site	PIL days	Shoot production (mg DW shoot ⁻¹ day ⁻¹)	Area production (g DW day ⁻¹ m ⁻²)
MM	10.98±1.24 ^a	3.08±0.64 ^a	4.92±0.08
MS	8.46±0.59 ^b	7.69±1.02 ^b	9.47±0.13
CS	8.17±0.39 ^b	9.51±1.35 ^c	7.48±0.07

Table 3. Relationship between the carbon, nitrogen and phosphorus contents (C:N:P atomic ratios) of third-youngest leaves of *T. ciliatum*, collected at the four sites in Gazi Bay and in Chale lagoon.

Site	C:N:P atomic ratio
MM	605 : 26 : 1
MS	545 : 24 : 1
CS	524 : 28 : 1
CC	583 : 25 : 1
Chale	454 : 17 : 1

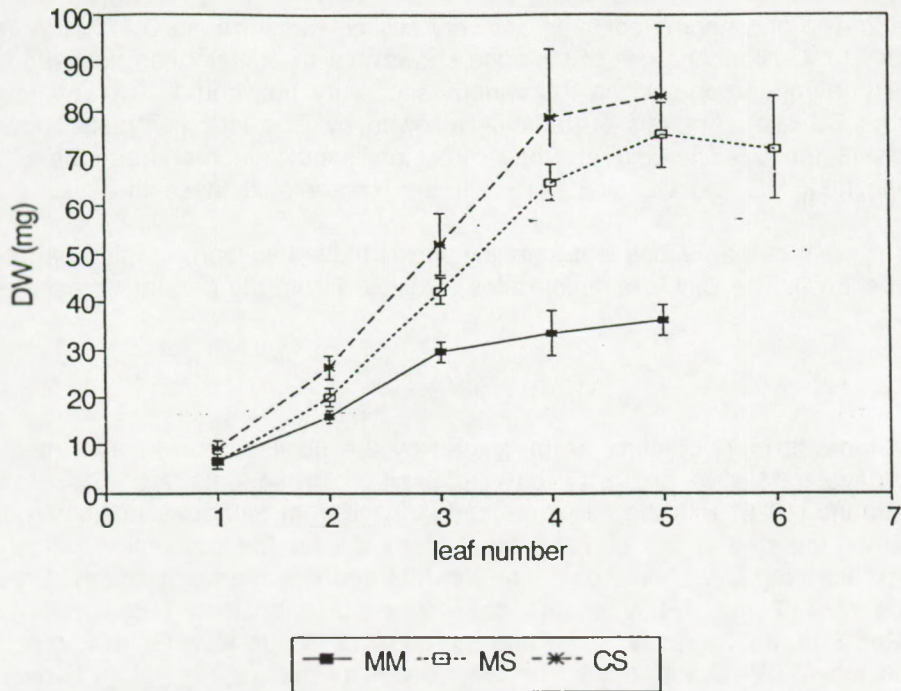


Fig.1. Dry weights (DW) of intact leaves of *T. ciliatum*, collected at the MM, MS and CS sites. Leaf 1 is the youngest leaf. Means and SD of 4 samples. Each sample (4 per site) consisted of 15 pooled leaves.

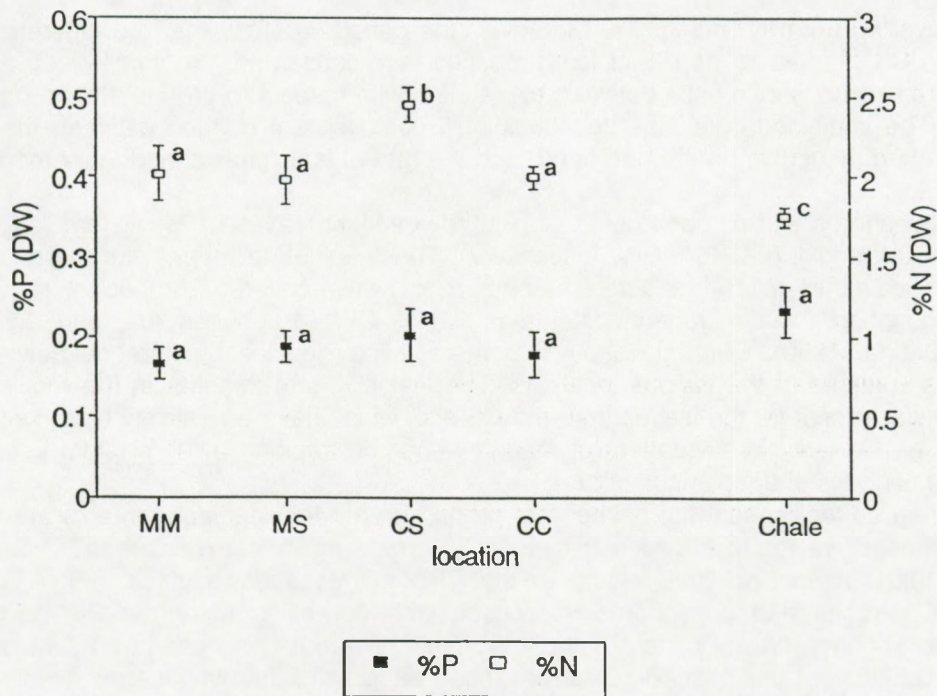


Fig.2. Phosphorus and nitrogen contents (in percentage dry weight, DW) of third-youngest leaves of *T. ciliatum*, collected at the 4 sites in Gazi Bay and at Chale lagoon. Means and SD of 4 samples. Data sharing a common letter are not significantly different.

Nutrient contents

The phosphorus and nitrogen contents of the third leaves of *T. ciliatum* on the different sites are shown in Figure 2. The phosphorus contents are very similar, ranging from 0.17% DW (at the MM site) to 0.23% DW (at Chale). Analysis of variance shows that the differences between groups are not significant. The nitrogen contents on the various sites vary between 1.76% DW (at Chale) to 2.46% DW (at the CS site). Analysis of variance followed by Post-Hoc contrasts shows that the nitrogen contents at the CS site and at Chale are significantly different from the other values determined at the MM, MS and CC sites. The nitrogen contents at these three sites are nearly identical.

The carbon content of the various leaf samples showed little variation, ranging between 37 and 42% (results not shown). The C:N:P (atomic) ratios calculated from the data are presented in Table 3.

DISCUSSION

The rate of leaf renewal in *T. ciliatum*, as measured by the plastochrone interval method, varied between 10.98 days (MM site) and 8.17 days (CS site). These data are close to the value determined by Brouns (1985) with the same method in *T. ciliatum* meadows in Eastern-Indonesian waters. This author reported a PIL of 7.20 days. Our data on the production per shoot range between 3.08 and 9.51 mg DW shoot⁻¹ day⁻¹ on the MM and CS site, respectively. Brouns (1985) reported a value of 4.22 mg AFDW shoot⁻¹ day⁻¹, whereas Johnstone (1984), who studied *T. ciliatum* in the Red Sea, on Thursday Island and the coast of Papua New Guinea, reported values of 4.18 and 3.56 mg AFDW shoot⁻¹ day⁻¹. The ash content of mature *T. ciliatum* leaves is around 20% (Brouns, 1985). Thus, it can be concluded that the data on production per shoot given by these authors are of the same order of magnitude as the results obtained in the present study.

The very low nitrate, ammonium and phosphate levels both in the incoming flood water from the ocean, and in the water flowing from the mangrove with ebb tide (Table 1), indicate that dissolved inorganic nutrients are efficiently retained within the mangrove. The data also make it likely that if there is a substantial nutrient input from the mangrove into the seagrass zone, this input must be connected with the trapping of particulate matter. In the present study we found that the rate of leaf renewal and leaf production were significantly lower at the MM site than at the MS and CS sites. The data on the stable carbon isotope analyses indicate that especially the MM site is exposed to carbon outwelling from the mangrove. Moreover, the data also show that the differences between the MS and CS sites as far as PIL or leaf production are concerned, are small or absent, although there is a conspicuous difference between these sites with respect to the input of mangrove-carbon (Table 1). The combined data thus do not point to a consistent relation between the trapping of carbon from the mangrove on the one hand, and the rate of leaf renewal and leaf production on the other hand.

The phosphorus and nitrogen contents of third-youngest leaves of *T. ciliatum* ranged between 0.17-0.23% DW and 1.76-2.46% DW, respectively. These values are typical for the nutrient content of seagrass leaves in general: a literature comparison, which covered 26 species, showed that the average phosphorus and nitrogen contents is 0.23% DW for phosphorus, and 1.92% DW for nitrogen (Duarte, 1990). Our data show that there is no significant difference between the leaf phosphorus contents at the various locations. The leaf nitrogen contents at the four sites in Gazi Bay are similar except for the leaves from the CS site, which have a relatively high content. Clearly, there exist no similarity in the pattern of mangrove-carbon trapping by *T. ciliatum* vegetations and the nutrient contents of the plants.

What can be the reason that neither leaf production nor leaf nutrient contents are increased in *T. ciliatum* meadows that are evident recipients of outwelling mangrove carbon? A first possibility would be that nutrients are not limiting to the *T. ciliatum* meadows in Gazi Bay. In that case, trapping of nitrogen and phosphorus associated with outwelling mangrove-POM would not be expected to enhance growth or leaf nutrient contents. The data on nutrient content of the leaves allow an evaluation of this possibility. As mentioned earlier, the third-youngest leaves of *T. ciliatum* had phosphorus and nitrogen contents very similar to the average values established in a dataset comprising 26 seagrass species. The values determined in the present study (approximately 0.2% DW phosphorus and 2.3% DW nitrogen), however, are much lower than the maximum phosphorus (> 0.7%) and nitrogen (> 5%) values reported by Duarte (1990). This author also made a comparison of nutrient enrichment studies which led him to the conclusion that seagrasses with phosphorus

contents below 0.2% DW and nitrogen levels below 1.8% DW were probably nutrient limited. In fertilization experiments, these seagrasses responded with significant increases in their tissue nutrient contents. In view of these literature data it is unlikely that in Gazi Bay phosphorus and nitrogen were available at saturation levels for *T. ciliatum*. We thus reject the possibility that nutrient sufficiency caused the lack of effect of mangrove outwelling on seagrass growth and nutrient content.

Having concluded this, two obvious possibilities remain to explain the present results: (1) the effect of any nutrient input on the seagrasses is masked by other factors; (2) the trapping of mangrove carbon in the seagrass zone does not coincide with nutrient enrichment.

The first possibility may be particularly relevant for the MM site. At this site the nitrogen content of the sediment is on average higher than at any other site (0.26%; Table 1); this high nitrogen content coincides with a relatively high sediment carbon content (3.78%; Hemminga et al., 1994). The comparatively high nitrogen levels, however, do not result in elevated nitrogen levels in the leaves or in increased primary production. The *T. ciliatum* at this site (the mouth of the mangrove creek) grows in shallow water (less than 1 m at ebb tide), at high current velocities. The functioning of the plants at the MM site therefore may be primarily determined by stressfully high irradiance levels (leading to photoinhibition) and flow velocities, offsetting any effects of increased nutrient supply. Comparable stressful conditions, however, cannot be indicated at the other investigated sites.

The second possibility that must be considered is that trapping of mangrove carbon in the seagrass zone does not coincide with nutrient enrichment. This could be the case if the outwelling mangrove carbon consisted of dissolved inorganic carbon compounds which lack nitrogen and phosphorus constituents, i.e. CO_2 , bicarbonate and carbonate molecules. The $\delta^{13}\text{C}$ of oceanic dissolved inorganic carbon normally is circa 0 ‰ (Boutton, 1991). Mangrove leaves, the major category of organic litter produced by the mangrove trees in Gazi Bay, have $\delta^{13}\text{C}$ values ranging from circa -25 to -28 ‰ (Hemminga et al., 1994). Uptake of ^{13}C -depleted CO_2 (resulting from leaf decomposition) in the tidal water inundating the mangrove thus would reduce the $\delta^{13}\text{C}$ value of its inorganic carbon pool. This ^{13}C -depleted inorganic carbon subsequently would become available to *T. ciliatum* when the ebb water crossed the seagrass zone, resulting in ^{13}C -depleted *T. ciliatum* plants. Recent observations (Slim & Hemminga, unpublished observations) show that the inorganic carbon flowing from Kinondo creek with ebb tide indeed shows some depletion in ^{13}C ($\delta^{13}\text{C}$ ca. -5 ‰). This is unsufficiently low for a full explanation of the deeply negative $\delta^{13}\text{C}$ values of the seagrasses in the proximity of the mangroves, but it indicates that at least part of the carbon export from the mangrove is not directly coupled to nutrient fluxes.

Trapping of mangrove carbon without a coinciding (net) nutrient enrichment of seagrass zone could also occur if the nutrient gain associated with the input of mangrove-derived POM in the seagrass meadows was offset by losses of nutrients due to export of seagrass detritus. As the C:N ratio of senescent mangrove leaves generally is much higher than that of senescent or dead seagrass leaves (Harrison, 1989; Rao et al., 1994), the exchange balance in the seagrass meadow could even be positive for carbon (net carbon input) without a net gain in nutrients. Substantial export of seagrass detritus from the meadows in Gazi Bay does occur, as can be gathered from the observation that approximately 60% of the macrodetritus in the water between mangrove and seagrass meadows is of seagrass origin (on dry weight basis; F.J. Slim, pers. comm.).

In conclusion, we assume that there are several reasons explaining the fact that trapping of mangrove carbon by the adjacent seagrass meadows does not coincide with increases in leaf production or in leaf nutrient content. Most likely, outwelling of mangrove carbon includes dissolved inorganic compounds without N and P constituents. The nutrient input associated with trapping of mangrove-POM in the seagrass meadows probably is limited, to the degree that its impact, if any, is masked by opposite influences of environmental conditions or nutrient losses caused by export of seagrass detritus. Thus, although in Gazi Bay seagrass beds are directly adjacent to a mangrove forest and connected with the forest via the tidal water flow, the influence of abiotic fluxes from the mangrove forest on the functioning of the seagrasses appears to be inconspicuous.

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PRODUCTIVITY OF SEAGRASSES WITH RESPECT TO INTERSYSTEM FLUXES IN GAZI BAY (KENYA)

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INTRODUCTION

Seagrasses ecosystems have been recognized as one of the richest and most productive ecosystems (McRey 1974, Zieman 1975). The high primary production is but one of the ways in which seagrasses function in maintaining the productivity and stability of nearshore marine and estuarine ecosystems and is therefore the most essential function of these ecosystems. Their role has been summarized by Wood et al (1969). Productivity studies have been confined to *Zostera marina* and *Thalassia testudinum*, although seagrass meadows are widespread in the oceans and make a more measurable contribution to coastal productivity that might otherwise be imagined.

In the tropics, the rate of productivity of seagrasses need long-term studies to look at the quantitative changes throughout the year. However the number of in-situ productivity studies of seagrasses over an extended period, even in Kenya, is small. Productivity and biomass of seagrasses may be influenced by hydrographic parameters and is also a function of many interrelating factors. The interrelations between mangrove, seagrass and Coral reef biotopes are biotic and abiotic whereby the abiotic level, intersystem fluxes of nutrients driven by 'trapped' tidal watermass within the coastal zone is likely to structure the biotic characteristics. The abundance and morphology of these seagrasses are more likely to be limited by the availability of nutrients. The productivity and growth data may provide information to quantify the functional characteristics inherent in these fluxes. An analysis of the total plant biomass is essential in the evaluation of growth dynamics.

The current study was carried out to determine the rate of accumulation of organic matter in the living tissues of seagrasses and whether the seagrass beds function in relation to intersystem fluxes in Gazi Bay.

METHODS

Study area

The study was carried out in Gazi Bay (Kenya). Sampling sites were selected on the basis of accessibility during the low waters and were along a transect that ran from a mangrove to coral reef constellation and was confined to areas in which the monospecific beds of *Thalassodendron ciliatum* supported continuous sampling. These were:

- (1) Mangrove Creek (MM). This site represents the sublittoral part of the seagrass zone represented by the creek system connecting mangroves, the sea and the coral reef. Its 0-10 cm layer of sediment is characterized by a mixture of quartz and organic material of biogenic origin. Massive calcareous algae cover the near-exposed fossil coral. The site has the highest tidal current velocity of approximately 0.62 m/s. *T. ciliatum* forms dense beds in this creek.
- (2) Intertidal area (SS). This site represents the shallow intertidal mud flats. Its 0-10 cm layer of sediment consists mainly of quartz and coarse sand in the deeper 10-20 cm. The tidal current velocity here is much reduced (0.25 m/s) and the low water marks often leaves the extensive mudflat exposed to heat and air. A mixture of seagrass species are found on the mudflat, but the dominant *T. ciliatum* characterizes the area. SS₁ refers to site where samples of mixed *Thalassia hemprichii* and *Cymodocea rotundata* were taken from.
- (3) Subtidal area (CS). This is the upper subtidal part of the seagrass zone where the lowest watermark is not less than 1 m. The site is further from the creek and has little influence of mangrove outwelling. The sediment is purely biogenic with fine to very fine grained mud in the deeper 10-20 cm. *T. ciliatum* dominates the sampling site.

Productivity measurements

The field work was carried out during April 94- July 95. To study productivity the Plastochrone Interval (PI), which is a replacement technique, was applied according to Brouns (1985). A small hole was punched in the tip of the youngest leaf reaching a minimal reference point of about 1 cm (Erftemeijer et al 1993). This was done for a number of shoots within quadrats measuring 25 by 25 cm. An average of twenty shoots was marked per quadrat. After 14 days, all new leaves reaching the reference point were counted. The PI was calculated according to Jacobs (1979):

$$PI = (N \text{ of shoots marked } * t) / N \text{ of new leaves}$$

where N = total number,
t = time interval between marking and harvesting (in days).

Triplicate samples were taken for each sampling site. Randomly collected adult leaves of the same species were averaged and the data together with biomass of leaves and shoots was used to calculate the daily production in gram per meter square. To measure the growth of leaves, the leaf marking (LM) technique described by Zieman (1975) was applied. All leaves of a seagrass shoot were punched using a special device. A 'makuti' stick was stuck in the sediment next to the shoot in question to mark a fixed reference point. This could only apply to *T. hemprichii* and *C. rotundata*. The reference point for *T. ciliatum* was determined by the level of the leaf blade furthest from the basic meristem.

After four days the leaves were re-punched at the reference point. Shoots were harvested, stored in a cool box and brought to the laboratory. Triplicate samples of random squares (25 cm X 25 cm) were taken for each sampling site. The distance between the first and second hole was taken as a measure of growth in length. These were cut out, oven dried to a constant weight and the dry weight determined. Relative growth rate and areal productivity were calculated from data on density and biomass.

For standing stock and total biomass estimates, all the seagrass from a 25 cm X 25 cm aluminium frame were harvested and partitioning of each harvest was assessed. All dead material was excluded from the samples. The biomass of epiphytic macroalgae was also assessed by cleaning and drying to constant dry weight at 60 °C.

The ash free dry-weight (AFDW) was determined by calculating the difference between the dry weight (DW) and ash weight after ignition at 550° C for approximately six hours.

Data analysis

Samples were pooled for different sampling sites in order to compare their growth productivity and biomass values. ANOVA was used to test any variations in productivity within the sampling sites. Comparison was also made of data collected during the wet (S.E. monsoon Apr.-July) and during the dry (N.E monsoon Nov.- Mar. of 1994/95). The comparison of areal productivity of the species was made from pooled data collected over the study period. The \pm refers to the standard deviation unless otherwise stated whereas n refers to the total number of samples used.

RESULTS

Biomass

The average total biomass values for *T. ciliatum* (Table 1) was within the range of 473-978 gram dry weight per meter square (values include above-ground and below-ground biomass); whereas the leaf biomass ranged between 53.8-139.8 g AFDW m⁻². Total biomass values were comparable for *T. ciliatum* at the mangrove creek (MM) and intertidal area (SS) but were lower at the subtidal area (CS). Below - ground biomass values were also comparable at all the sites, but the percentage of below ground in the total biomass was considerably higher at CS (65%) than at MM and SS (49% and 45% respectively). However, relatively higher biomass (up to 82.8 gm⁻²) of epiphytic macroalgae was recorded at MM than at SS and CS (57.7 \pm 39 and 44.2 \pm 29 g dw m⁻² respectively). Biomass values did not vary during the wet and dry period.

Density

Thalassia hemprichii had lower leaf density in cluster per m² ranging between 3944 - 3990 with an average of four leaves per shoot as compared with the high densities of *T. ciliatum* ranging between 3000 - 6628 with an average of eight leaves per shoot. The same trend applied for shoot density (n

Table 1. Average biomass of *T. ciliatum* at different sites in Gazi Bay.

Sampling site	MM	SS	CS
Shoot biomass g dw m ⁻² (M±SE)	345.5 ± 17.2	368.6 ± 10.2	234.3 ± 3.7
Below ground biomass g dw m ⁻² (M ± SE)	378.6 ± 18.4	326.3 ± 12.1	399.5 ± 14.7
Total biomass g dw m ⁻² (M ± SE)	700.1 ± 23.6	740 ± 21.6	564 ± 21.7

Table 2. Average net productivity and growth rate of *T. ciliatum* measured during the N.E. monsoon.

	Sampling site		
	MM	SS	CS
Leaf growth (cm/shoot/day)	1.92 ± 0.48	2.08 ± 0.43	2.21 ± 0.3
Productivity (gAFDW m ⁻² day ⁻¹)	2.28 ± 0.9	3.5 ± 0.9	3.9 ± 0.6
R. growth rate (gg ⁻¹ AFDWday ⁻¹)	0.02 ± 0.002	0.02 ± 0.004	0.03 ± 0.003
P:B	0.02 ± 0.002	0.02 ± 0.004	0.03 ± 0.003

Table 3. Density and leaf length of *T. ciliatum* sampled at Gazi Bay.

Sampling site	MM	SS	CS
Average length of full grown leaves (cm)	7.4±1	9.8±0.2	8.18±0.9
Shoot density (n m ⁻²)	1108±450 (n=18)	643±246 (n=22)	702±171 (n=19)
Leaf density (cluster m ⁻²) (M±SE)	5053± 64	4060±62	5198±64

m²) whereby *T.ciliatum* was more dense (708 ± 100) than *Thalassia hemprichii* (555.9 ± 122). The Kinondo mangrove creek (MM) had the highest seagrass shoot density compared to the intertidal (SS) and subtidal (CS) areas. More details on density, leaf length values of *T.ciliatum* are presented in Table 3.

Growth

In general the seagrasses had remarkably high growth with absolute leaf growth rate of up to 2.3 cm per shoot per day. No significant variation was observed in the different sites in terms of growth rates. This was further confirmed by the constant relative growth rates of 0.02 g g^{-1} (Table 2) and constant production to biomass ratios (P:B). However, the average length of full grown leaves (cm) was small in the mangrove creek (MM) and highest in the intertidal area (SS)(Table 3). The lengths of full grown leaves did not change significantly during the dry or wet period (9.8 ± 0.2 and 10.18 ± 0.8 cm respectively).

Plastochrone Interval (PI_{leaves})

The average PI_{leaves} measured during the study period was 9.9 ± 2.3 (n=14) days for *T. hemprichii* and 6.3 ± 0.9 (n=32) days for *T. ciliatum*. The values of PI_{leaves} was comparable in the N.E as well as the S.E monsoon periods (5.8 ± 0.5 and 6.2 ± 1 days respectively). These measurements (seasonal) were taken only at the intertidal area (SS) on *T. ciliatum* species only. Similarly, very little variation was observed on PI_{leaves} values taken at different sites (Table 5).

Productivity

There was detectable seasonal variation in productivity - the wet period (S.E monsoon) having higher values ($F = 3.53$ (1,10) $\alpha = 0.05$) than the dry period (N.E. monsoon). A one- way analysis of variance test revealed that there was a gradient in seagrass productivity levels from the mangrove creek (MM) - having the least values - to the subtidal (CS) area having the highest values. The difference between MM and CS was significant ($F = 6$ (1,15) $\alpha = 0.025$). Results of productivity from leaf marking measurements are summarized in Table 2.

Table 4. Average net productivity of *Thalassodendron ciliatum* in comparison with mixed *Thalassia hemprichii* and *Cymodocea rotundata* as measured with Plastochrone Interval (PI_{leaves}).

Species	Plots	areal productivity (g dw m ⁻² day ⁻¹)
<i>T. ciliatum</i>	n=15	4.43 ± 2.7
Mixed <i>T. hemprichii</i> and <i>C. rotundata</i>	n=14	2.4 ± 0.6

Table 5. Average Plastochrone Interval (PI_{leaves}) values.

Sampling site	MM	SS	CS
<i>Thalassodendron ciliatum</i>	6.7 ± 0.9	5.89 ± 0.5	6 ± 0.6
<i>Thalassia hemprichii</i>	—	9.9 ± 2.3	—

DISCUSSION

Seagrass leaves may constitute a variable amount of the weight of the plant depending on the substrate, season and nutrient availability. The highest leaf and biomass weights have been found in the coarser sediments (Zieman, 1980). Our results indicate that leaf lengths at the intertidal and the subtidal areas are higher than those at the mangrove creek. Erftemeijer (1993) also noted that much longer leaves of the same species were found on terrigenous sediments and attributed this to richer

sediment nutrient conditions. The net production and biomass values recorded in Gazi Bay during the study correspond with other studies carried out in the subtropics by Erftemeijer et al 1993, and confirms that the rate of seagrass productivity is remarkably high (Jacobs, 1979; Den Hartog, 1979).

The net production at the SS and CS was quite comparable and was relatively higher than at MM. This can be attributed to a direct terrestrial influence from two seasonal rivers - Mkurumuji and Kidogoweni which drain into this area directly. The run-off from rivers deposit terrigenous sediments which characterizes an environment of richer nutrient supply. As such lower productivity values at MM relative to CS and SS may have been due to the little river influence at the Kinondo creek. However a constant relative growth rate and production to biomass ratios (P:B) observed at the mangrove creek (MM), intertidal area (SS) and subtidal area (CS) indicate that the seagrasses in Gazi Bay are equally efficient in nutrient recycling and uptake regardless of their situation. The high tidal current velocity at the Kinondo creek may enhance nutrient uptake by the leaves.

Nevertheless, the permanent availability of water at the subtidal (CS) as compared with the intertidal area and mangrove creek (MM and SS) implies that seagrasses here have longer hours to obtain sufficient nutrients from the environment, and could account for the higher productivity values recorded at CS than at MM and SS. Jacobs (1979) reports 85% growth at places with a minimum tidal coverage, but optimum growth at places with 95% to 100% tidal coverage. The temperatures of the tide pools have been reported to rise by up to 5°C (Coppejans et al 1992), and the seagrasses thereby experiencing a notable 'burning'. The seasonal temperature elevation with periodic exposure to air and high temperature during low spring water may enhance photoinhibition and desiccation which are likely to affect the vigor and vegetative reproduction of *T. ciliatum*. This factor explains why the productivity values at CS are significantly higher than at MM and SS. Ogata and Matsui (1965) also found that strong dehydration suppressed photosynthesis. CS is subtidal area, always submerged and therefore lacks a large diurnal variation.

The subtidal seagrasses (at CS) lack potential outwelling mangroves. The investment of most of their biomass below ground (65%) compared to mangrove creek (MM) and the intertidal (SS) seagrasses (less than 50%) may be contributing to their efficiency in nutrient incorporation from the sediment. Seagrasses have been known to utilize nutrients from the sediments (Erftemeijer et al 1994). The mangrove creek (Kinondo) reflects a nutrient poor environment, but the thin sediment layer underlain with coral fossil does not encourage the investment of a high below ground biomass. The seagrasses here compensate this by having a more dense above ground cover which then can take up nutrients in this site with a high tidal current velocity. However, the high density of seagrasses in this creek compared to the subtidal and the intertidal sites may also contribute to low production rate due to competition.

The present study did not reveal any seasonality in the total biomass. This is characteristic of the tropical region where the relatively uniform temperatures sustain a persistent biomass; although Erftemeijer and Herman (1994) reported seasonal changes in biomass in the seagrass beds of South Sulawesi, Indonesia. The relatively high areal productivity of the intertidal seagrass during the S.E. monsoon (April-June) can be attributed to relatively elevated nitrogen concentrations brought into the bay by the rivers as has been indicated by studies on 'dissolved inorganic nutrient fluxes' under the EEC STD-3 project; the influence of the rivers is small in the Kinondo creek, where tidal current velocity is also very high (0.62m/s).

In conclusion, the subtidal seagrass of the same species has higher productivity than the intertidal and mangrove creek sites in the shallow lagoon system of Gazi. The spatial variation in productivity of *T. ciliatum* is attributed to the tidal regime which often leaves the intertidal area exposed to high insolation during low waters, thereby increasing the temperatures and salinity, causing burning and inhibiting photosynthesis. The subtidal area is always covered during low waters hence the seagrasses here exhibit higher production. The rivers Mkurumuji and Kidogoweni bring nutrient-rich terrigenous sediments directly into the intertidal and subtidal areas with little influence in the mangrove creek; as a result the production in these areas is higher than the mangrove creek. The river influence is greater during the S.E. monsoon bringing in more nutrients thereby increasing the productivity of the seagrasses as compared to the N.E. monsoon period.

The higher tidal current velocity at the mangrove creek contributes in enhancing nutrient incorporation by the seagrass leaves thereby compensating the plants' efficiency in the otherwise considered relatively nutrient-poor creek.

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COMMUNITY PRODUCTION AND NUTRIENT FLUXES IN SEAGRASS BEDS (UNGUJA ISL., TANZANIA)

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INTRODUCTION

In addition to playing a support role, the Stockholm component has aimed at specifically addressing the following aspects of the inter-linkages project:

1. To make a comparison of the community function of seagrass meadows (sink and source function) in two contrasting situations, i.e. in between mangroves and reefs, and in the absence of mangroves in back reef lagoons.
2. To examine the water column nutrient dynamics in seagrass meadows adjacent to mangroves and remote to mangrove influences.

In this section of the final report, the results obtained with respect to the first aspect are summarised. Experiments conducted in mangrove influenced areas will be compared with the data collected from seagrass and sandy benthic areas remote to mangrove influences.

As has been presented in earlier reports, studies in the open lagoon at Paje (Fig. 1) show there to be an active benthic remineralisation of organic material and that, in certain areas, this returns a considerable amount of dissolved inorganic nitrogen (DIN) to the water column. Also, subsequent studies have shown that there is an active micro-algal community on large areas of the lagoon floor which appears to account for a part of this DIN; photosynthesis of this community averaged $450 \text{ mg C.m}^{-2}.\text{d}^{-1}$. In the adjacent seagrass communities community production was significantly higher with a mean of $567 \text{ g C.m}^{-2}.\text{d}^{-1}$. Further, these seagrass communities were heterotrophic; i.e. community production exceeded respiration (mean P:R ratio of 1.1).

In the light of these observations and the overall aims of the project, similar benthic studies are being conducted in Chwaka Bay (Fig. 1). Compared to the lagoon at Paje, this ecosystem consists of a bay surrounded by mangrove forests which are drained by tidal creeks flowing into the bay. Also, throughout the bay the benthos is dominated by seagrass communities of varying densities and there is a clearly visible particulate load in the water column which is not seen at Paje. Further, work conducted in the mangrove forest creeks has shown that, whilst there is a strong tidal exchange between the mangrove forest and the bay, there appears to be no net export of dissolved nutrients from the mangroves (Mohammed and Johnstone, 1995). No data has yet been collected on the level of particulate or dissolved organic matter (POM, DOM) which might be transported by the creeks, however, given both the levels of production and deposition within the forests (Shanula, 1989), as well as the apparent particulate load in the creek waters, POM and DOM may represent a significant output to the bay.

The work thus described here has attempted to determine the production of the benthic communities along a transect from the mouth of the mangrove creek to the bay proper. The intention with this is that by estimating the relative nutrient status and requirements of these communities, it is possible to make a first estimate as to whether these communities require (and thus receive) an external input of material to meet their production requirements. This approach has been used elsewhere with success (e.g. Johnson and Johnstone, 1995), and permits the construction of a mass balance model for the large scale assessment of community status; from which more specific investigations can be initiated.

METHODS

Study area

The two sites investigated lie in the south western corner of Chwaka Bay directly outside Mapopwe Creek which is one of the main drainage channels for the surrounding mangrove forest. Site 1 is closest

to the mouth of the creek and site 2 along the same current path approximately 0.7km away. It should be noted that both sites lie outside a shallow sill which essentially isolates the creek water from the bay at low tide (Wollanski, 1992) and which hinders water flow close to low tide. Both sites are described here as seagrass areas or communities but there are marked differences in their seagrass density. At both sites, seagrasses represent $\geq 80\%$ of the macroflora biomass however, at site 1 (closest to the creek mouth) seagrasses gave a benthic coverage of approximately 50%, compared to approximately 80% at site 2. Also, Site one was dominated by *Thalassodendron* sp. ($\geq 70\%$ of seagrass biomass) with *Halophila* sp. and *Thalassia* sp. also represented. This compares with site 2 which was dominated by a mixture of *Thalassodendron* sp. and *Cymodocea* sp. In addition, there were fewer macro-algae at site 2 and *Halimeda* sp. was common.

Both sites have a tidal fluctuation of $\approx 1.5\text{m}$ and a mean low water depth of 0.5m. Also, both sites were within 10m of the deeper central channel which drains this part of the bay; mean low water depth of $\pm 2\text{m}$.

Community Production Measurements

Given that the rate of release of oxygen during photosynthesis is directly proportional to the rate of carbon fixation the method used here monitored the rate of oxygen release from the seagrass community and then calculated primary production. It should be noted, however, that the measurements taken represent the total community entrapped under the benthic chambers, so this includes the various epiphytes and the associated fauna. Thus the measurements are in fact of community production. There has been some discussion as to whether this method gives an underestimation of the primary production because oxygen may be transported to the roots, and there is the possibility of oxygen storage. Also, factors such as photorespiration, leakage of dissolved organic carbon, and the formation or translocation of carbon reserves may cause a discrepancy between net photosynthesis and actual growth (Larkum and West, 1983). Despite this, the method has been demonstrated to give a good estimate with a possible underestimation in the order of 10-15% (Jayasuriya, 1991; West and Larkum, 1983; Peduzzi and Vukovic, 1990).

Two different production values are obtained from the method. *Gross community production*, which is the total amount of organic matter produced by the communities photosynthesising members, and *net community production*, which is gross primary production minus organic material used by community inhabitants in respiration. Net production therefore represents the amount of resource which may be utilised by other organisms. For the sake of comparing different sites, this balance between production and respiration can also be expressed as the P:R ratio so that communities with $P:R > 1$ are said to be autotrophic (*in situ* production above *in situ* demand), or heterotrophic with $P:R < 1$ (*in situ* demand exceeds *in situ* production).

Measurements were carried out by using four replicate water tight plexi glass domes built as taller and somewhat more automated replicas of those described by Johnstone *et al.* (1989). These were placed over the seagrass communities at each site and anchored by pushing them 5 cm into the sediments to prevent dome movement and water exchange under the dome edge. Each dome had a volume of 216 litres with a basal area of 188 cm^2 . The water inside was stirred by an Attwood Miniking 360 pump, pumping at a speed of approximately 600 litres per hour. This speed was chosen because preliminary dye tests showed this to best simulate the ambient water mixing rate.

Sampling was done at different time intervals for the different parameters over a period of six hours each sampling day. Oxygen and temperature were measured every hour through a re-sealable port in the dome using a WTW Oximeter 191. Respiration was carried out during the day by measuring oxygen uptake in the domes covered with black plastic and it was then assumed that the respiration by the community during the dark was the same as the respiration during light (Ertmeijer *et al.*, 1993). All oxygen values were converted to carbon equivalents using a conversion factor of 0.31 (Schramm *et al.*, 1984). Also, as a control for water column activity, a water column sample of 2 litres was enclosed in a flask at the beginning of the experiment and this was monitored for changes in oxygen concentration. The flask was incubated *in situ* and the production or consumption obtained was subtracted from the dome data.

Nutrient and Salinity Measurements

In addition to primary production measurements, water samples for nutrient and salinity analyses were taken from each dome every second hour using a 50 ml syringe and needle pushed through self-sealing sampling ports on the side of the dome. An equal amount of water was allowed to enter the dome through a similar needle and port on the opposite side of the dome. This prevented interstitial

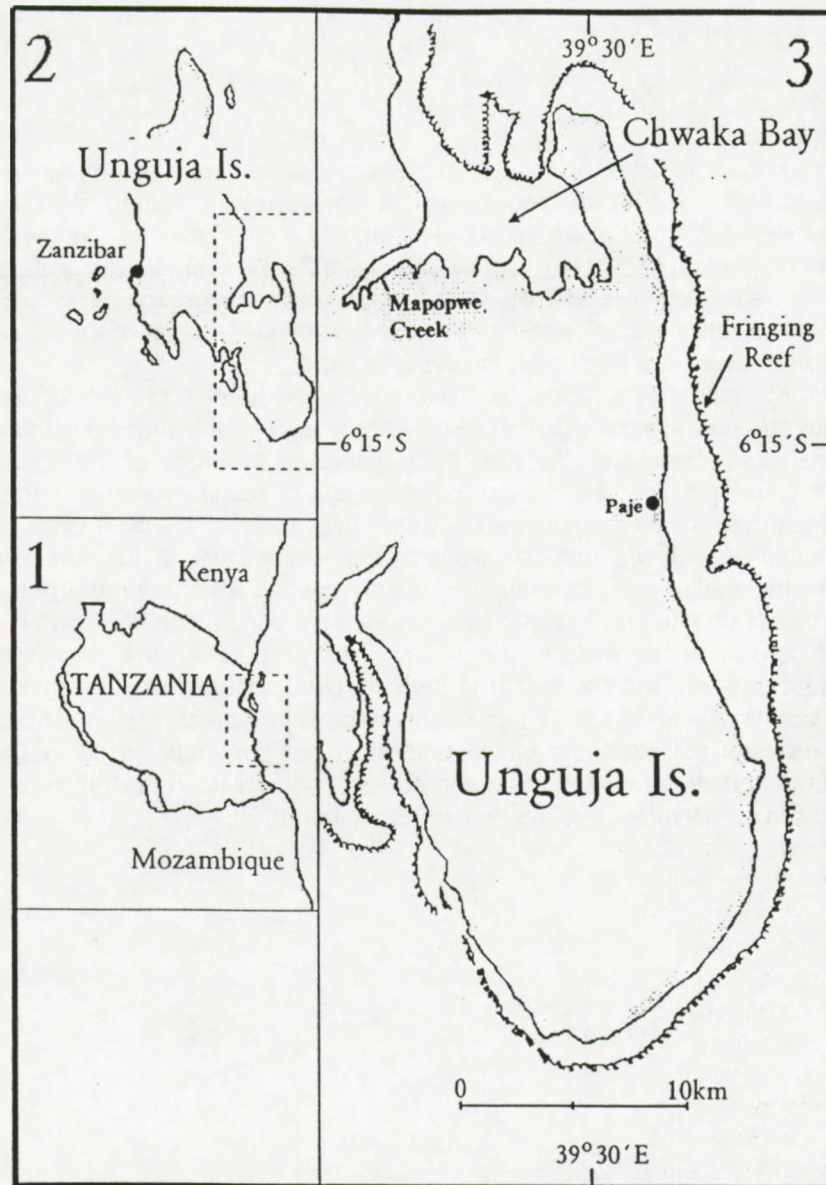


Fig. 1. Map of Unguja Island (Zanzibar) showing the study areas at Chwaka Bay and Paje

water (with another nutrient concentration) from being drawn from the sediment. Samples were also taken from the water adjacent to the domes for ambient nutrient determinations. All samples were immediately put on ice for transport to the research station to be frozen until analysed and all nutrient analyses were carried out according to standard methods (Parsons *et al.*, 1984; Johnstone and Preston, 1993). Flux rates were determined by plotting the change in concentration over time for each dome and nutrient, and then applying a linear regression to the data (least squares method); the slope of this curve was taken as the rate of release or uptake. The rates for each site were then averaged and the standard deviation calculated. Also, a water column control was conducted as for oxygen measurements as a check on water column nutrient regeneration. Water column values were

subtracted from dome values to give the flux component due to the benthos.

Light conditions at each site were measured every hour for the same six hours, using Secchi disks of different colours. Salinity was measured with a Meiji Techno Salinometer S-1. The data for each site was averaged over the time of incubation.

RESULTS

Community metabolism

Benthic chamber experiments showed the two stations to have different community production levels with site 2, (more remote to Mapopwe Creek) having a higher production than site 1; gross community production values were $123 \pm 52 \text{ gC.m}^{-2}.\text{y}^{-1}$ at site 1 and $182 \pm 45 \text{ gC.m}^{-2}.\text{y}^{-1}$ at site 2. Notably, site 1 also had a lower respiration ($228 \pm 16 \text{ gC.m}^{-2}.\text{y}^{-1}$) than site 2 ($278 \pm 25 \text{ gC.m}^{-2}.\text{y}^{-1}$) but the communities at both sites were heterotrophic with P:R values of 0.54 and 0.66 respectively. These values are corrected for water column production within the chamber by subtraction of the control flask values. Examples of the flux curves are presented for site 2 in Fig. 2.

As shown in Table 1, the production values recorded here are in the low end of the range reported in the literature for seagrass communities. One reason for this may be light availability as the waters are consistently coloured and/or turbid depending on the state of the tide. The turbidity is typically worst at or near to low tide presumably because of resuspension of benthic material. By comparison, the transparent brown colouration exists over most of the tidal cycle and is presently thought to be humic substances resulting from organic breakdown of the forest litter; this being transported out by the tidal stream. Unfortunately, an underwater light meter was not available for this work but as the secchi disk results indicate (see below) light penetration is generally low. Of course, ambient nutrient concentrations were also considered here but given the prevailing water column concentrations (see below), and the fact that there is a significant efflux of ammonium from one community, this seems unlikely to have a significant effect. This is presently being further assessed by determining the nutrient requirements of the different plant communities using C:H:N ratios and comparing this to the observed uptake rates and nutrient availability. This work is an offspring of the current work and will be completed by the end of November 1995.

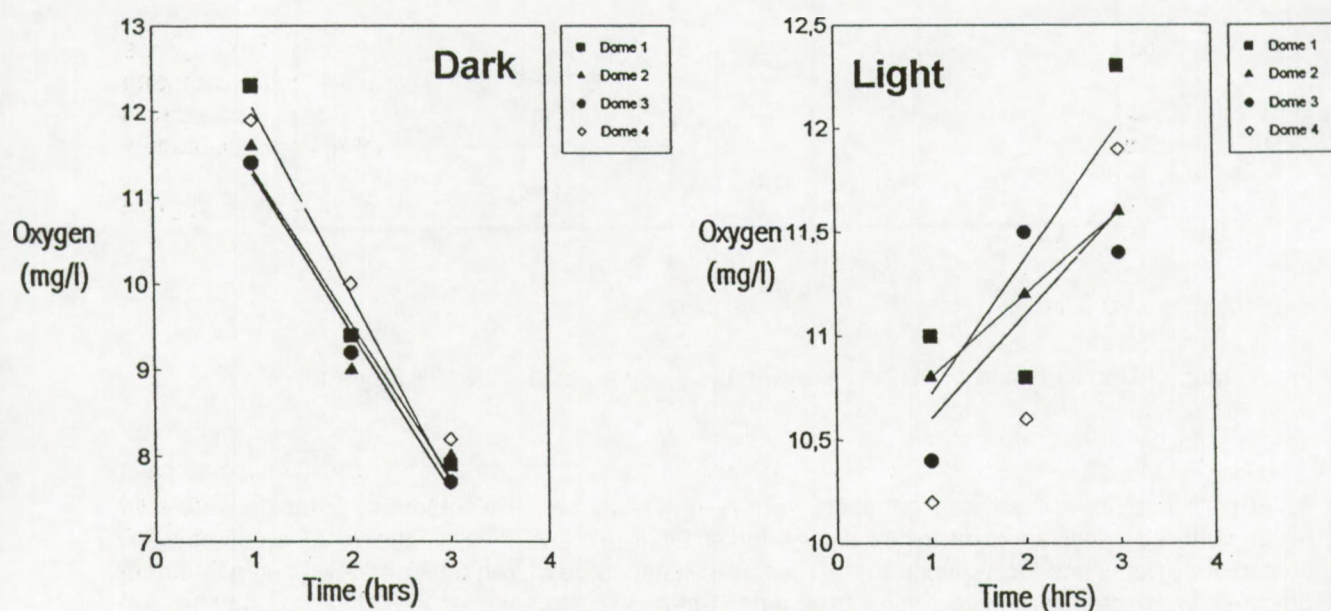


Fig. 2. Oxygen flux data from site 2 in Chwaka Bay. The dark and light plots represent respiration and photosynthesis measurements, respectively.

Production C (g/m ² /year)	P:R ratio	Species	Remarks	Source
2190	1.20	<i>Cymodocea rotundata</i> <i>Thalassia hemprichii</i>	Communities	Pollard & Moriarty, 1991
1460-3285	0.81-1.67	Various	Communities	
219-1752	0.94-2.25	Various	Communities	Moriarty et al., 1990
328-1606	0.55-1.17	Mixed species	Communities	Erfmeijer et al., 1993
182	N.A.	<i>Cymodocea rotundata</i>	Seagrass only	Pollard & Moriarty, 1991
36-365	N.A.	<i>Cymodocea rotundata</i>	Seagrass only	Moriarty et al., 1990
1058	N.A.	<i>Cymodocea rotundata</i>	Above ground, seagrass only	Erfmeijer et al., 1993
365	N.A.	<i>Cymodocea rotundata</i>	Leaf production,	Hillman et al., 1989
150-800	N.A.	Various	seagrass only	
73-255	N.A.	Various	Net production, seagrass only	Valiela, 1991
45-1314	N.A.	Various	Leaf production, seagrass only	West & Larkum, 1983

Table 1. Examples of primary production values taken from the literature. The five top rows indicate community production and are directly comparable with each other, whilst the rest are seagrass productivity. The latter are included to give an idea of the potential contribution of the seagrass itself. Where published figures were in g dry weight, a conversion factor of 0.36 was used to convert to grams carbon, and organic (ash-free) dry weights were multiplied by 0.5. A range of values indicates multiple values.

Community nutrient fluxes and physicochemical parameters

Nutrient flux measurements showed considerable variation both within sites and between sites. Also, fluxes were only recorded for ammonium (NH₄⁺); no fluxes were observed for either soluble phosphate (SRP) or nitrate+nitrite (NO₃⁻+NO₂⁻). At site 1, ammonium fluxes were consistently positive among replicates so that the mean community flux rate was 413 ± 275 mM. NH₄⁺.m⁻².d⁻¹. This compares with site 2 which showed both positive and negative fluxes between replicates so that the mean community flux was -220 ± 485mM. NH₄⁺.m⁻².d⁻¹.

Ambient water column concentrations of nutrients were the same at both sites with mean values of 62mg N.l⁻¹ for ammonium, 11mg N.l⁻¹ for nitrate+nitrite, and 97mg P.l⁻¹ for SRP.

Salinity was consistently between 34.8‰ and 35‰. Also, secchi disk measurements showed the mean penetration of light to be 48 ± 7 cm at site 1 and 73 ± 9 cm at site 2.

CONCLUDING REMARKS

In accordance with the original goals of the project, the benthic component has now collected data describing the community metabolism of the different biotopes within an open lagoon system devoid of mangroves, Paje, and within an embayment encircled by mangrove forests, Chwaka Bay. Unfortunately, some of this data is still being collated and calculated as this report is submitted but at this stage it seems apparent that the seagrass communities in these two different ecosystems behave differently. Specifically, the seagrass beds in Paje lagoon gave not only a higher production but also produced more than was consumed within the community (P:R 1.1). By comparison, the seagrass communities outside Mapopwe Creek both gave P:R ratios <1 indicating that the communities did not produce an excess that could be exported but required an input to meet their needs. As mentioned earlier, it would appear from the data so far collected that mangroves around Mapopwe Creek may

export an amount of their production, however, this material is not exported as dissolved inorganic substances but rather as dissolved organic/particulate organic material (Mohammed and Johnstone, 1995). This notion would now appear to be supported in part by the fact that the seagrass communities which receive the outgoing waters from this creek are dependent on an organic input. Clearly there may be other inputs from, for example, seagrass beds further out into the bay, however, this has not yet been adequately investigated and the turbidity of the outgoing creek water would suggest a considerable particulate load. The actual quality of this material is presently being investigated by a graduate student at IMS, Mr Mohammed.

In addition to the one publication so far produced from this work, it is expected that the data presently being collated will lead to the production of at least one more which will deal specifically with the situation in Chwaka Bay and the comparison between it and the seagrass beds in Paje lagoon. Copies of these will be forwarded on completion.

In addition to the production of scientific data, it should be pointed out here that this work has also assisted in the training of Mr Salim Mohammed who is a Ph.D. student from the Institute of Marine Sciences (IMS) on Zanzibar. Mr Mohammed is supported by a scholarship from the Swedish Agency for Research Co-operation in developing countries (SAREC), however, this provides only limited research support and so programs such as this provide an avenue for the development of such students.

This project has also enabled the maintenance and developed use of the chemical analysis facilities at IMS. Specifically, the project has helped to assist in training Mr Mohammed and a technician at IMS in the use of a range of analytical equipment including an auto-analyser for nutrients, benthic incubation chambers, and sediment incubation techniques for laboratory sediment investigations.

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Part 3: The hydrodynamics and nutrient contents of tidal waters flushing mangrove forests and seagrass meadows

WATER CIRCULATION DYNAMICS, WATER COLUMN NUTRIENTS AND PLANKTON PRODUCTIVITY IN GAZI BAY (KENYA)

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INTRODUCTION

Research on coastal water circulation dynamics and its relation to water column nutrients and plankton productivity in tropical waters has been receiving growing attention in the recent past as a result of increasing awareness of the importance of coastal water circulation dynamics to the short- and long-term sustainability of coastal marine ecosystems (Boto, 1982., Swenson et al 1983., Wolanski 1986, 1994). The description of the relationship between water circulation and spatial-temporal variations of water-column nutrients and plankton productivity in tropical coastal waters is also crucial to the understanding of the tropical ecosystem dynamics and land-ocean flux studies (Koutitonsky, et al. 1990, Swenson and Chuang 1983., Ho 1977 and Bowman 1977). The spatial-temporal distribution of dissolved inorganic nutrients in tropical coastal marine ecosystems (mangroves, seagrass beds and coral reef) is influenced by a wide range of factors of which hydrodynamic processes and river discharges are important (Bowman, 1977., Ho, 1977). The tidal water movement characterised by ebb and flood flows, has been known to serve as a vehicle for the fluxes of dissolved inorganic nutrients between the different coastal ecosystems (Wolanski, et al 1980). The incoming flood tide water is thought to be a source of dissolved nutrients to the mangroves, seagrass beds and the coral reef ecosystems. The outgoing ebb tide water could leach nutrients from the mangrove swamp soils and act as a net exporter of dissolved inorganic nutrients from the mangroves and adjacent coastal ecosystems (Boto, 1982). The tidal transport of particulate matter as a source of nitrogen loss in tropical coastal waters is balanced by tidal import of dissolved nitrogen from the rivers along with nitrogen fixation. The net annual exchange of dissolved materials between mangrove creeks and the coastal waters has been reported to be negligible and insignificant, although a significant net export of the particulate matter mostly as mangrove litter occur in creeks with dominant tidal asymmetry (Alongi, 1990). The productivity of phytoplankton and zooplankton in coastal waters is determined by the seasonal abundance of dissolved inorganic nutrients and hydrodynamic processes (Wheeler and Kichman, 1986). However the patterns of plankton productivity variation and response to seasonally varying rates of nutrients and freshwater input in tropical coastal waters is not well known. Coastal water circulation, coupled with seasonal river freshwater input, has been known to affect nutrient distribution and plankton productivity in semi-enclosed bays, but the mechanisms of this influence in tropical coastal waters is still inadequate. Where the input of freshwater from the rivers is seasonal, the plankton productivity shows highly seasonal signals which may be a reflection of the seasonally-varying nutrients input. In regions where there is no direct surface freshwater supply, nutrients may be derived from the groundwater seepage and from the static sources such as nitrogen-transformation processes in sediments and other dynamic sources such as tidal transport (Boto, 1982). In the framework EEC-STD 3 research programme on the linkages between the Eastern Africa Coastal ecosystems, the influence of water circulation in the distribution of dissolved inorganic nutrients and plankton productivity in the mangroves, seagrass beds and coral reef ecosystems of the tropical Gazi Bay in southern Kenya was undertaken between 1993-1995. The objective of the study was to establish, by focussing on Gazi Bay, the importance of riverine freshwater input and coastal water circulation, in determining the spatial-temporal distribution of dissolved inorganic nutrients and productivity of plankton in different tropical coastal marine ecosystems.

METHODS

study area

Gazi (Maftaha) bay is a shallow bay with mean depth often less than 5.0 m (Fig. 1). The total area of

the bay excluding the area covered by the mangroves is 10.0 km². The seagrass zone is found in the central region and covers an area of 7.0 km². The bay is open to the Indian Ocean through a relatively wide (3,500 m) and shallow entrance in the south. This entrance, which for the purpose of this study is represented by a transect running from the Chale Island to the lower parts of the Mkurumuji estuary, is rather shallow with depths ranging between 3.0 and 8.0 m in the eastern and western region respectively. There are also a number of narrow and shallow cuts through the coral reef ecosystem, which is submerged most of the time but emerges at spring low tide. There are two tidal creeks (Kidogoweni and Kinondo) draining the upper region which is dominated by mangrove vegetation. Kidogoweni and Kinondo creeks have lengths of 5.0 and 2.5 km respectively. Kidogoweni Creek receives freshwater from Kidogoweni River, but Kinondo lacks direct surface freshwater input, but there may be groundwater influx as salinity of water fluctuates significantly in wet season. Finally there is Mkurumuji River which has higher flow rates and discharges into the southwestern region of the bay. The drainage basin of Mkurumuji and Kidogoweni Rivers extends into the coastal ranges of Shimba hills with the drainage areas being 164 and 30 km² respectively. River discharge is important in wet seasons and reach up to 5.0 and 17.0 m³sec⁻¹ for the Kidogoweni and Mkurumuji Rivers respectively. The climatic seasons are the southeast monsoon which is responsible for the long-rains (April-June) and the north-east monsoon, which causes short-rains (November-December). Annual rainfall based on data from the Meteorological Department Nairobi, is between 1000 and 1500 mm. The rates of evaporation range between 1950 and 2200 mm per annum (Meteorological. Dept. 1964).

Sampling Stations

Data on the hydrography, water column nutrients and plankton productivity were obtained in the mangroves, seagrass beds and coral reef zones by applying different standard measurement techniques. Data were obtained at the coral reef zone at station 1 and seagrass bed zone at station 2 and at five stations in the mangrove zone (K1, K2, K3, K4 and 3) in the Kidogoweni creek and stations R1 and R2 in the Kinondo creek. There were also two additional stations (K1 and M1) in the lower reaches of Mkurumuji and Kidogoweni rivers for the measurements of freshwater influx and nutrients supply into the bay (Fig. 1).

Hydrographic measurements

Measured hydrographic parameters were salinity, temperature, current speed and sea-level variations. Measurements of salinity, temperature, and dissolved oxygen were at three levels in order to represent surface, middle and bottom water column. Water samples were obtained by using a Nansen bottle equipped with a closing mechanism. Salinity of water was determined in the field using a Atago hand-held refractometer and occasionally with a salinity-temperature sond. Temperature was measured using either a WTW LF/95 conductivity meter or a temperature-salinity sond. The dissolved oxygen (DO) in water samples was determined at the Kenya Marine and Fisheries Research Institute laboratories using the Winkler method. Tidal current velocities were also measured at three levels (surface, middle, bottom) using three C-31 Ott current meters and a direct reading CM-2 Dentan current meter. The current flow direction was based on visual observation of the direction of the vane of the current meters suspended in water. Tidal elevations during neap and spring tides were measured at an interval of 2-3 h using a tide-pole installed at station 3. The sampling frequency for the measurement of above water physical parameters was twice per month during neap and spring tide, in dry and wet seasons and in low and high waters.

Freshwater influx measurements

The freshwater influx into Gazi Bay from Kidogoweni and Mkurumuji Rivers was determined through river gauging operations at stations K1 and M1 respectively. The river discharge is computed using the following relation

$$Q_i = \sum a_i \cdot v_i \cdot \cos (\Theta \cdot \pi/180)$$

Where a_i is the cross sectional area (m²), v_i is the cross component velocity (ms⁻¹) and Θ is the deviation of the current velocity in relation to the flow direction (Linsley, 1988).

In the study of the influences of fresh water influx, it was also necessary to determine circulation and stratification parameters since these are the key indices of the influence of freshwater influx in coastal waters. The stratification and water circulation parameters (S_i and U_i) were calculated

using the method of Hansen and Rattray (1965, 1967). The stratification parameter (S_i) was computed as the difference between bottom (S_b) and surface salinity (S_s) divided by the depth-averaged salinity (S_d). This relation is presented in the following equation:

$$S_i = S_b - S_s / S_d$$

The circulation parameter (U_i) was calculated by dividing net surface velocity with the net depth-averaged velocity.

Water exchange

In the evaluation of the importance of water exchange in Gazi Bay, volume-conservation approach involving the determination of exchange fluxes as well as salinity changes, was applied. The volume conservation in semi-enclosed coastal waters is represented in the following equation (Rydberg, 1991., O'Kane, 1988).

$$V \cdot ds/dt = (Q_r \cdot S_r + Q_a \cdot S_a) - (Q_o \cdot S - Q_r \cdot S)$$

Where Q_r is the river freshwater supply ($\text{m}^3\text{sec}^{-1}$), Q_a is the exchange flux ($\text{m}^3\text{sec}^{-1}$), S_r is the salinity of river water (0 PSU), S_o is the salinity of ocean water (PSU), V is the volume of the bay (m^3), S is the salinity of the bay (PSU), ds/dt is the salinity change with time (PSUday^{-1}), Q_o is the ocean water influx ($\text{m}^3\text{sec}^{-1}$), S_o is the salinity of ocean water influx Q_o (PSU). The simplified version of the above equation is written as:

$$Q_a = (V \cdot ds/dt) + (Q_r \cdot S) / S_a - S$$

The oceanic water influx (Q_o) is equivalent to river influx (Q_r) and exchange flux (Q_a) [$Q_o = Q_r + Q_a$]. The residence time is then computed using the following relation V/Q_o where V is the volume of the bay (m^3) and Q_o is the oceanic water flux (Rydberg, 1991; O'Kane, 1988). Residence time is also calculated as L/U where L is the adjective length of the bay (m) and U is the mean current velocity (ms^{-1}).

Dissolved nutrient and particulate organic material (POM) analysis

The concentrations of dissolved inorganic nutrients (ammonium, nitrate + nitrite and orthophosphate) were determined according to the methods of Parsons et. al. (1984) and occasionally by the same methods but with minor modifications for use with a Technicon Autoanalyzer II system. Samples for particulate organic material (POM) determination were collected by filtering about 4 litres of water sample through a $0.45 \mu\text{m}$ millipore glass filters. These were transported to the laboratory where they were dried at 80°C for 2 days. The samples were stored until taken to the University of Brussels for carbon, nitrogen and $\delta^{13}\text{C}$ analysis.

The plankton

Plankton samples were collected from August 1993 to July 1995, and mainly aimed at covering both the dry and the rainy season. Three main sampling stations were demarcated representative of the Mangrove, Seagrass and Coral reef biotopes (Fig. 1). The samples for phytoplankton standing stock (chlorophyll a) were collected from the three biotopes at about high tide. Water samples were collected at one or two hour intervals for half and full tidal cycles using a Nansen bottle. The samples were then fixed with magnesium carbonate suspension and filtered using a hand pump on glass fibre filter (Whatman GF/F). A few samples were pre-filtered using a $20 \mu\text{m}$ net to determine the nanoplankton fraction. Samples were transported to the laboratory in ice and kept frozen until analysis was carried out.

Chlorophyll-a was determined using the method of Parsons et al. (1984). The pigment was extracted from the filter papers using 12ml of 90% acetone for 20 hrs and determined using the absorption spectrophotometer at wavelengths of 630, 647, 664, and 750 nm. Primary production was determined by using light and dark bottles incubated for 6 hours in different biotopes. The incubation of the chlorophyll-a samples was carried out either between sunrise and mid-day or between mid-day and sunset in order to take into account the changing daylight conditions. Phytoplankton primary production was determined using the oxygen method.

The results for phytoplankton biomass and production were computed by averaging individual

observations for each biotope between August 1993–July 1995 into monthly means. The monthly means were then used to compute seasonal means by averaging April–July; Nov/Dec as the wet months, and Jan–March; Aug–Oct as the dry months.

Near surface zooplankton samples were collected from a rubber dingy by towing a 332 μm mesh size plankton net for five minutes in stations 1, 2 and 3 (Fig. 1). Sampling was carried out once a month in both neap and spring tides. The collected samples were fixed with 5% formaldehyde. Biomass was estimated using displacement volume method. Samples were sorted under a Wild Stereo Microscope and major taxa recorded. The taxonomic identification of the zooplankton was attempted upto species level (Smith, 1977., Todd et al. 1991).

RESULTS

The hydrographic features

Astronomical tide is the main forcing function driving water circulation in Gazi Bay. The tide generates strong reversing current in the deep and narrow tidal channels in the mangrove zone but not in the seagrass and coral reef. The bay experiences semi-diurnal tides (Kruyt and van den Berg 1993) with a spring tide range of 3.2 m and neap tide range of 1.4 m. The strength and magnitude of tidal currents vary depending on the cross-sectional area of the channel, depth and tidal regime. The current speed is 90° out of phase with tidal elevations and is approximately 50 % higher during spring tide as compared to neap tide. On most occasions, the peak ebb and flood currents were symmetrical particularly in open waters (seagrass and coral reef zone) implying that their durations and magnitudes are equal (Table 1 and 2). In the mangrove creeks, tidal asymmetry was more clearly defined with ebb currents slightly stronger than flood currents (Figs. 2, 3 and 4). The peak current speed in the mangrove creeks reach 0.60 ms^{-1} and duration of flood and ebb currents differs by up to one hour (Table 1). The tidal asymmetry in the mangroves is partly attributed to the flow retarding effects of the dense mangrove vegetation during spring high tide when flood waters inundate most parts of the mangrove forest. Tidal asymmetry contributes toward the maintenance of deep narrow tidal creeks through tidal flushing (Wolanski, 1980). Currents were lower in the wide and shallow open region of the bay covered with seagrass and coral reef ($<0.25 \text{ ms}^{-1}$). The tidal asymmetry in the mangrove zone also promotes the net-downstream longitudinal current which is responsible for carrying away of organic detritus to the seagrass zones in the open region of the Gazi Bay. This may also enhance the export of nutrients from the mangrove zone to the seagrass beds (Wolanski et al. 1980; Pylee et al. 1990; Van de Kreek, 1976).

Results shown in Fig. 5 demonstrate that variations in the level of salinity are a result of the evaporation, freshwater and oceanic water influx. At low tide, oceanic water is flushed out of the bay during ebb period, paving the way for brackish water from Kidogoweni River in rainy season to occupy the mangrove creek. This leads to lowering of salinity. As the oceanic water starts getting into the bay during flood tide, salinity starts to rise (from 28 PSU to 34 PSU in Fig. 5) reaching its peak at highwater when most parts of the bay are covered with oceanic water. The brackish water at this time is pushed back into the mangroves (Figs. 5 and 6). This pattern is repeated in several tidal cycles until brackish water is totally mixed with oceanic water. The complete mixing of the different water masses happens mostly in dry seasons when freshwater influx becomes negligible as a result of decline in rainfall in the Kidogoweni and Mkurumuji River basins (Fig. 7). Rainfall was experienced in the months of December 1993 and June–July 1994. The months of August, October 1993 and March, August and November 1994 were relatively dry. Salinity at station 3 over August to October 1993 remained fairly constant at 35 PSU. During the short rains in December, salinity dropped upto 15 PSU in the esuaries and in the mangrove zone, as a result of river water influx. During the long rains in June 1994, salinity fell further to about 2 PSU at station K 2 in the Kidogoweni mangrove creek. This is attributed to influx of fresh water from the seasonal river R. Kidogoweni. In stations 1 and 2 (Coral and Seagrass), salinity fell to about 33 and 31 PSU respectively. The diurnal variations of temperature based on measurements at station 3 shows that the main temperature control is the intensity of solar radiation heating effect. However, there are also temperature variations related to tidal dynamics (Fig.5). The highest temperature is reached during the day when cloud cover is low and solar heating effect is at its maximum. However, since the oceanic water is cooler ($27.0\text{--}27.5^\circ\text{C}$) than mangrove water, the influx of oceanic water into the bay often leads to slight lowering of water temperature (from 28.5°C to 27.0°C). Spatial observation on temperature distribution shows that, water temperature changes can be as large as 2.5°C . Highest temperature was 31.5°C during the month of December 1993, and the

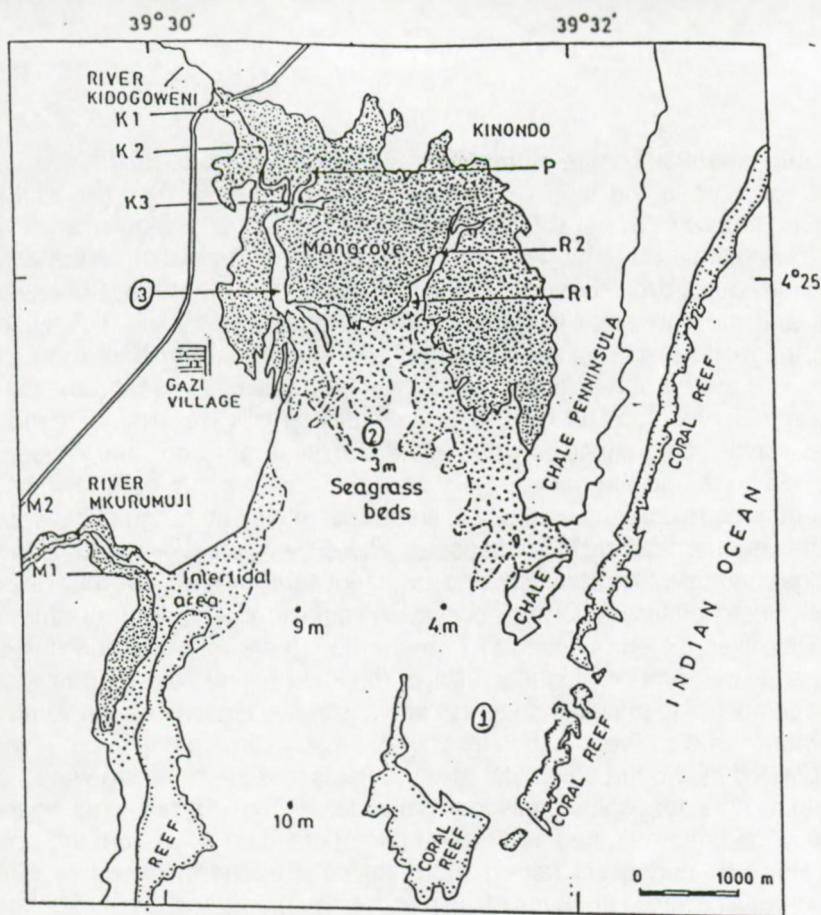


Fig. 1. Gazi bay with sampling stations.

Table 1. The magnitude and duration of tidal currents in Gazi bay. Highest current velocity recorded at station R1 in Kinondo creek during the spring tide (0.62 ms^{-1}). Kidogoweni creek has maximum current velocity of 0.60 ms^{-1} during the spring tide. Current velocities for seagrass and coral zones are less than 0.25 ms^{-1} . Longshore current has peak velocity of 0.34 ms^{-1} . Within the Mangrove swamp, current velocities are less than 0.10 ms^{-1} .

Date	Tidal phase	Current (ms^{-1})	Duration (h)
23-24 Sep 93*	Flooding	0.19-0.12	8
	Ebbing	0.22-0.10	7
3-4 Nov 93*	Flooding	0.27-0.22	7
	Ebbing	0.20-0.10	5
17 Dec 93+	Flooding	0.55	6
	Ebbing	0.60-0.45	7.5
13 Jan 94+	Flooding	0.50-0.45	6
	Ebbing	0.50-0.45	6

* Measurements during southeast monsoon. + Measurements during northeast monsoon.

lowest was 25.5°C recorded in August 1993. Temperatures were slightly lower (25.5- 30.7°C) at the coral station (near the bay entrance) while the inner mangrove stations were warmer (27-31°C). Temperature variations by day tend to follow diurnal solar radiation patterns. In the shallow mangrove zone, temperature variations shows diurnal patterns while in the open ocean, semi-diurnal patterns which are as a result of the tidal influences are observed. There are also spatial differences between the mangroves, seagrass beds and the coral reef in terms of temperature distribution. The water temperature difference between the mangroves and seagrass bed zone was in the order of 0.6°C. It reached 2.0°C for the mangrove and the coral reef zones. Water temperature of the seagrass zone differs from that in the coral reef zone by as much as 1.5°C, but these differences are minimal in most periods of the year. Although these spatial differences between mangrove, seagrass beds and the coral reef appear to be small, they are important in the net export of heat energy from the inshore waters to offshore waters. The vertical temperature differences are also small occurring in the range of between 0.5 to 1.5°C in most periods of the year, particularly in dry seasons. The dissolved oxygen in Gazi Bay vary diurnally in response to algal photosynthetic activity and turbulent tidal mixing. The dissolved oxygen which is an important physico-chemical factor for ecosystem sustainability, is in the range of between 3.0 and 6.0 mg O₂ l⁻¹. Dissolved oxygen is seen to increase during the rainy season due to greater mixing of the fresh and sea water. The coral station always recorded higher dissolved oxygen readings (mean value: 5.68 mg/l) compared to the inner seagrass and mangrove stations (mean values: 5.28 and 3.76 mg/l). The maintenance of dissolved oxygen level of 3.0 mgO₂l⁻¹ in the bay even, in the absence of sunlight, is partly facilitated by the turbulent tidal mixing effects and the breaking waves in the coral reef zone which tends to mix the atmospheric oxygen with water (Fig. 5). Turbidity during the dry seasons was low and normally the bottom of the bay (3 to 4 meters) could be seen from the boat especially in stations 1 and 2. However during the rainy period, station 3 is characterised by high turbidity (secchi depth <0.5m) as a result of large amounts of suspended sediments and organic detrital matter brought in by Kidogoweni River.

Table 2. Water circulation and stratification parameters for various stations in Gazi Bay. U_r represents circulation parameter and S_r represents stratification parameter. Stations K2, K3, K4 and 3 are in the Kidogoweni tidal creek while stations R1 and R2 are in Kinondo mangrove tidal creek. Stations 1 and 2 are in coral reef and seagrass zones respectively.

Date	U _r			S _r	
	Max	Min	station	Max	station
18 Aug 93	1.08	0.66	R1	0.068	R1
24 Aug 93	1.15	0.82	K2	0.045	2
10 Sep 93	1.33	0.97	2	0.033	2
23 Sep 93*	1.40	0.90	3	0.028	3
23 Sep 93+	1.75	0.92	3	0.028	2
4 Nov 93	1.32	0.80	3	0.015	3
12 Nov 93	1.11	1.00	K3	-	-
9 Dec 93	1.00	0.80	K2	-	-
28 Apr 94	1.23	0.01	3	0.125	K2
13 May 94	-	-	-	1.000	K2
28 Aug 94	1.24	0.00	2	0.020	2
30 Aug 94	1.00	1.00	R2	0.014	R2
31 Aug 94+	-	-	-	0.330	K4
31 Aug 94*	-	-	-	1.310	K2

* ebb tide measurements. + flood tide measurements.

Table 3. Water exchange and tidal ranges in Gazi Bay, Kenya. The computations on water exchange was based on modified tidal prism method.

Type	HIGH WATERS		LOW WATERS		MEAN WATERS
	Mean spring	Mean neap	Mean sea-level	Mean neap	mean sea level
Sea-level	3.3	2.4	0.5	1.0	1.8
Volume (m ³)	49.5x10 ⁶	36.0x10 ⁶	7.5x10 ⁶	15.5x10 ⁶	27.0x10 ⁶
Tidal prism (m ³)	42.0x10 ⁶	21.0x10 ⁶			
Exchange	85.0 %	58.0 %			

Freshwater influx and salinity gradient

Figs. 4, 6 and 10 are presentations of spatial salinity distribution in the mangroves, seagrass beds and the coral reef zones. The low salinity, brackish water is found during rainy seasons in the Kidogoweni Creek and in the southwestern region of Gazi Bay (Fig. 6). As a result of freshwater influx, a negative horizontal salinity gradient of 2.0 PSU km⁻¹ in Kinondo Creek and 5.0 PSU km⁻¹ in the Kidogoweni Creek was measured in wet season. The dry season lateral salinity gradient in both creeks is often less than 1.0 PSU Km⁻¹. While wet season salinity fluctuations are mainly as a result of freshwater influx from the rivers and surface runoff including also direct rainfall, dry season variations are mainly as a result of high evapotranspiration rates which often reach 7.0 mm day⁻¹ in the southern coastal region of Kenya (see also studies by Wolanski 1980). In order to establish whether the freshwater influx in the bay causes any measurable buoyancy effects, water stratification and circulation parameters (S_i and U_i) were calculated using procedures of Pylee et al (1990) and Hansen and Rattray (1965 and 1967). The results of calculation of these parameters shows that, water circulation parameter (U_i) is less than 1.75 while the stratification parameter (S_i) is often less than 1.3. The maximum S_i and U_i values were both 1.31. These results indicates existence of measurable buoyancy effects in the Kidogoweni creek in the mangrove zone in wet season when the freshwater influx through Kidogoweni River is greater than 3.0 m³sec⁻¹ (Fig. 4 and 6). In both dry and wet seasons, the U_i and S_i values for seagrass and coral reef zones were found to be often less than 0.01, implying there is no stratification and the bay waters and dissolved inorganic nutrients are well-mixed and homogeneous.

Nutrients distribution

Rates of discharged nutrients from rivers Mkurumuji and Kidogoweni were calculated from the observed concentration levels and discharged volumes. The mean daily river freshwater supply from Mkurumuji River is in the order of 4.13 ± 3.38 ($\times 10^5$) m³day⁻¹ in the rainy seasons. The freshwater influx from Mkurumuji River, with the maximum rates reaching 17.0 m³sec⁻¹ was associated with nutrient discharge rates of 12.21 ± 9.98 kg N day⁻¹ as NH₄⁺, 37.45 ± 30.59 kg N day⁻¹ as NO₃⁻ + NO₂⁻, and 31.66 ± 25.86 kg P day⁻¹ as PO₄³⁻. During the dry seasons, the river had a mean discharge rate of 3.67 ± 2.23 ($\times 10^4$) m³day⁻¹. This resulted in corresponding nutrient discharge rates of 0.28 ± 0.17 kg N day⁻¹ as NH₄⁺, 0.27 ± 0.16 kg N day⁻¹ as NO₃⁻ + NO₂⁻, and 0.93 ± 0.57 kg P day⁻¹ as PO₄³⁻.

Similarly, Kidogoweni River with a mean discharge rate of $2.02 \times 10^5 \pm 1.76 \times 10^5$ m³/day⁻¹ during the wet months of the study period, had estimated nutrient discharge rates of 5.37 ± 4.69 kg N day⁻¹ in form of NH₄⁺, 9.83 ± 8.59 kg N day⁻¹ as NO₃⁻ + NO₂⁻, and 9.00 ± 7.87 kg P day⁻¹ as PO₄³⁻. During the dry periods, the river had a mean discharge rate $1.56 \times 10^3 \pm 1.05 \times 10^3$ m³day⁻¹, which corresponded to nutrient discharge rates of 0.013 ± 0.009 kg N day⁻¹ as NH₄⁺, 0.0057 ± 0.0038 kg N day⁻¹ as NO₃⁻ + NO₂⁻, and 0.035 ± 0.023 kg P day⁻¹ as PO₄³⁻.

Time series observations conducted at the mangrove zone (st. 3, Fig. 1) to ascertain the extent to which riverine nutrient loads from Kidogoweni river influence the nutrient distribution in the bay revealed that in wet periods, nutrient levels were generally higher during low tide and decreased with flood tide to almost oceanic levels at high tide. Fig. 8 shows a nutrient profile (mean values - excluding SD for clarity) for nine 24hrs time series experiments conducted at st.3 during rainy season (May/June) of 1992 to 1994. At high tide (t=0, 12 and 24h) all the nutrient concentrations were found to be below 0.3μM but increased steadily to slightly higher values at low tide. Though the low tide average nutrient peaks for NH₄⁺, NO₃⁻ and PO₄³⁻ were found to be averagily 1.37 ± 0.56 ; 0.87 ± 0.31 and 1.19 ± 0.47 μM

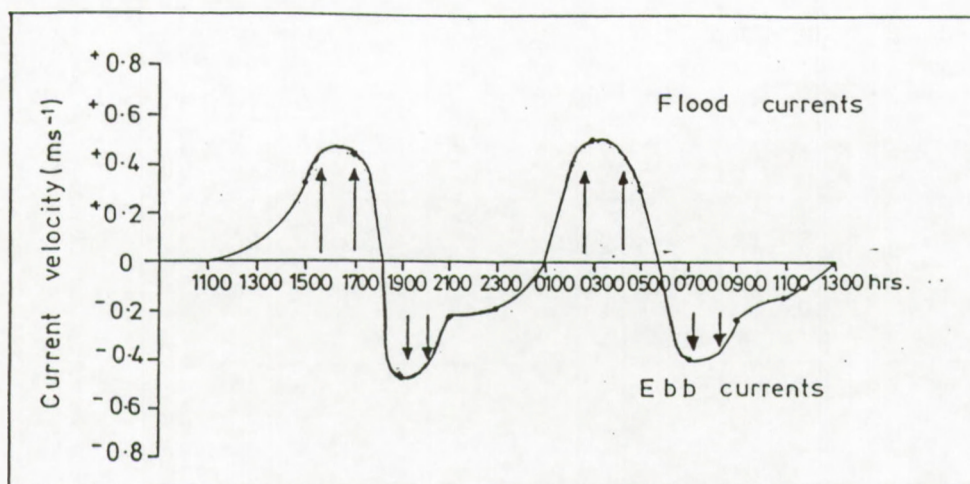


Fig. 2. Current patterns during flood and ebb periods at Kidogweni creek (Gazi bay) between 13 and 14 January 1994. Measurements were made during the post north east monsoon season at station 3.

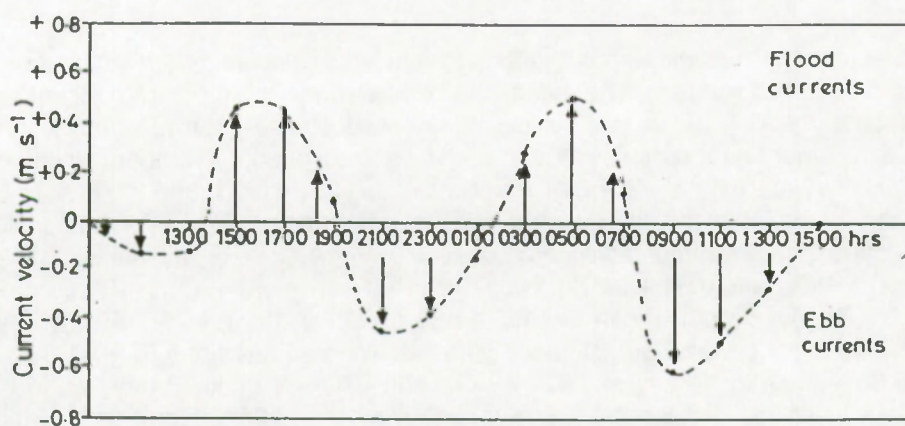


Fig. 3. Current patterns during flood and ebb periods at Kidogweni Creek in Gazi bay, Kenya. Measurements were made during the north east monsoon season 17 December 1993 at station 3.

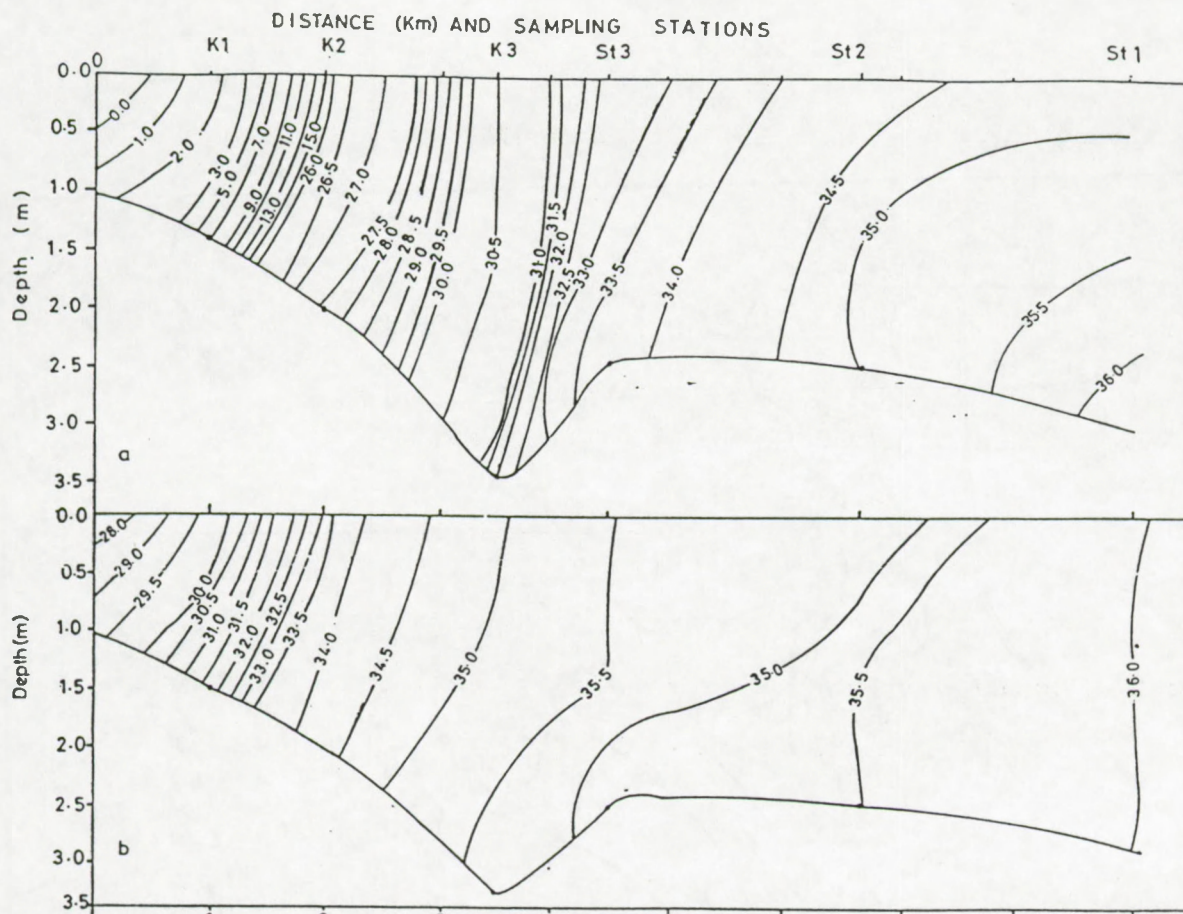


Fig. 4. Longitudinal distribution of salinity on 27-28 April 1994. a. Flood period b. Ebb period. Contours in ‰.

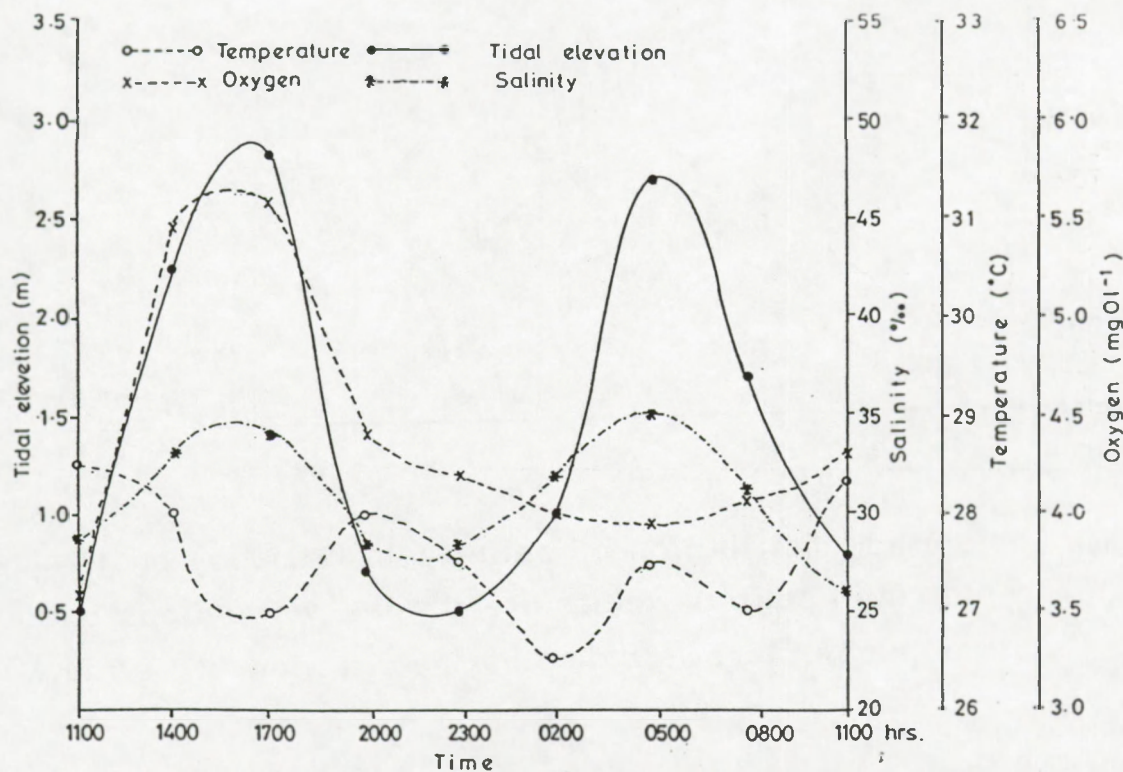


Fig. 5. Diurnal variability in physical hydrologic parameters in Gazi Bay during the South-East Monsoon Season. Measurements for station 3 at Kidogweni Creek.

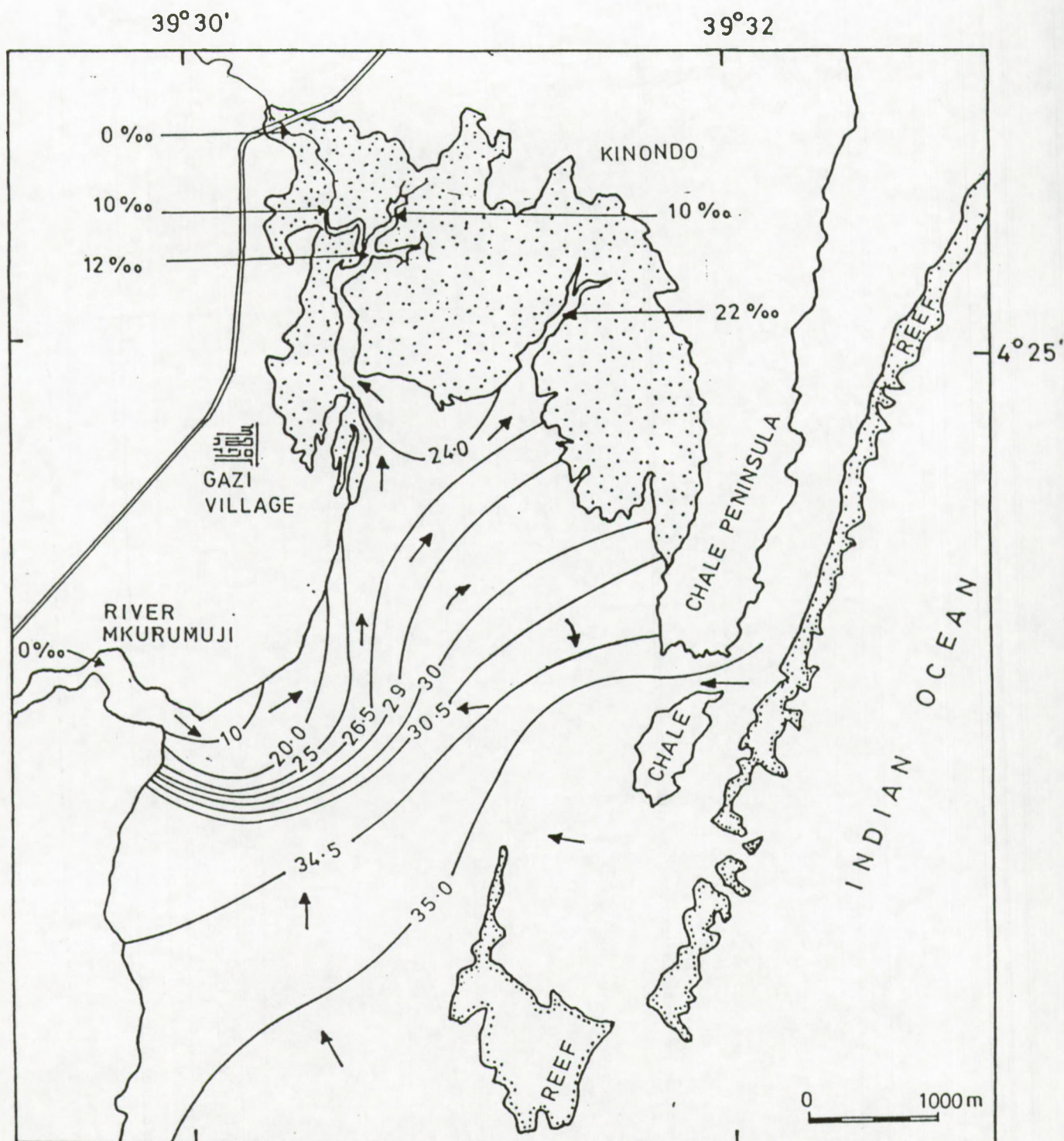


Fig. 6. The spatial distribution of salinity in Gazi bay on 13 may 1994. The indicated salinity values are for the wet periods of south east monsoon. Arrows indicates the direction of flow of water.

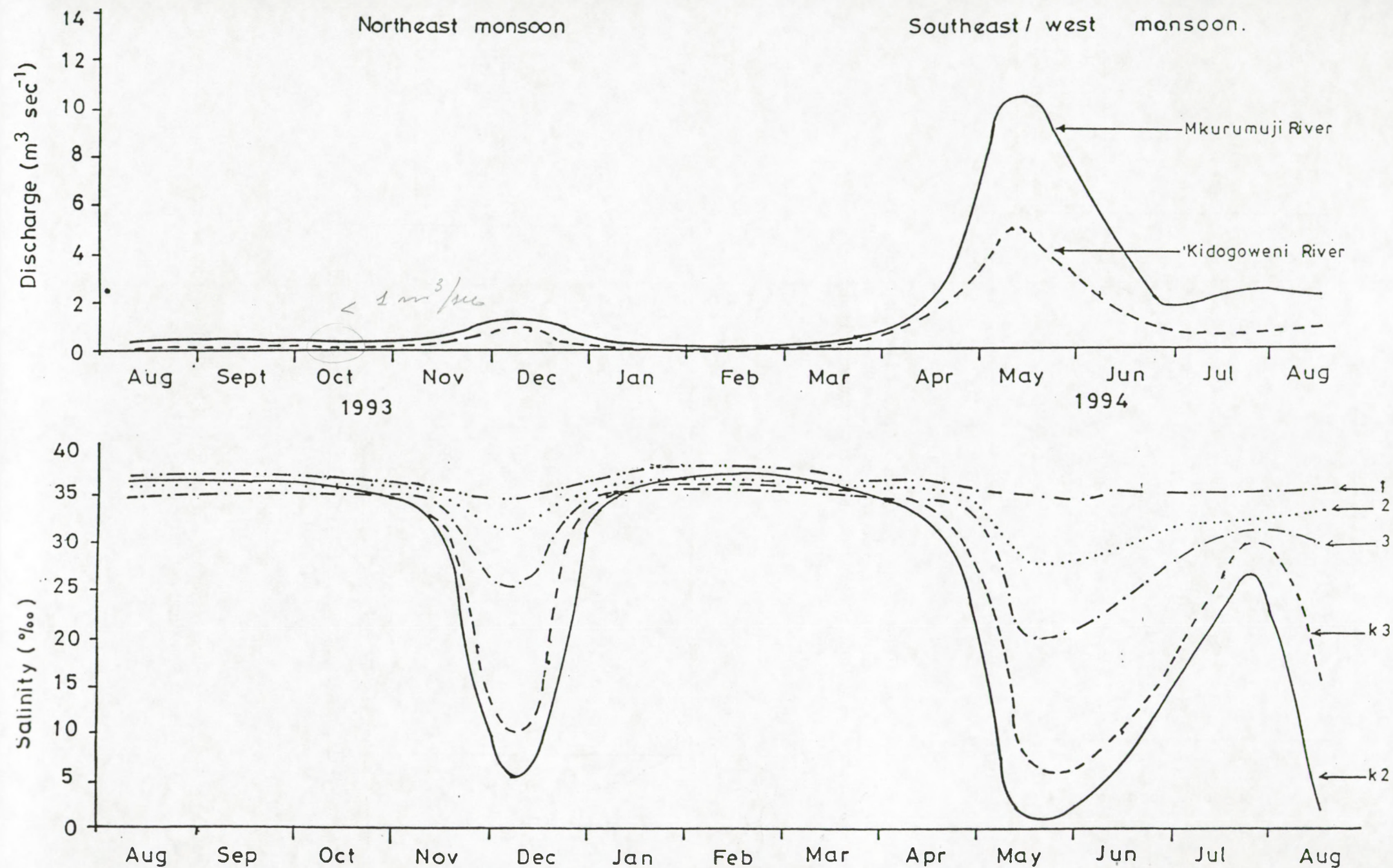


Fig. 7. The influence of river discharge on seasonal salinity variations in Gazi Bay, Kenya.

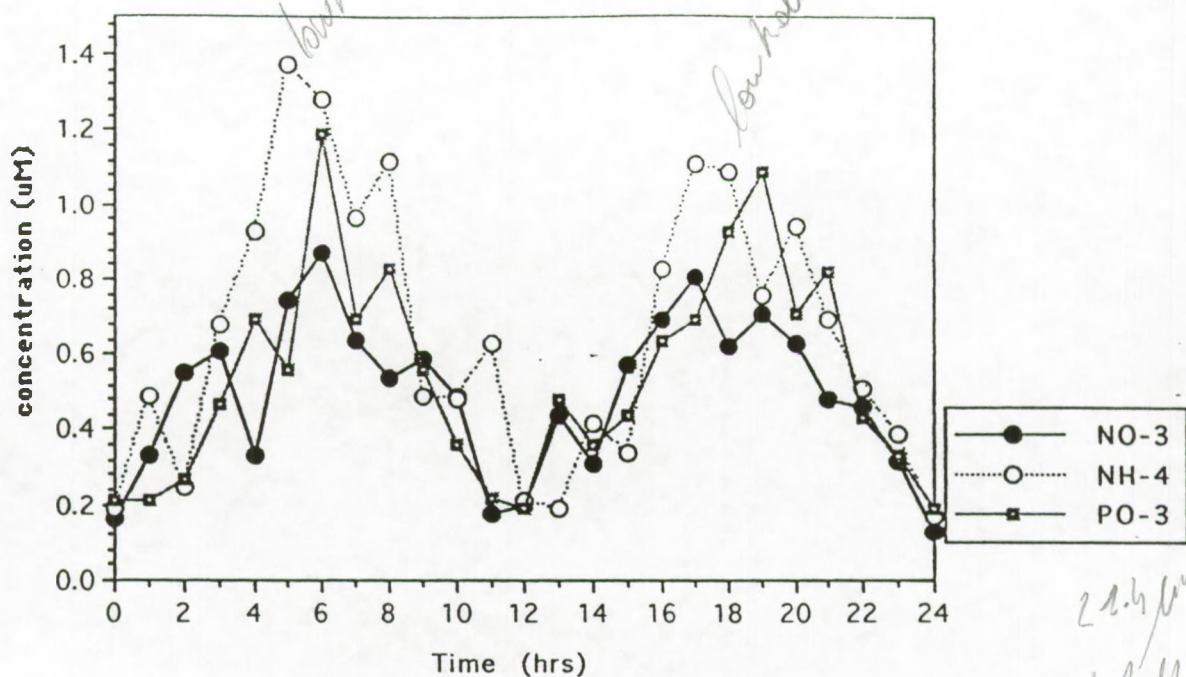


Fig. 8; Time series observation of Dissolved Inorganic Nutrients (DIN) at st.3 during rainy season of (May/June) 1992/3/4. Mean value of nine observations shown without S.D. for clarity. Low tide; $t=6$ & 18

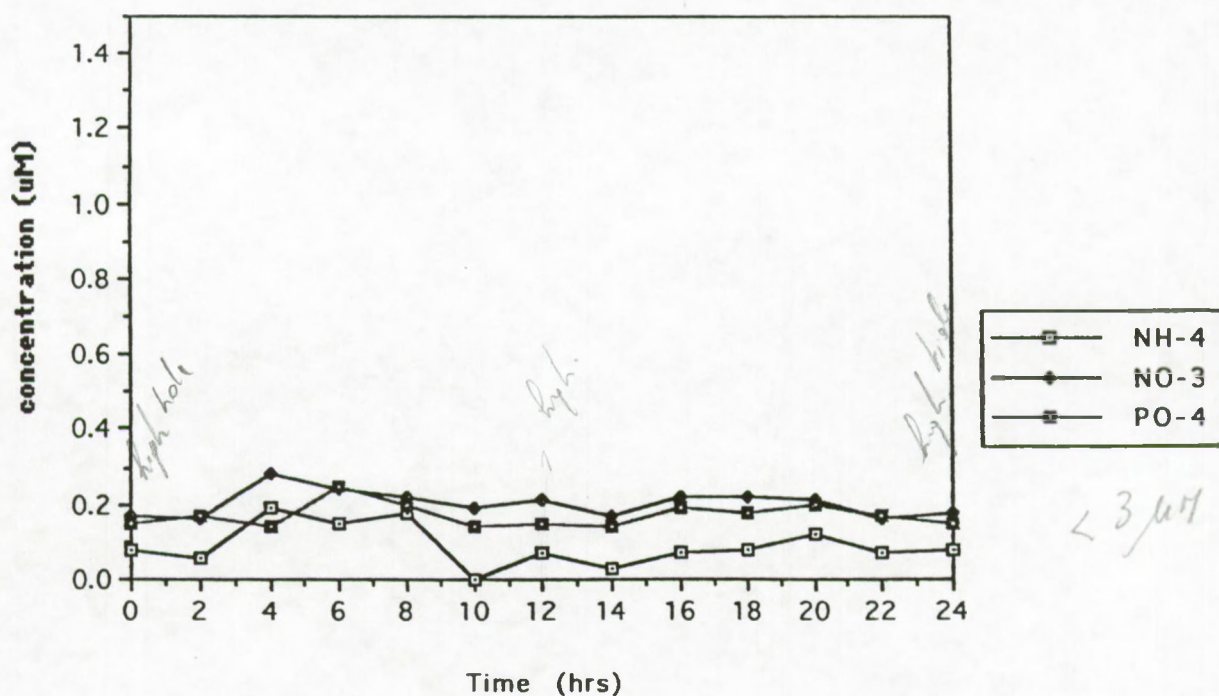


Fig. 9; Time series (hrs) observation of DIN at st.3 in Feb. 1994 (dry period). High tide at 0, 12 and 24hrs. $t=0$ was at 4 pm during spring high tide.

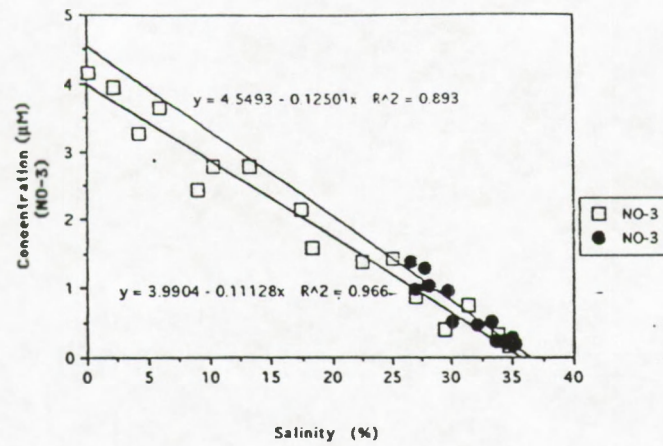


Fig. 10 A

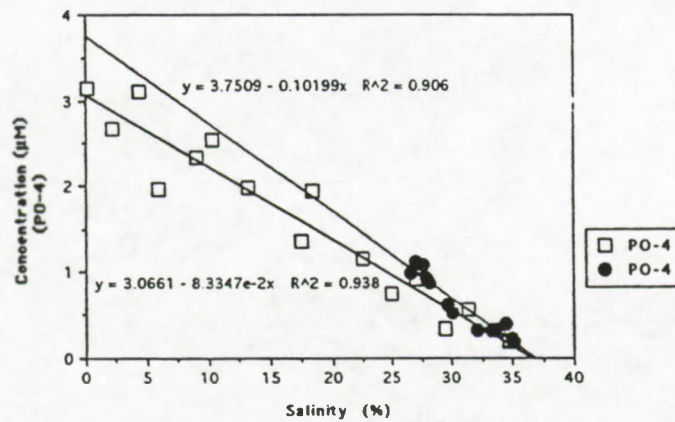


Fig. 10 B

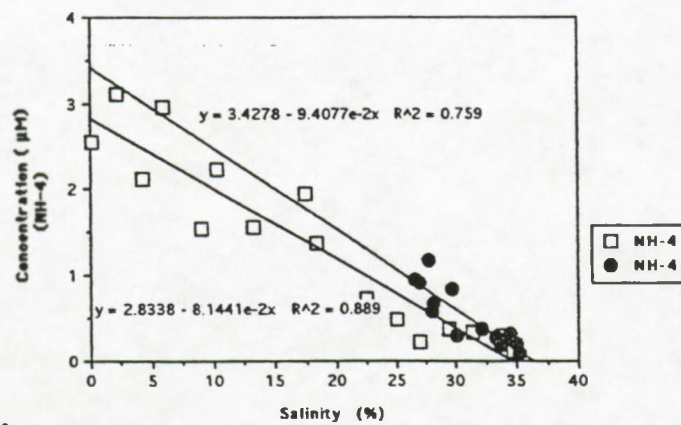


Fig. 10 C

Figs. 10 A, B, C; Nutrients profiles Vs. salinity for 17 stations between St. K1 and st. 3 with 12 hrs time series values at st. 3 superimposed. May 1993.

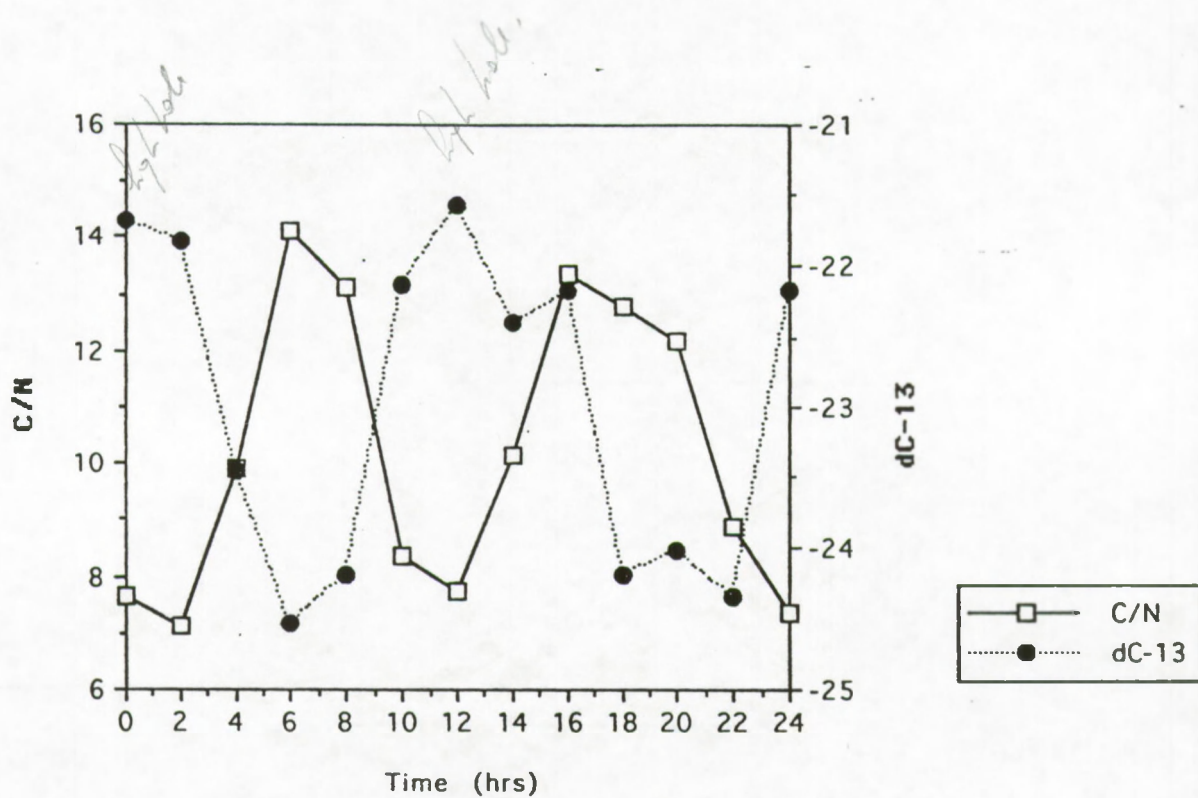


Fig. 11; A time series plot of C/N atom ratio and dC-13 values of POM at st. 3 in May 1993. $t = 0, 12$ and 24 hrs corresponds with spring high tide and $t = 0$ was at 5pm.

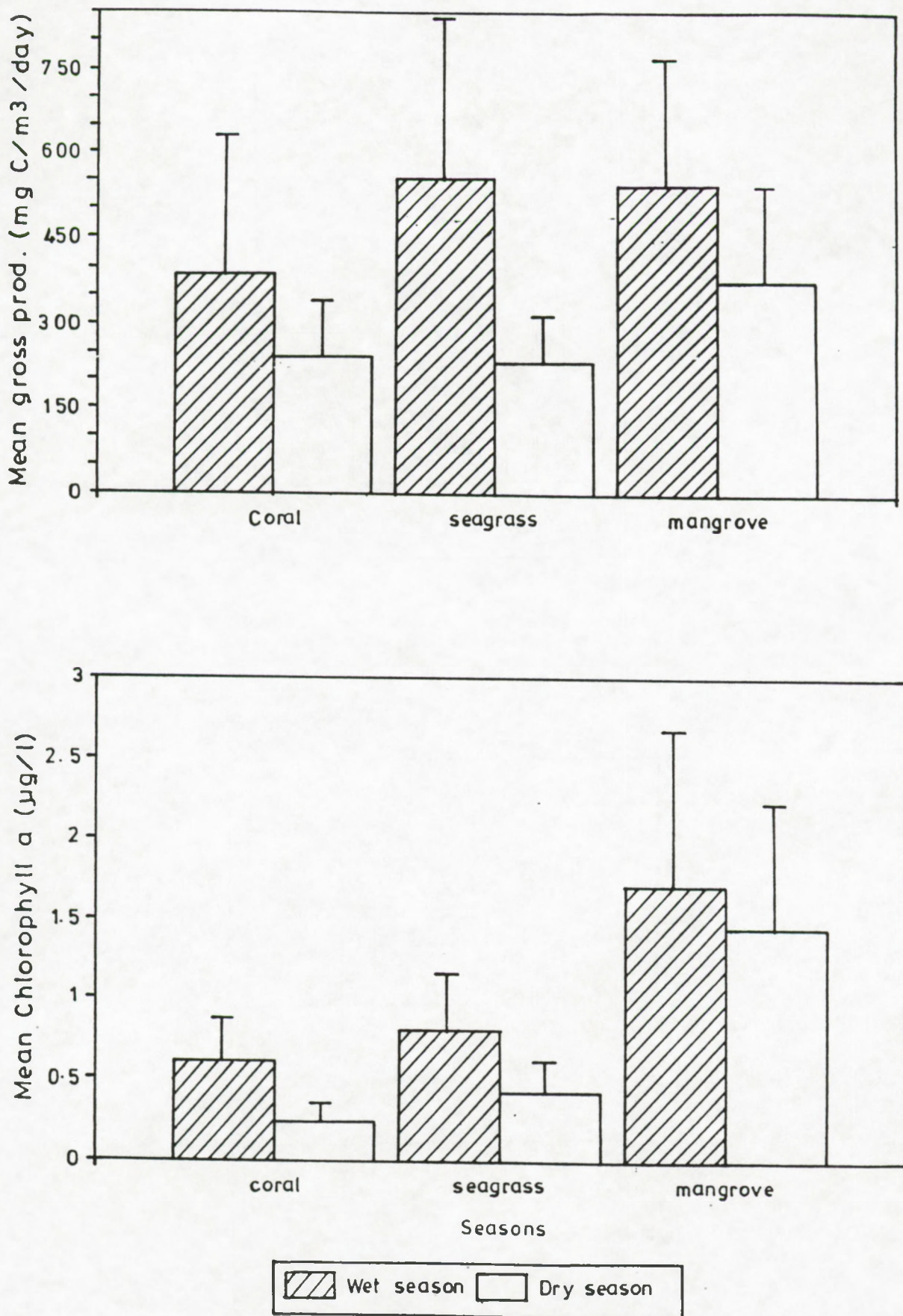


Fig.12 Spatial and seasonal phytoplankton production and standing stock of Gazi bay.

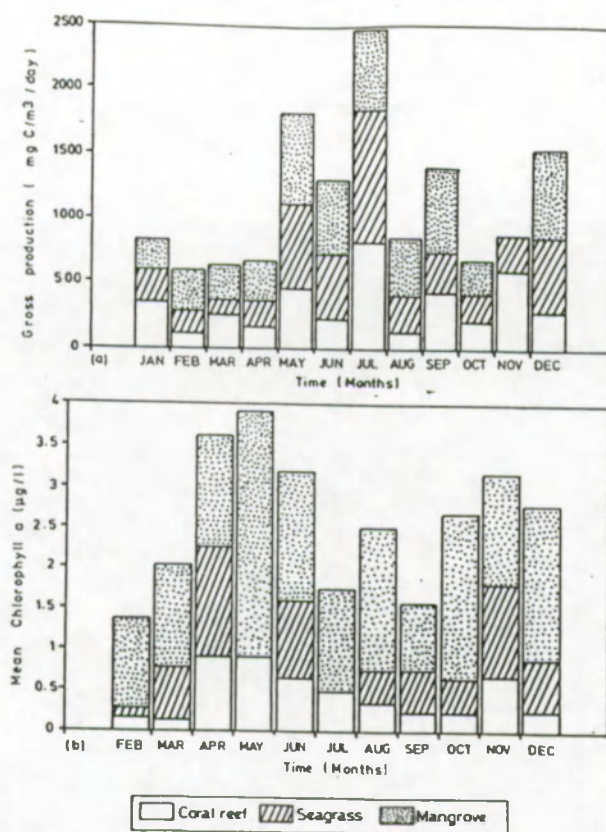


Fig. 13 The seasonal phytoplankton productivity (a) and biomass (b) in the mangroves, seagrass beds and coral reef ecosystems.

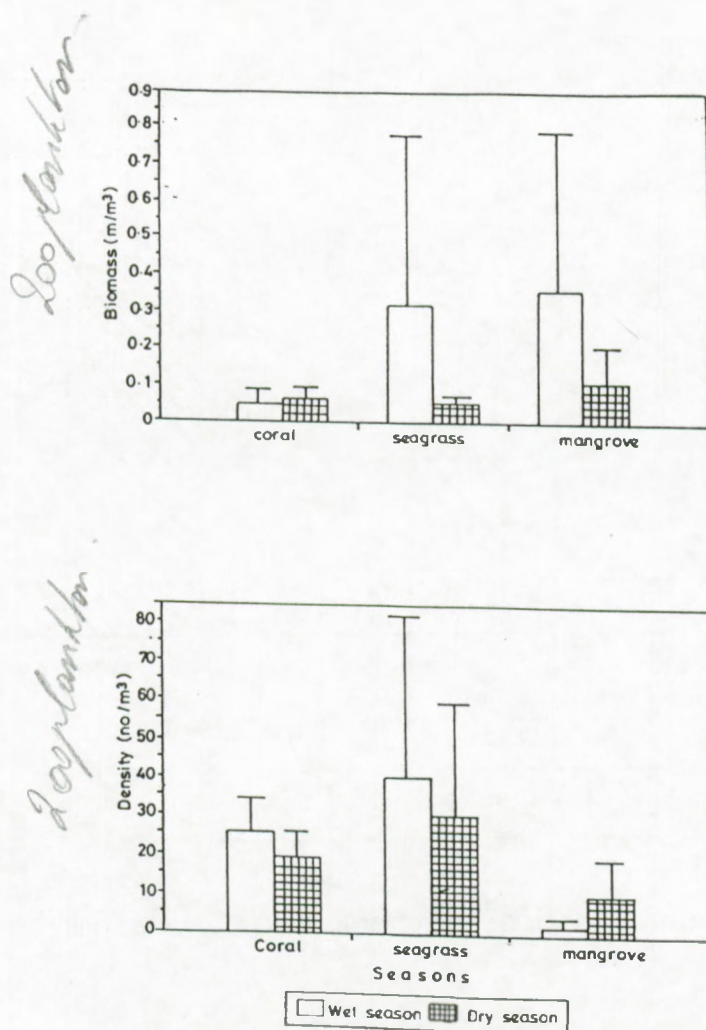


Fig. 14 Seasonal zooplankton biomass and density in Gazi bay during wet and dry seasons in the mangroves, seagrass beds and the coral reef zones.

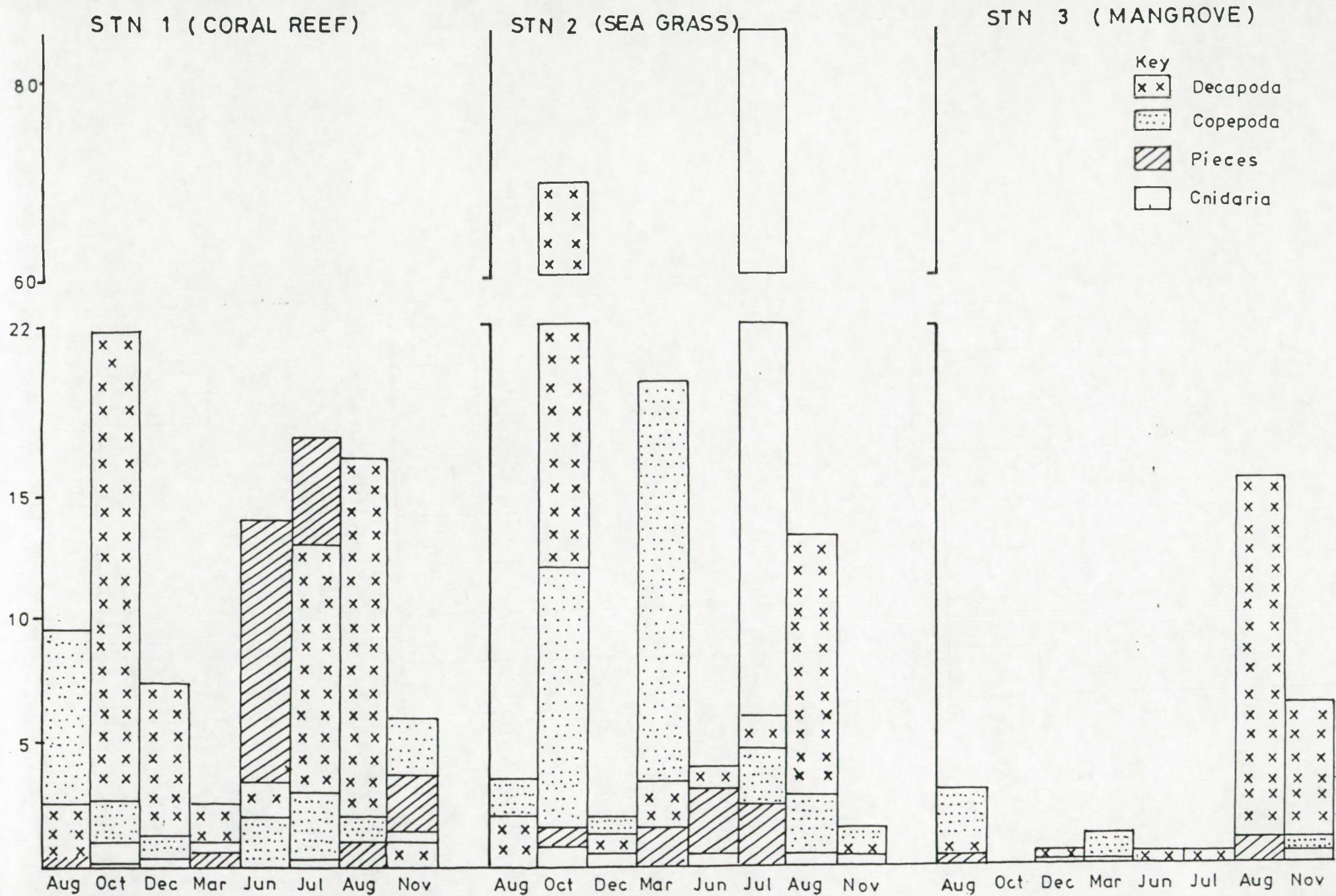


Fig15 Distribution of four most abundant groups of zooplankton along three biotopes Gazi bay.
Aug. 1993 - Nov. 1994.

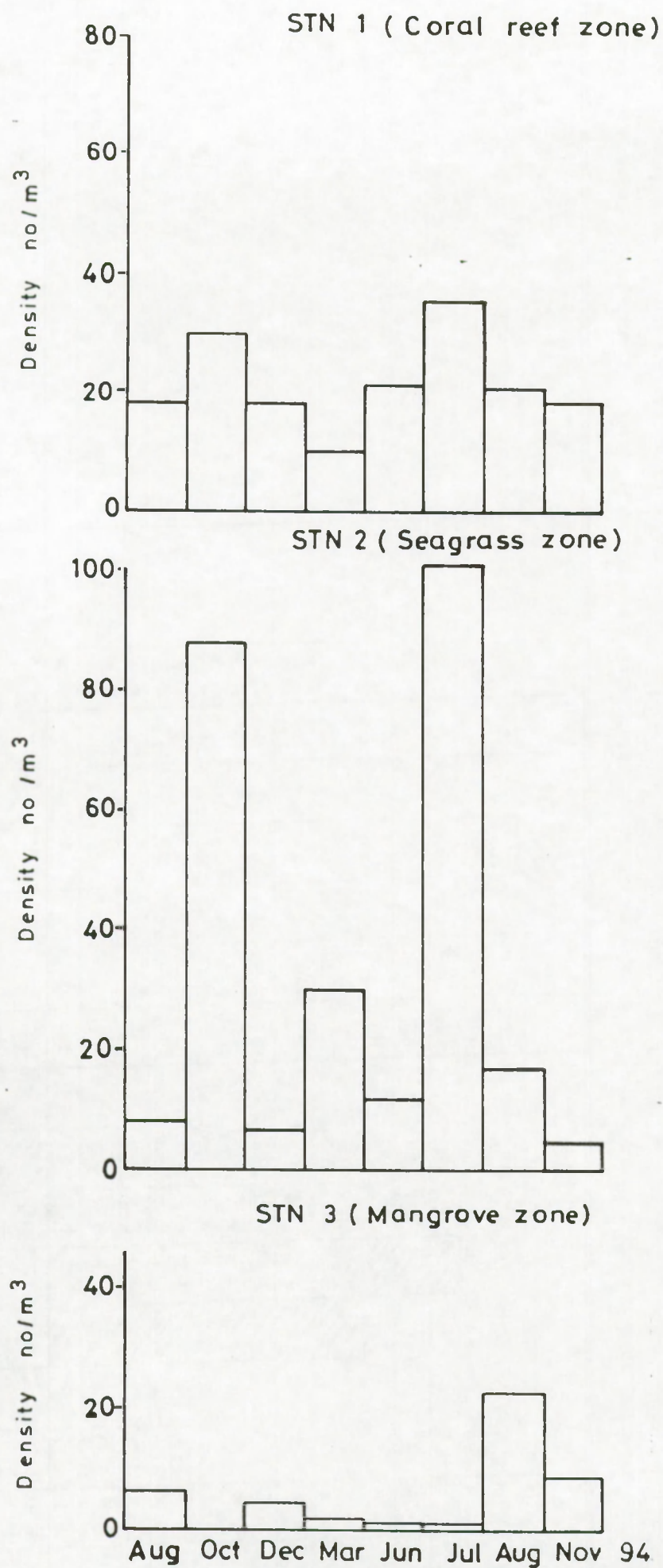


Fig:16 Zooplankton density in three biotopes, Aug 93 -Nov 94, Gazi bay .

Table 4. Zooplankton taxa collected in Gazi creek, August 1993-
November 1994

Taxa	Aug	Oct	Dec	Mar	Jun	Jul	Aug	Nov
1. Cnidaria	X	X	X	X	X	XXX	X	XX
Hydromedusae				X				XXX
Siphonophora								
2. Annelida								
Polychaete larvae	X		X	X	X		X	X
Polychaete adult	X	X		X	X	X	X	
3. Branchiopoda								
Cladoceran								
4. Ostracoda								
Ostracods	X		X	X	X			
5. Copepoda								
Calanoida	XXX	XXX	XXX	XXX	XX	XX	X	XXX
Cyclopoida	XX	X	X	XX	X	X		XX
Harpacticoida	X	X	X	X				
Monstrilloida	X		X	X			X	
6. Cirripedia								
Cirripede nauplii	X							
7. Mysidacea								
Mysiids	X	XX			XX	X		X
8. Cumacea								
Cumacean (diastylis)				X				
9. Isopoda								
Isopoda sp.		X	X	X			X	
Cryptoncid larvae				X				
Paragnathia larvae		X						
Sphaeroma sp.				X		X		
10. Penaidae								
Lucifer adults	X	X				X	X	X
11. Decapod larvae								
Brachyuran zoea	XXX	XXX	XXX	XX	XX	XXX	XXX	XX
Brachyuran mega.	X	X	X	X	X	X	X	X
Caridean larvae	XXX	X	XX	XX	XXX	XXX	XXX	X
12. Mollusca								
Bivalve veligers			X		X	X	X	X
Pteropoda		X	X	X	X			X
Gastropod veligers	X	X	XXX	XX	X	X	X	X

Heteropods		X	X	X	X		X	X
Cephalopod larvae	X	X	X		X		X	X
13. Lophophorates								
Bryozoan (cyph. larvae)			X		X			
14. Stomatopoda								
Stomatopoda larvae	X			X	X	X	X	X
Alima		X	X					
15. Chaetognatha								
Sagitta sp.	X	X	X	X	X		X	X
16. Salpida								
Thalia sp.	X							X
17. Pieces								
Fish eggs	X	X	X	X	XXX	XXX	X	X
Fish larvae	X	X	X	X	X	X	X	X
18. Appendicularia								
Oikopleura				X				XX
Flitillaria	X			X				XX
19. Protozoan								
Foraminifera	X	XX	XX	XX	X	X	X	
20. Water mite					X			X
21. Insecta								
Halobates	X			X	X		X	X
22. Tunicates								
Ascidacea larvae	X	X	X					
23. Euphausiacea								
Euphausiids	X	X						X
24. Nematoda			X		X	X		X
25. Amphipoda								
Gammaridea	X	X	X	X	X	X	X	X
Caprellia amphipod					X	X		

25 taxa identified: xxx = Abundant
 xx = Common
 x = Rare

respectively, the actual levels depended very much on the sampling day within the season. Kidogoweni being a seasonal river, discharged volumes on any particular day depended on the rainfall pattern within the season.

Time series nutrient profile (7 obs.) for the same station during dry period (Feb/Mar) of 1992 to 1994 indicated low nutrient levels with no significant variations within the tidal cycle. Fig.9 gives as an example, one of the profiles obtained during dry season (Feb. 1994). Nutrient values are all found to lie below $0.3\mu\text{M}$ throughout the tidal cycle.

A plot of nutrients against salinity between st. 3 and K1 (a total of 17 stations, about 100m apart) during spring high tide (figs. 10 A, B, & C) indicates conservative mixing for all the elements during rainy season. When time series values taken at station G3 over the same tidal cycle (12 hour low tide-high tide-low tide cycle) are superimposed, they are again found to lie within the same regression line boundary. However, they are all found to have a slightly bigger slope indicating a possibility of more nutrients being washed into the bay from the mangrove forest during ebb flow. During the rainy season, the nutrient supply by Kidogoweni river may act as a background leaving any additional input from the mangrove vegetation to be unnoticed. The conservative mixing noticed within Kidogoweni creek and the slightly higher slope seen for the time series plot may actually support Boto's (Boto, 1982) suggestion that outgoing ebb flow could leach nutrients from mangrove swamp soils. During the dry period, this supplied nutrients from the mangroves may be immediately taken up for primary production (since in dry season there is no significant riverine input and the water is less turbid) hence may not be easily noticed.

Investigation of particulate organic matter flow from mangrove zone into the open sea was also undertaken. Fig. 11 shows time-series profiles of carbon-13 stable isotope ($\delta^{13}\text{C}$) associated with particulate organic material as it passes through station 3. Isotope analyses were carried out at the Free University, Brussels. Corresponding C/N values are also displayed. Though this is a specific example of a 24hr sampling done in May 1993, all other results (including results for dry season) display the same trends. At high tide, POM with relatively low C/N values (7-8) and $\delta^{13}\text{C}$ isotope signature of ca. -21.5 per mille dominates, while at high tide the $\delta^{13}\text{C}$ signature becomes more negative decreasing upto ca. -24.5 per mille with a C/N value of ca. 14. Particulate organic material associated with offshore waters have been found to have $\delta^{13}\text{C}$ signature of ca. -21 per mille while that associated with mangrove waters have $\delta^{13}\text{C}$ of ca. -26.7 per mille (Rezende et al., 1990). The less negative $\delta^{13}\text{C}$ signature found at station 3 during high tide is therefore of marine origin and it becomes more negative with ebb flow indicating export of mangrove dominated POM. This process is found not to be affected by seasonal changes as witnessed with dissolved inorganic nutrients.

It is still not very clear how much the seagrass within the bay would contribute to the overall POM content within the water column. Though a remarkable decrease of $\delta^{13}\text{C}$ isotope signature of *Thalassodendron ciliatum* (one of the most common seagrass species in the bay) from the open waters into the mangrove creeks (Hemminga et. al., 1994) was noticed, C/N values of the same remained more-or-less uniform at ca. 20 (unpublished data). The low C/N value (ca. 7-8) of the POM at low tide and its high (less negative) $\delta^{13}\text{C}$ values (ca. -21 to -22 per mille) may therefore imply very minimal seagrass contribution on the water column POM during high tide. It is also observed, that the highest C/N value (ca. 14) found at station 3 during low tide is still very low compared to the average C/N values determined for mangrove vegetation (Rao, et. al., 1994). Since the carbon-13 isotope signature of mangrove sediment indicates that the major contribution of organic matter is the mangrove vegetation (Hemminga, et. al. 1994), the big difference in C/N may imply a major transformational process of the released mangrove organic material resulting in increase of nitrogen and therefore lowering of the C/N value. This aspect is discussed in detail in other sections of this report.

From the above results, it is seen that although riverine freshwater influx accounts for less than 1.0% of the total volume of the bay it actually acts as the main supplier of dissolved inorganic nutrients into the bay, particularly in rainy seasons. The mangrove vegetation also supplies organic material in particulate phase to the adjacent bay. However, as a result of high exchange rates and rapid mixing of the different water bodies in the bay, there are no major differences in the spatial distribution of dissolved inorganic nutrients between the mangrove, seagrass and coral reef zones of Gazi bay apart from the upper part of Kidogoweni creek leading to Kidogoweni river. This is further supported by the fact that residence time of the water in the bay is rather short (3 to 4h) and does not allow the development of highly distinct water bodies with special characteristics different from the oceanic water. As a result of location near the discharge point of the River Mkurumuji which also has higher river discharge rates (upto $17.0\text{ m}^3\text{ sec}^{-1}$) and displays semi-perennial characteristics, the coral reef and seagrass biotope zones near Mkurumuji river may have slightly elevated concentrations of N-nutrients

during the wet seasons especially at mid-flood tide when part of the river Mkurumuji's water enters the bay. Since there is a significant tidal asymmetry in the tidal creeks with relatively stronger ebb flows as compared to flood flows, a net export of nutrients brought from the river (and mangroves?) occurs, thereby promoting the linkage with the mangroves and seagrass beds. The net export of nutrients from the rivers, coupled with high rates of water exchange between the offshore and inshore waters, reduces the occurrence of eutrophic conditions since nutrients are not completely retained in the bay, but are flushed out of the creeks and estuaries and rapidly mixed by the breaking waves and tidal currents whose maximum speed often reach 0.60 msec^{-1} in spring tide. The flood tide which is associated with the influx of nutrient-poor water from the offshore waters results in decrease in nutrients levels at high flood waters. This phenomena is partly promoted by tidal mixing and dilution effects.

Phytoplankton and zooplankton

Mean phytoplankton primary production and biomass indicate spatial-temporal variability which can be related partly to water circulation patterns and the distribution of nutrients in the bay (Figs. 6, 8 and 9). The highest rates of primary production in the mangroves, seagrass beds and in the coral reef zones were measured in rainy seasons. These were the periods with high river discharge rates of freshwater and nutrients. The mean gross productivity during the wet season was $540.41 \pm 222.63 \text{ mg C/m}^3/\text{day}$, $552.22 \pm 291.36 \text{ mg C/m}^3/\text{day}$ and $388.88 \pm 247.12 \text{ mg C/m}^3/\text{day}$ for the mangrove, seagrass, and coral reef biotopes respectively (Fig. 12). The rates of primary production were low during the dry season (Jan-March; Aug-Sep) averaging $377.67 \pm 159.7 \text{ mg C/m}^3/\text{day}$, $230.84 \pm 84.75 \text{ mg C/m}^3/\text{day}$ and $240.27 \pm 115.29 \text{ mg C/m}^3/\text{day}$ for the mangrove, seagrass, and coral reef biotopes respectively. However, the analysis of variance (ANOVA) carried out on the pooled data for the three biotopes, do not show major significant differences between the wet and dry seasons ($p < 0.05$).

The wet season with increased nutrients input from Kidogoweni and Mkurumuji Rivers, exhibited more phytoplankton biomass than the dry season for all the biotopes. Mean chlorophyll-a level for mangrove zone was $1.74 \pm 0.94 \mu\text{g/l}$ for the wet season and $1.45 \pm 0.77 \mu\text{g/l}$ for the dry season as compared to $0.80 \pm 0.35 \mu\text{g/l}$ (wet season), $0.42 \pm 0.17 \mu\text{g/l}$ (dry season) for seagrass and $0.61 \pm 0.26 \mu\text{g/l}$ (wet season), $0.24 \pm 0.1 \mu\text{g/l}$ for the coral zone (Fig. 12). A gradient in pigment concentration is evident with a significant difference between stations (ANOVA, $p > 0.05$). The highest values were recorded from the mangrove zone (Figs. 12 and 13) with the lowest values recorded from the coral reef zone. The tidal flow of water in the bay also influences the level of phytoplankton biomass with diurnal influences being more predominant. The ebb tide in wet seasons, which is characterised by low salinity and higher nutrients, is associated with high primary production. The influx of nutrient poor oceanic water at flood tide leads to a corresponding decline in the rates of primary production and phytoplankton standing stocks in the creeks. However, this pattern is not so pronounced in the dry season (with low nutrients concentrations) as the spatial differences of primary production between the offshore and backwaters is negligible. The trends of the diurnally tidally-influenced variations of phytoplankton standing stock are only distinct in the mangrove zone and to a certain extent in the seagrass zone, but not in the coral reef biotope where such diurnal changes are undiscernable. This is because the coral reef ecosystem is not highly influenced by the riverine nutrients input responsible for increased primary productivity. The nutrient-laden water is coastally-trapped along the southwest coast and therefore prevented from reaching the coral reef ecosystem. The wet season values for chlorophyll-a tended to be higher than dry season values in ebb and flood phases of the tidal cycle ($1.90\text{--}5.7 \mu\text{g/l}$ for wet season, $1.5\text{--}3.3 \mu\text{g/l}$ for dry season in the mangrove). Microscopic analysis of the phytoplankton samples have revealed that diatoms and dinoflagellates are the predominant species in Gazi Bay.

Seasonal zooplankton biomass (Fig. 14) indicate higher biomass (0.315 ± 0.366 and $0.355 \pm 0.45 \text{ ml/m}^3$) in rainy season as compared to the dry season (0.062 ± 0.021 to $0.106 \pm 0.087 \text{ ml/m}^3$). The highest zooplankton density occurred in the seagrass station during the wet season ($40.2 \pm 43.2 \text{ no./m}^3$). Lowest zooplankton abundance was found in the mangrove station during the wet season ($2.0 \pm 1.57 \text{ no./m}^3$). In most periods of the year, high zooplankton density occurs in the coral reef and seagrass zones, but not in the mangrove backwater zone (Fig. 14, 15 and 16). The most common zooplankton groups encountered were *Copepoda*, *Decapoda* and *Pisces*. Others were *Cnidaria*, *Protozoa*, *Amphipods*, *Appendicularia*, *Mollusca* amongst others (Table 4). The spatial distribution and abundance of zooplankton groups varied seasonally between the different biotopes.

Species diversity

The mean monthly Shannon index species diversity was highest in the month of August 1993 ($H =$

1.25). In October, 1993 at the onset of the short rains, the diversity fell to its lowest ($H = 0.45$) and it remained fairly low until it peaked again in March 1994 during the dry season. During the long rains May - July, 1994, species diversity declined again (Average $H = 0.7$), peaked again just before the short rains in November ($H = 1.1$). The species diversity is affected by the changes in freshwater input in the bay which is a response to rainy seasons. The low levels of salinity (2.0 to 25 PSU) created during the rainy season as a result of an increase in river freshwater supply led to a decrease in species diversity. The onset of rainy season and associated increase in the rates of fresh water input, leads to physico-chemical conditions which are not suitable for certain species of zooplankton (Osore, 1994; Okemwa, 1986). In comparing the average zooplankton species diversity between the mangroves, seagrass beds and coral reef stations in the bay, we note that the highest value was for the mangrove zone ($H = 0.92$). The different zooplankton groups were found to be more evenly distributed in the mangrove zone ($J = 0.62$). The coral reef also had high and stable species diversity ($H=0.89$) and an evenness comparable to that of the mangrove zone. The seagrass and mangrove waters are constantly interchanged in light of close proximity and the water physical characteristics in the two zones, does not differ much. The lowest zooplankton diversity was in seagrass zone which is found between the mangrove and coral reef zones.

There was no direct relationship between zooplankton abundance and phytoplankton production and biomass in the bay. The areas with high phytoplankton production in the mangroves and backwater zone were not associated with high zooplankton abundance. These weak correlations may indicate that zooplankton in the bay does not totally rely on phytoplankton as food items.

DISCUSSION

The freshwater input through direct rainfall and river runoff is in the order of $300,000 \text{ m}^3 \text{ day}^{-1}$ (rainfall amount; $1000 \text{ mm year}^{-1}$, freshwater influx rate; $3.4 \text{ m}^3 \text{ sec}^{-1}$). The freshwater influx volume accounts for 1.0 % of the total volume of the bay. The loss of freshwater through evaporation is equivalent to 20 % of the total freshwater supplied through river runoff and direct rainfall falling into the bay. The remaining 80 % is retained in the bay and is transported through the seagrass beds by eddy diffusion and advection and eventually mixed away through tidal turbulence in the more saline water offshore. This study has however not established the contribution of groundwater seepage to the total freshwater and nutrients supply in the bay.

In the determination of water exchange bay, mass-balance approach was adopted. The exchange flux (Q_a) in the bay is approximately $3800 \text{ m}^3 \text{ sec}^{-1}$ with the mean ocean flux (Q_o) at the bay entrance of $4200 \text{ m}^3 \text{ sec}^{-1}$ (bay width at the entrance; 4.0 Km at high tide, mean depth; 3.0 m and maximum current speed; 0.35 m sec^{-1}). The exchange rate using the volume-conservation approach has been found to be 90.0 % in spring tide (Kitheka, 1995). However, with the modified tidal prism method, the exchange rate was found to vary between 60 and 85% in neap and spring tide respectively. The residence time of the oceanic water is short and varies between 3.1 and 3.6 hrs. The high exchange rates are as a result of the presence of a wide shallow entrance, absence of topographic controls (sills), and the orientation of the bay in respect to the dominant tidal water flow paths. This high rate of water exchange has significant implications in as far as the linkage between mangroves, seagrass beds and coral reef ecosystem is concerned (Kitheka, 1995).

The presence of drainage creeks coupled with the occurrence of dense vegetation in the mangrove zone, promotes the tidal asymmetry and therefore seaward net-transport of organic matter and nutrients from Kidogoweni River and links the mangroves with the seagrass ecosystem. Previous hydrographic study restricted in the Kinondo Creek area in the north east of Gazi Bay, has shown that, the tidal creek act as an export system with net seaward transport of organic matter (Kruyt and van der Berg 1993).

The semi-seasonal Mkurumuji and Kidogoweni Rivers plays an important role in the spatial-temporal distribution of dissolved inorganic nutrients in Gazi bay coastal waters. The role of the discharges of the two rivers is more pronounced during the rainy seasons when the influx of riverine freshwater into the bay often reaches $17.0 \text{ m}^3 \text{ sec}^{-1}$ and $6.0 \text{ m}^3 \text{ sec}^{-1}$ in the Mkurumuji and Kidogoweni Rivers respectively. The freshwater discharge greater than $1.0 \text{ m}^3 \text{ sec}^{-1}$ results in high concentrations of dissolved nutrients which are derived from terrestrial surface runoff and drainage from agricultural lands. Tropical rivers with large seasonal differences in discharge rates, are characterised by an increased output of chemical compounds during stormy situations. Due to a higher discharge rate of Mkurumuji river as compared to Kidogoweni river, nutrients levels at the coral reefs and seagrass

biotope close-by could have elevated values which are slightly higher than those noticed for the mangrove zone. Conservative mixing of the nutrients supplied by river Kidogoweni has been demonstrated with a possibility of minimal input of nutrients from the mangrove vegetation. The direct response of the N-nutrient concentrations increase in the coastal waters as a result of river freshwater influx has been reported by Morris et al. (1985) who observed that concentrations of nitrite and ammonium in the coastal waters vary in direct response to increasing river discharge rates. The quantities of any river-borne dissolved chemical compounds being transported via the estuarine zone, depends on river discharge (Duinker, 1989). The principle source of nitrogen to the coastal regions is evidently riverine inputs, as higher levels are normally measured close to the river mouths (Owens et al 1990). Low river discharges during dry seasons implied minimal riverine influence on the distribution of dissolved inorganic nutrients in the mangroves, seagrass beds and the coral reef zone, with the resulting minimal variations in the spatial distribution of nutrients between the three biotopes. It also indicated that there is very minimal contribution of nutrients from the mangroves, seagrass beds and the coral reef zones. The contribution of these ecological systems to the total nutrients budget of the bay is therefore very low.

The freshwater input in Gazi bay is therefore associated with an increase in inorganic nutrients level in the seagrass, mangrove and the near-coral reef zone. However a result of modification by tidal action, the levels tends to lower within the bay waters as compared to the rivers. The observations made on salinity distribution, which is an important indicator of water circulation patterns in the bay, shows that the river brackish water plume which is nutrient-laden is trapped along the southwestern coast and in the mangrove zone (Fig. 6). The coastal trapping of this brackish water is enhanced by onshore wind, wave-breaking in the coral reef zone which generates westward flowing current throughout the year. The coastal trapping of this plume is further enhanced by the long-shore current generated along the southwest coast of the bay. The longshore currents generated in flood tide links with the tidal currents to facilitate further trapping of the plume. The nutrient-laden water does not therefore reach the coral reef ecosystem (reaches the near coral reef biotope zone) where its impact on the sustainability of the coral reef ecosystem could be disastrous, since the reef ecosystem cannot withstand high nutrients and salinity fluctuations as observed in the mangrove zone in wet seasons. It is important to note that nutrient analysis results obtained for Gazi Bay were much lower than those reported in Tudor Creek (Kazungu et.al, 1989) where the rate of water exchange is relatively lower.

Zooplankton density and biomass in the mangroves, seagrass beds and the coral reef zones increases in the rainy period and reach a peak of 101 no./m³ in July in the seagrass zone (Mwaluma, 1993., Mwaluma et al. 1993). In previous studies in the bay, zooplankton abundance peaks were associated with rainfall and occurred in March, April and May (300-550 no./m³) (Osore (1992., 1994). River Kidogoweni influence the distribution and abundance of zooplankton in the mangrove zone which is close to the river mouth by causing lower salinity in the creek in rainy seasons. The mangrove zone with greater riverine influences thus recorded low zooplankton counts (2 no./m³) while higher densities (36 and 101 no./m³) were recorded in the seagrass and coral stations which had higher salinity (35 PSU) in the same period. During the dry season, the distribution was more even among the stations because salinity of water was more evenly distributed (35 PSU). Apart from rainfall, zooplankton groups are found distributed differently within the three biotopes. *Brachyuran larvae*, *Brachyuran megalopae*, and *Caridea* seem to be distributed more in the seagrass and coral reef stations whereas fish eggs were mostly found in the coral reef station (Table 4). This distribution is partly caused by food availability, spawning patterns, tidal rhythms and varying tolerance to changing salinity levels.

Increased phytoplankton production (upto 1110.7 mg C/m³/day) during the rainy season is as a result of an increase in amount of nutrients discharged by the the Kidogoweni and Mkurumuji Rivers (Fig. 8 and 9). During the dry season with low freshwater input and corresponding low nutrients supply, the phytoplankton production and biomass reduce considerably (Figs. 8 and 9), since part of it is used to sustain zooplankton biomass. The mean gross phytoplankton production (540.41 mgC/m³/day) and zooplankton abundance (58 ind. /m³) are low when compared to similar tropical creeks. For example Tudor creek, the gross phytoplankton production has been estimated to be 350 mg C/m²/hr (Okemwa 1989). These differences are as a result of high exchange rates (60 to 90%) between the offshore and inshore waters and short residence time (upto 4hrs) in the bay. The high rates of water exchange means that nutrients supplied by the rivers are rapidly flushed out of the bay system and therefore cannot accumulate to cause high primary and secondary productions. The mangrove zone has significantly more phytoplankton biomass than the other two biotopes during both the dry and wet seasons, partly because of the low water volume and more stable conditions in the creeks as compared to the frontwaters which are highly unstable (Wave breaking) and have large water volume and high

dilution effect.

Summarizing, Gazi bay is well-flushed estuarine coastal water system with a very high rate of exchange (60 to 90%) and short residence times. The short residence time, coupled with high rate of water exchange prevents the formation of highly eutrophic conditions, despite high rates of nutrients supply from the rivers. Mangrove biotope produces very low amount of dissolved nutrients which are likely to be taken up and used for primary production within the mangrove zone and not noticed as net export. This nutrient source could easily be the reason as why primary production in mangrove zone was found to be relatively higher than the other two biotopes. These are relative differences, however, rates of phytoplankton and zooplankton production are generally still low as compared to other tropical creeks partly because of high rates of water exchange in the bay. The strong reversing current in the mangrove tidal creeks (0.60 m sec^{-1}) and weak current in the seagrass and coral reef zones ($<0.35 \text{ m sec}^{-1}$) coupled with tidal asymmetry, promotes the net-seaward export of nutrients from the rivers in rainy seasons and export of organic matter from the mangroves to the seagrass beds. The influence of freshwater influx on salinity and nutrients distribution in the bay is important in rainy seasons of both northeast and southeast monsoons. The drastic increase in nutrients level in rainy season promotes increased rates of primary production, but eutrophic conditions do not develop because of high tidal flushing rates. The most important nutrients source that partly sustains the mangroves, seagrass beds and coral reef ecosystems, are the two semi-seasonal rivers located in the lower and upper regions of the bay. The increased input of nutrients in rainy season from the rivers causes an increase in primary production in the mangroves, seagrass beds and the coral reef zone, although levels vary from one biotope to another. The increase in primary production and phytoplankton biomass is not however followed by a corresponding increase in zooplankton biomass, density especially in the mangrove zone as a result of seasonally fluctuating salinity. The turbid, nutrient-laden brackish water plume is trapped along the coast, in the southwestern region of the bay by wave-breaking, longshore currents and perennial onshore wind. The onshore wind combined with wave-breaking, tidal and longshore currents, facilitates the rapid mixing of the water column leading to the formation of well-mixed homogeneous water observed in dry seasons (salinity; 34.5 to 35.5 PSU). The turbid, brackish water from the mangroves and the estuaries, reach the seagrass beds where changes on nutrients, turbidity and salinity may occur before this water reach the near-coral reef zone. These changes in the water physical characteristics are enhanced by tidal turbulence, advective mixing and wave-breaking.

The generation of dissolved inorganic nutrients in the mangroves, seagrass beds and the coral reef ecosystems are very low and insignificant to the total water-column nutrients budget of the bay, as the levels of nutrients in the bay were very low during dry seasons with minimal river discharges.

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SPATIAL AND TEMPORAL VARIATIONS IN WATER COLUMN NUTRIENT CONCENTRATIONS IN A MANGROVE CREEK (CHWAKA BAY, ZANZIBAR)

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INTRODUCTION

Mangrove swamps generally exhibit production rates among the highest observed in tropical environments (Morell and Corredor, 1993) with estimates of around 25 Kg C ha⁻¹ d⁻¹ not uncommon (e.g. Boto and Bunt, 1981). This reputed high production of mangroves coupled with their physical proximity to nutrient limited ecosystems, such as coral reefs, has led to the supposition that mangroves may act as a major source of material necessary for the sustenance of adjacent ecosystems. Several authors have postulated the existence of chemical linkages between mangroves and other adjacent biotopes, however, whilst some studies have reported an export of material from mangrove areas (e.g. Boto and Bunt, 1981; Woodroffe, 1985; Robertson, 1986; Boto and Wellington, 1988; Hemminga et al., 1994), other studies have shown some mangrove ecosystems to behave as a sink for different dissolved and particulate materials (e.g. Odum et al., 1982; Nixon et al., 1984). The conclusion to be drawn from these studies is probably that mangroves may behave as both a sink or a source depending on the constraining factors of the particular ecosystem and that factors such as the hydrodynamics and geomorphology of a given mangrove area play an important role (Boto and Bunt, 1981; Boto and Wellington, 1988; Woodroffe, 1992; Wolanski et al., 1992). Furthermore, as highlighted by Wolanski (1989) and Woodroffe (1992), mangrove swamps are characterised by bi-directional tidal fluxes which gives them great potential as suppliers of material to the adjacent coastal waters and related biotopes.

The present study set out to examine the spatial and temporal variation in dissolved nutrients along a mangrove creek in north eastern Zanzibar. This work is intended as a first step in assessing whether the mangroves are exporting dissolved nutrients and to provide baseline data for later comparative work.

METHODS

Study area

This study was carried out in the Chwaka Bay situated 34 Km east of Zanzibar Town (Fig. 1). The bay is a shallow water body of approximately 35km² and is fringed in the south by a limestone reef which is covered by a dense mangrove forest with an estimated area of approximately 3000 ha. A series of tidal creeks drain the forest and these include the Mapopwe Creek where the present study was conducted (Fig. 2). None of these waterways has any significant fresh water input except during heavy rains when salinity gradients develop and the creek assumes estuarine characteristics. A total of seven mangrove species occur in this forest including *Rhizophora mucronata*, *Ceriops tagal*, *Bruguiera gymnorhiza*, *Sonneratia alba*, *Avicennia marina* and *Xylocarpus granatum* (Shunula, 1989). On the seaward side, immediately adjacent to the forest, the bay opens up to large intertidal flats which are covered by a mixed assemblage of seagrasses and algae or, to a lesser extent, by monospecific seagrass stands. A coral reef, which is part of the extensive reef that fringes the coast of Zanzibar, occurs at the entrance of the bay. The tidal regime and bathymetry of the Chwaka Bay and the Mapopwe creek have been previously investigated (Parson et al., 1984; Mgendi, 1994). The relative topography of the bay and the tidal creek are shown in Fig. 2. The major features of the bathymetry of the bay are the presence of the deep tidal creek (Mapopwe Creek) on the western side of the bay (cell 14; Fig. 2a), a limestone sill (cell 15; Fig. 2a), and the elevated mangrove swamp on the southern

reaches of the bay. The two studies also showed that the bay has a semidiurnal tidal pattern with a strong tidal asymmetry; ebb currents being stronger than flood currents. This tidal asymmetry is responsible for maintaining the deep tidal creek. Also, Wolanski (1989) showed that the sill at the mouth of the creek hinders water exchange between the Mapopwe creek and the bay.

Sampling

In order to effectively cover both the dry and wet seasons, sampling was conducted during the months of August and December 1993 and February, June and July 1994. To assess the spatial variability of dissolved nutrients in the creek water, samples were collected during flood tides from six sampling positions located along the length of the creek (Figure 2b). All stations were very shallow (< 2 m) so it was assumed that the water was well mixed and samples were consequently taken approximately 50cm below the surface. This was done using a clean polycarbonate container for sample collection and then filtering the sample through a $0.45 \mu\text{m}$ prewashed polycarbonate membrane filter. The samples were then stored under ice for transportation to the laboratory where they were stored frozen (-20°C) until analysed.

Temporal variability of nutrient concentrations was assessed by measuring nutrient concentrations over eight tidal cycles during both the dry and rainy seasons. Sampling positions were established at the entrance of the creek proper, as well as over a mixed seagrass/algal assemblage immediately beyond the sill at the mouth of the creek (Site 7; Figure 2b). Water samples were collected at half hour intervals over a complete 12 hour tidal cycle and were handled as described above.

All samples were analysed for ammonium, soluble reactive phosphate, nitrate, and nitrite in accordance with the colorimetric methods of Parsons et al (1984). All ammonium analyses were conducted within 24 hours of collection and all other analyses within one week.

Replicate samples were also taken on each sampling occasion for salinity determinations. Samples were only taken at the head and at the mouth of the creek, and salinity was determined in the field with a refractometer.

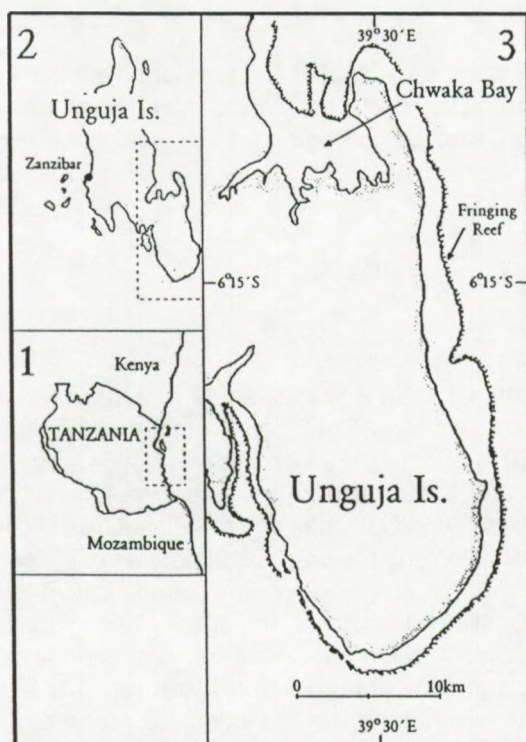
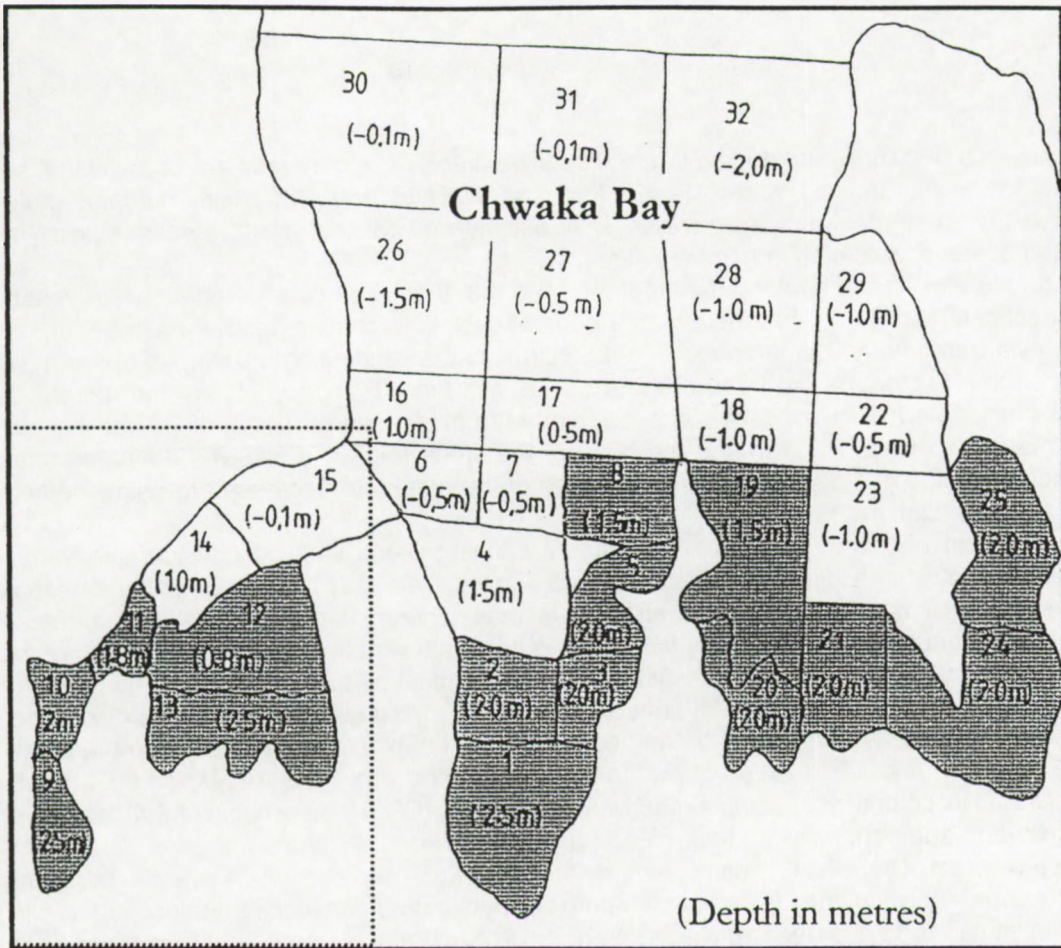


Fig. 1 Map of Tanzania and Unguja Island showing the location of Chwaka Bay and the Mapopwe Creek.

A



B

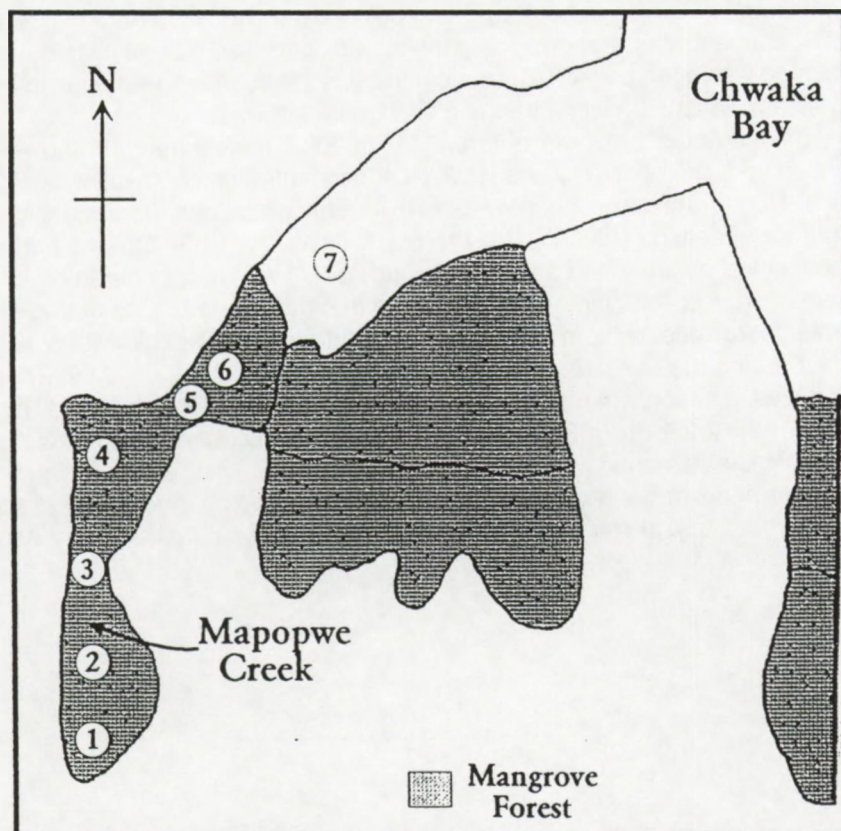


Fig. 2. Broad scale bathymetric map of Chwaka Bay (A), and Mapopwe Creek (B) showing the the location of sampling sites within the creek.

RESULTS

Concentrations of dissolved nutrients in the Mapopwe creek were generally low and within the range reported for similar tropical waters (e.g., Boto and Wellington, 1988). Also, random analysis of standards during sample analysis gave an error estimate of < 2% of the true value which was well below the observed variation in sample values.

Nutrient measurements along the creek showed that there was considerable spatial variability in nutrient concentrations and that there was a general decline in concentration for all nutrients as one moved toward the mouth of the creek (Fig. 3). Nitrate/nitrite concentrations ranged from an average of $0.32 \mu\text{g-at N.l}^{-1}$ towards the head of the creek to less than $0.01 \mu\text{g-at N.l}^{-1}$ at the mouth. Soluble reactive phosphate (SRP) concentrations also varied from a mean of $0.1 \mu\text{g-at P.l}^{-1}$ at the mouth to approximately $0.6 \mu\text{g-at P.l}^{-1}$ towards the head of the creek (Fig. 3). Dissolved ammonia showed a mean concentration of $1.39 \mu\text{g-at N.l}^{-1}$ at the head of the creek but decreased to below detection by the next station (station 2).

Examination of temporal changes in nutrient concentrations showed considerable variation in concentrations over time for all nutrients measured (Fig. 4). On a daily basis, it was often observed that dissolved inorganic nitrogen (DIN) concentrations increased during the period of low tide, however, this was not consistent and appeared to be linked to the particular weather and tidal conditions of the day. This dependency could not be accurately tested here but must certainly be abetted by the hindrance effect of the shallow sill at the creek mouth as described by Wolanski (1989). This is discussed later. The mean concentration ranges for the respective nutrients at high and low tide along the creek were 0 to $2.0 \mu\text{g-at N.l}^{-1}$ and 1.0 to $7.0 \mu\text{g-at N.l}^{-1}$ for NO_3+NO_2 ; and 0 to $1.2 \mu\text{g-at N.l}^{-1}$ and 0.4 to $9.5 \mu\text{g-at N.l}^{-1}$ for NH_4+ . By comparison, soluble reactive phosphorous (SRP) was consistently variable over time and showed no apparent link with tide, time of day, or prevailing weather.

Measurement of tidal fluctuations of ammonia, nitrate/nitrite and phosphate over the seagrass/algal assemblage immediately outside the creek mouth showed that nutrient concentrations at this site were within the same range observed within the creek except that mean ammonium levels were generally slightly lower than observed in the creek water. Nitrate/nitrite ranged from $0.3 \mu\text{g-at N.l}^{-1}$ to $2.0 \mu\text{g-at N.l}^{-1}$ at high tide and between $1.0 \mu\text{g-at N.l}^{-1}$ to $7.0 \mu\text{g-at N.l}^{-1}$ at low tide. Ammonium concentrations ranged from a maximum of $0.7 \mu\text{g-at/l}$ at low tide to below detection limits at high tide. Also, both NO_3+NO_2 and NH_4+ concentrations showed a change with tide that was similar but generally not as dramatic as observed within the creek. SRP concentrations also behaved similarly to inner creek levels and showed no clear relationship with changing tide or time of day.

Seasonally, the nutrients behaved differently with SRP concentrations showing no significant seasonal correlation ($p=0.05$) but NH_4+ and NO_3/NO_2 concentrations both gave significant differences between seasons. During the dry season, mean NH_4+ concentrations were significantly higher than observed during the wet season (ANOVA, $f = 11.75$; $p < 0.01$; $df = 1,96$). On one particular dry season sampling day, concentrations reached a peak of $9.5 \mu\text{g-at N.l}^{-1}$ with a daily mean of $3.4 \mu\text{g-at N.l}^{-1}$. This was the maximum observed. It is perhaps worth noting that this day was also during a particularly long period of high temperatures without any rain. By comparison, NO_3/NO_2 concentrations were significantly higher during the wet season (ANOVA, $f = 50.1$; $df = 1,96$; $p < 0.00$). There was also one occasion during the wet season when NO_3+NO_2 concentrations were significantly higher than for the other days (ANOVA, $f = 2.22$; $df = 23,96$; $p = 0.004$), with a peak of $6.91 \mu\text{g-at N.l}^{-1}$. This difference occurred on a day which was amidst a period of intense rains.

Salinity measurements at the head of the creek and at the mouth gave salinity ranges of 5 to 6‰ and 26 to 28‰ respectively in the wet season, and 35 to 38‰ during the dry season with 35‰ occurring regularly.

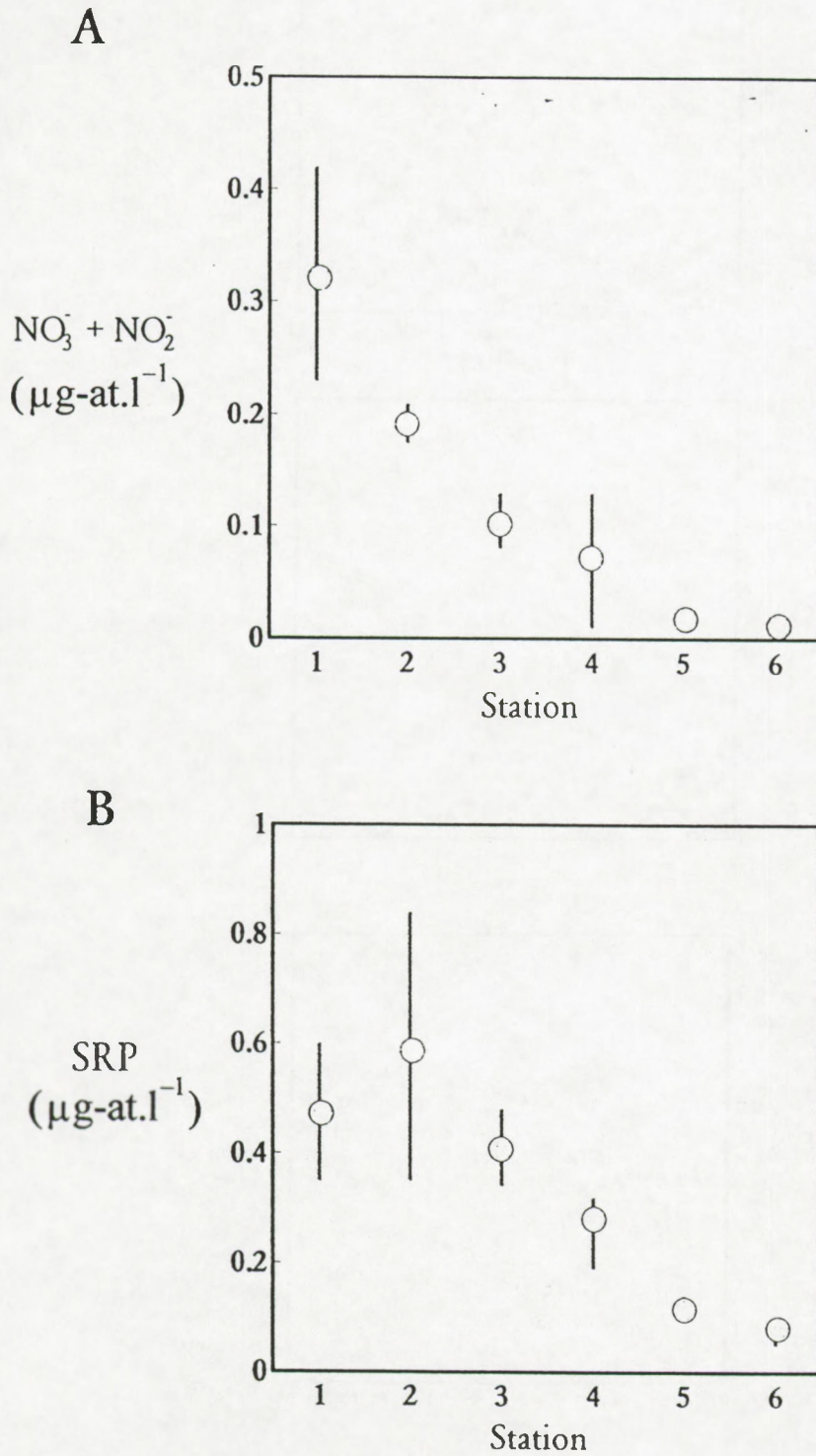


Fig. 3. Mean concentrations of nitrate+nitrite and soluble reactive phosphorous (SRP) along the Mapopwe Creek. The bars represent the 95% confidence limits for the means.

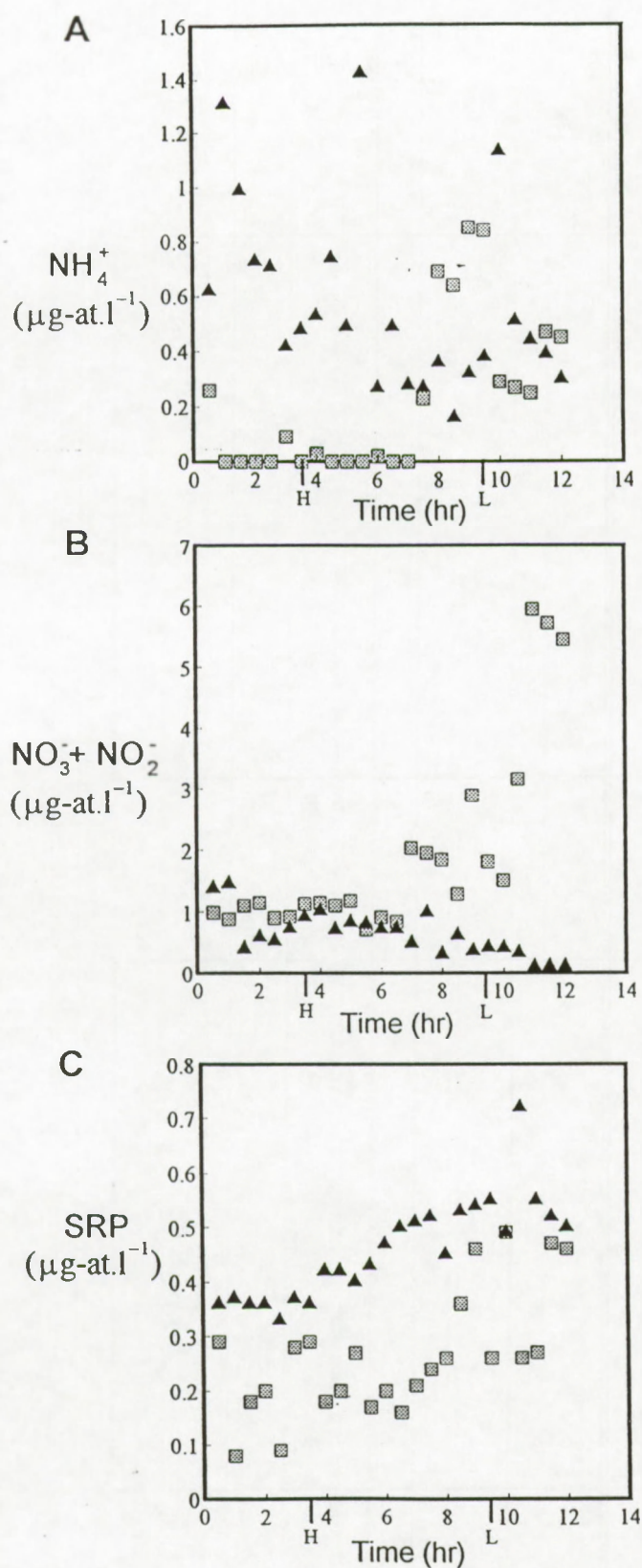


Figure 4. Mean concentrations of ammonium, nitrate+nitrite and SRP during the wet season (■) and dry season (▲). The x axis represents time of sampling over the 12 hour daylight period and tidal status is given on the x-axis; L low tide, H high tide.

DISCUSSION

Mapopwe creek is a good example of a tropical mangrove waterway which receives minimal and infrequent freshwater inputs. Accordingly, the observed results concur with other observations from mangrove waterways which are influenced almost entirely by tidal movements and which have little or no freshwater input from terrestrial sources (e.g. Boto and Wellington, 1988), as compared to those which have significant freshwater input (Wong, 1984). Even though the Chwaka mangrove forest is contiguous to the Jozani groundwater forest (a potential source of groundwater), it seems that this is not an important source of nutrients to the creek; the observed nutrient concentrations do not reflect the often characteristically elevated nutrient levels observed in mangrove swamps receiving significant groundwater inputs (see e.g. Nixon et al., 1984; Wong, 1984). The seasonal differences observed appear to reflect changes in localised nutrient processes and potentially a localised input of nutrients from forest run-off. In the case of ammonium, the elevated dry season concentrations may be attributable to changes in benthic nitrogen cycling. As discussed by Wolanski (1986), in creeks such as Mapopwe creek with its restrictive sill and minimal freshwater input, extended dry periods with high evaporation rates may lead to changes in the salinity regime which, in turn, may result in partitioning of water bodies and an inverse water circulation within the creek. The poor mixing that results from this, especially during neap tides, may therefore increase water residence times and a depletion of dissolved oxygen in bottom waters; even in very shallow systems. In Mapopwe creek, the observed peak in NH_4^+ concentrations occurred during dry, hot weather with neap tides when salinity's were highest. It seems conceivable, therefore, that vertical mixing of creek waters may have been more restricted than was assumed when this study was commenced. Unfortunately, salinity measurements were only for surface waters, and only from two stations, so our ability to fully describe the situation is limited. This is discussed further below.

Despite this, however, given the sill at the mouth of the creek, and the observed conditions, it seems likely that bottom waters were not well mixed and may well have been oxygen depleted. In this situation, elevated NH_4^+ concentrations would be expected as the anaerobic interface moved higher in the benthos and perhaps into the water column. Under these conditions anaerobic ammonification would increase and processes such as nitrification, which utilise NH_4^+ , would be greatly reduced so that more NH_4^+ is released to the water column. By comparison, $\text{NO}_3^-/\text{NO}_2^-$ concentrations were elevated during the wet season. Given the enhanced local terrestrial inputs that accompany the wet season via run-off, the observed concentrations may be expected. In line with this, the eight days of data collected within each season showed a significant seasonal difference and one sampling period, on the 10th of February, showed a $\text{NO}_3^-/\text{NO}_2^-$ level which was significantly higher than the other wet season samples. This day was amidst an extended period of intense rains so that inputs of terrestrial nitrates was likely to be high.

With regard to the apparent disparity in the sampling regime used here which assumed good water mixing, and the observation that this may not be the case, it should be noted that the waters at station 7 immediately outside the creek are generally well mixed (Wolanski, 1989), and that the data from this site showed no apparent export of dissolved nutrients during ebbe tides. Consequently, conclusions as to whether dissolved nutrients are exported seem valid and any errors in measurement are restricted to missing the possibly higher ammonium concentrations in creek bottom waters.

In the light of the above discussion it appears that the nutrient dynamics of the Mapopwe creek are driven by both *in situ* processes in the benthos and water column, as well as terrestrial inputs under rainy conditions. Given the inherent limitation of the eularian approach used in this study, it is difficult to assess the significance of benthic nutrient inputs to the water column, however, preliminary studies (Mohammed, unpublished data) show there to be strong nutrient gradients in the creek sediments (Fig. 5), and thus it is likely that they must play a role in supplying nutrients to the water column; as either dissolved nutrients or as particulate/living material derived from the benthic biomass supported by sediment nutrients. The fact that such sediment concentration gradients do not lead to water column concentrations higher than those observed is not unrealistic. A number of contributing factors and processes may play a role in this.

As reported by Kannan and Vasantha (1992) from south eastern India, such mangrove creeks often have a significant phytoplankton community and thus it is possible that any nutrients released by the benthos are immediately taken up by this community so that the dissolved water column pool is consistently small. Preliminary phytoplankton production studies using ^{14}C in Mapopwe creek indicate the presence of an active phytoplankton community (Johnstone, unpublished data) such a coupling may help to explain the

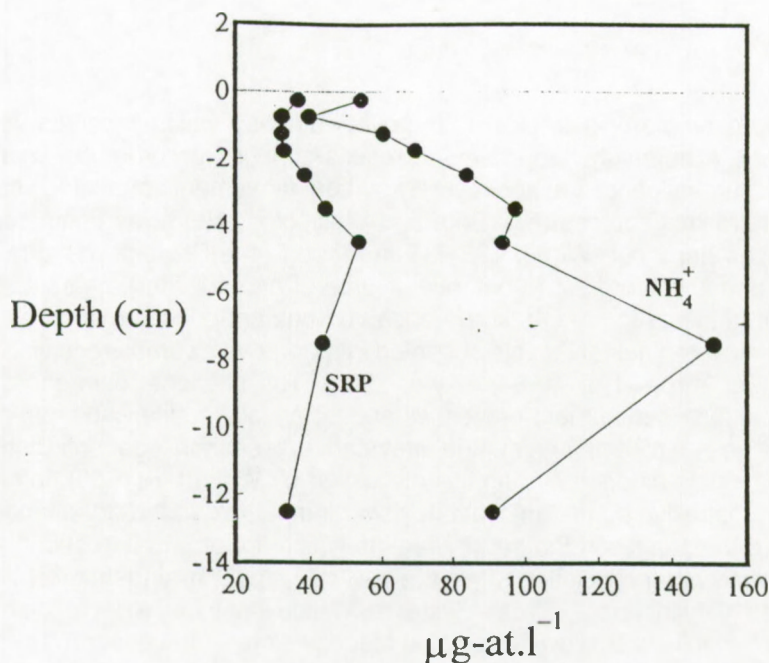


Fig. 5. Mean sediment depth concentration profiles for SRP and ammonium from sediments in Mapopwe creek. These profiles are the means of 4 core samples taken from the central creek channel.

results observed here. Further, it is also possible that there is active uptake by microautotrophs on the sediment surface which results in a further depletion of nutrient pools at the sediment water interface. It was often observed during the study that considerable areas of the benthos were covered by a discernibly green film of microalgae. Such microalgal communities have been shown elsewhere to take up sediment nutrients directly (Johnstone et al., 1988) and so they may also play a significant role here in controlling water column nutrient levels.

Presumably then, a significant fraction of the nutrients are locked up in the sediments as biomass but, as indicated earlier, strong DIN gradients in the sediments indicate the potential for a wide range of microbial mineralisation processes. Given this, microbially driven transformation processes such as denitrification may also be important in removing ammonium and nitrate/nitrite. The result of these different processes is that only a fraction of the sediment DIN actually escapes into the water column. Accordingly, only a relatively small concentration maximum was observed during low tide; when there was stationary water in the creek and presumably the greatest chance of nutrient enrichment in the water column. This is an area that requires further investigation.

In conjunction with the above observations the observed decrease in dissolved nutrients along the creek (Fig. 3) would suggest that little dissolved nitrogen or phosphorous leaves the creek into the adjacent bay. Clearly, the observed minimum concentrations at the mouth of the creek could be the result of dilution by incoming, less nutrient rich, bay water, however, as the measurements were taken at different times and over different tidal states, tidal dilution does not adequately explain the observed results. Consequently, it appears that there is no discernible release of dissolved nutrients from the mangrove creek ecosystem. As mentioned previously, such a situation has been reported elsewhere (e.g. Nixon et al, 1984; Odum et al., 1982) and is thus not unlikely especially given the protracted water residence times in this particular creek due to the sill at the creek mouth. Exactly how and where this material is conserved or bound is not clear from the present study, but both benthic and water column microbial processes must play a role. Also, it is possible that there is an export of nutrients as particulates or biomass generated from the dissolved nutrient pool but the extent of this export is not clear. It is apparent from the present investigation that both of these areas need to be further investigated before a more complete understanding of the creeks nutrient dynamics can be constructed, and the role of Mapopwe creek as a supplier or sink for nutrients be fully elucidated.

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Part 4: The biological diversity of the coastal zone and the population dynamics of economically relevant species

STRUCTURAL AND STABLE ISOTOPE DIFFERENCES IN THE FISH COMMUNITIES OF MANGROVE CREEKS, SEAGRASS MEADOWS AND SAND FLATS IN GAZI BAY (KENYA)

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INTRODUCTION

Shallow bays with mangroves and seagrass beds are considered to be important nursery grounds or feeding areas for many fish species. Such a nursery role of mangroves and seagrasses is widely accepted for tropical mangrove and tropical and temperate seagrass habitats in the USA, Africa, Asia and Australia (Austin, 1971; Middleton *et al.*, 1984; Wright, 1986; Thayer *et al.*, 1987; Little *et al.*, 1988; Chong *et al.*, 1990; Blaber *et al.*, 1992; McNeil *et al.*, 1992; Laegdsgaard & Johnson, 1995). Although seagrass meadows and mangroves often coexist in close proximity, in many cases species assemblages in seagrass beds differ from those in nearby mangroves and sand habitats (Pollard, 1984; Ferrell & Bell, 1991; Blaber *et al.*, 1992). To date only few studies have evaluated the importance of mangrove habitats as nursery areas relative to adjacent habitats such as seagrass beds and mud flats that are also associated with estuarine areas. Robertson and Duke (1987) and Thayer *et al.* (1987) have undertaken comparisons of mangroves and proximal habitats, and both studies recorded more number of fish species in mangroves than in surrounding seagrass habitats. It is also reported that the sub-tropical seagrass systems harbour fewer number of species than tropical systems (Stephenson & Dredge, 1976; Quinn, 1980; Thayer *et al.*, 1987; Morton, 1990; Laegdsgaard & Johnson, 1995).

Stable carbon and nitrogen isotopes can be used as a tool to trace the flow of organic matter through ecosystems (Peterson & Fry, 1987). The combined measurement of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provides a powerful tool to determine the sources of nutrition for consumers and indicates trophic relationship among organisms. Stable isotope abundance of carbon and nitrogen in animals are largely determined by isotope composition of their diet. Heavy isotope enrichment occurs between animals and their food. Such a isotope enrichment is estimated at about 1‰ per trophic level for carbon and at 3-4 ‰ per trophic level for nitrogen (Fry & Sherr, 1984; Minagawa & Wada, 1984). In general, $\delta^{13}\text{C}$ measurements primarily indicate which sources of carbon are important to consumers in food webs, rather than indicating trophic level.

This study elaborates on the findings outlined in Netherlands Indian Ocean Programme (NIOP) and STD III Programme. The main objective of this study is to compare the species composition, the abundance, biomass and size ranges of different fish species in the mangrove creeks, seagrass meadows and sand flats of Gazi bay in Kenya. The evaluation of the feeding behaviour of different size classes of fishes was also investigated using stable carbon and nitrogen analysis.

METHODS

Study area

The present study was carried out in Gazi bay (Kenya). The bay is dominated largely by seagrass beds and a mangrove stand (area 6.61 km²). A description of the mangrove and seagrass vegetation in Gazi bay is given in Coppejans and Gallin (1989), Coppejans *et al.* (1992), Van Avesaath *et al.* (1993) Slim and Gwada (1993) and Hemminga *et al.* (1994). The present study was undertaken at several locations in the Gazi bay (Fig. 1). In order to study the fish assemblages, the Gazi bay was divided into five

zones, each representing a particular biotope (see Fig. 2). However, it was not possible to fit all the sampling locations into five zones, due to practical constraints. Therefore, the fish species obtained out of these five zones were listed but not used for subsequent detailed studies.

Zone I (mangrove creek): This western mangrove creek is generally fed by the river Kidogoweni and in upstream direction the salinity gradient is evident from the decreasing water conductivity (46 mS/cm to 3 mS/cm, at 25 °C during low tide). The bottom of the creek is bare and sandy with only small cover of vegetation towards the ocean side. The vegetation mainly consists of *Cymodocea rotundata*, *C. serrulata*, *Halophila stipulacea* and *Thalassia hemprichii* and the dominant mangrove species is *Rhizophora mucronata*.

Zone II (mangrove creek): This eastern mangrove creek is not fed by a river but only carrying tidal water (conductivity 49 mS/cm at 25 °C) and has a dense cover with seagrasses like *Thalassodendron ciliatum*, *Cymodocea rotundata* and seaweeds. The creek also has only a few minor side channels and is bordered by *Rhizophora mucronata*.

Zone III (Seagrass beds and intertidal flats): The seagrass beds are generally covered by the vegetation (seagrass) of 30% - 100%; in intertidal flats, the seagrass vegetation is restricted to less than 30%. At many places there are dense stands of vegetation mostly consisting of *Thalassia hemprichii*, *T. ciliatum*, *Enhalus acoroides*, *Cymodocea rotundata* and *Gracilaria salicornia*. The seaweeds of *Halimeda macroloba* and *Avrainvillea obscura* are also typical for this zone (Coppejans *et al.*, 1992). In some places, particularly towards the reef, coral rubble is found in between the vegetation.

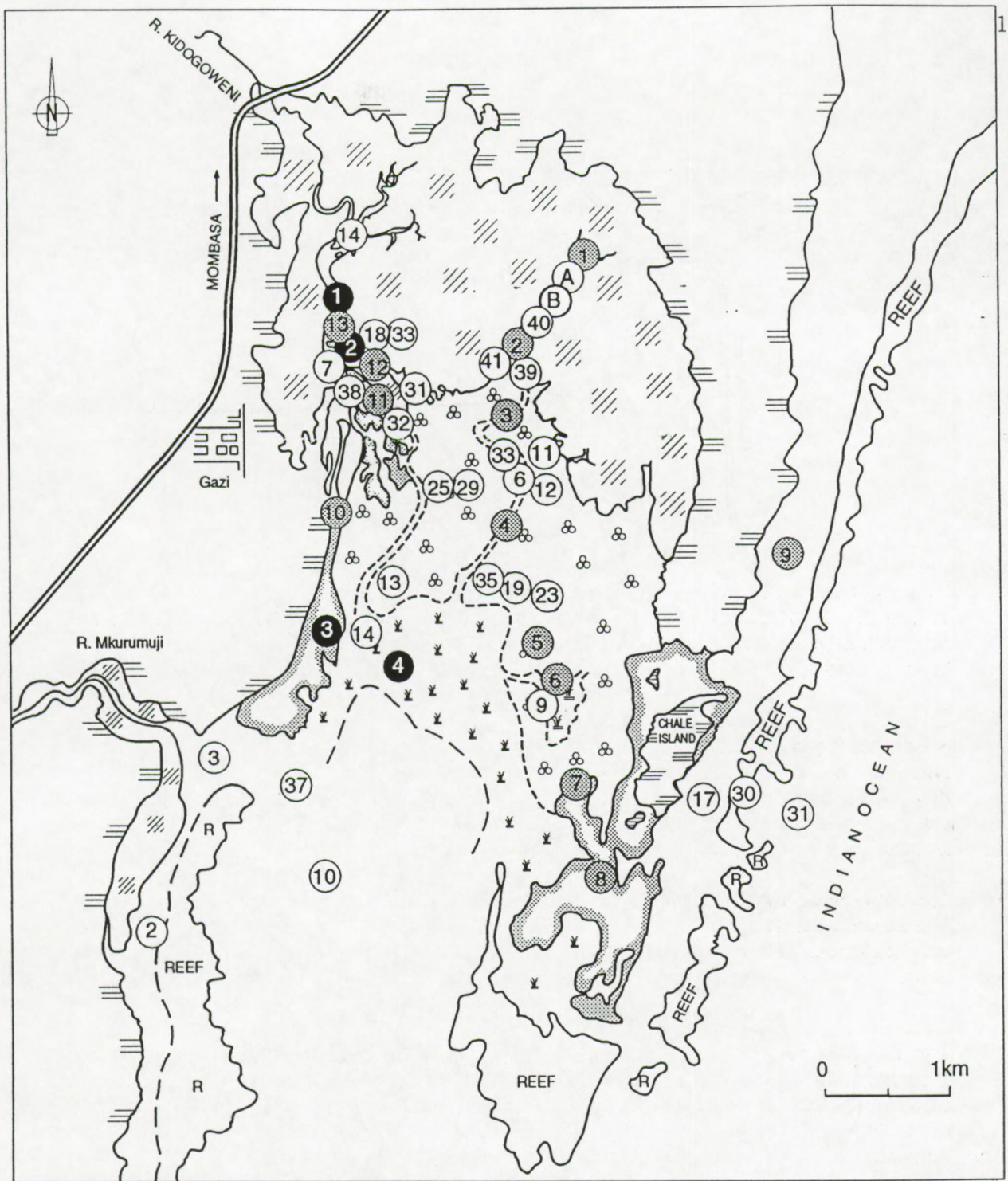
Zone IV (Open sea/coral reef): This zone consists of a partially open sea and a lagoon-like area to the west. This lagoon is situated between the mainland (mangroves) and a coral reef. River Mkurumui enters the sea near the sampling site of 3 (NIOP, see Fig. 1). The lagoon's vegetation is dominated by *Cymodocea rotundata*, *Syringodium isoetifolium*, *Halophila ovalis* and *H. stipulacea*. The area near the river mouth has bare vegetative cover of *C. rotundata*, *C. serrulata*, *H. stipulacea* and *S. isoetifolium*.

Zone V (fringing reef/intertidal flat): This zone is situated at the east of Gazi bay, near Chale Island. The salient features are sandy bottom on hard rock with sparsely corals and coral rubble and a often very scarce seagrass cover. The true coral reefs are sited towards the east. Some samples were taken at the east side of the reef, facing the Indian ocean.

Assessment of fish assemblages

The fish assemblages of Gazi bay, Kenya were collected during the Netherlands Indian Ocean Programme (NIOP) in June 1992, and as part of the the STD III Programme, during a intensive fishing campaign in October 1994. Various fishing techniques were used to describe the community structure of the fish assemblages at different locations in Gazi bay. The details of different fishing techniques, and preservation of samples are presented elsewhere (Van der Velde *et al.*, 1995). The preserved fish samples in 70% ethanol were transported to The Netherlands for definitive identification to establish the fish fauna composition. Sub-samples of muscle tissue of various species were taken from fresh fishes and subsequently dried and later on analysed for stable isotopes.

The fishes were identified to the species level using the literature (Randall & Lubbock, 1981; Randall & Randall, 1981; Allen, 1985; Allen & Talbot, 1985; Smith & Heemstra, 1986; Pietsch & Grobecker, 1987; Compagno *et al.*, 1989; Randall *et al.*, 1990; Randall & Heemstra, 1991; Randall, 1992; Heemstra & Randall, 1993; Van Egmond & Randall, 1994). After identification into species and measuring of their total length, each fish specimen was blotted dry and weighed for its wet weight. Percentage calculations were made at family level in order to get a broad view of dominance in abundance and biomass. Based on the total lengths, the fish fauna of each zone was divided into length classes (using 5 cm intervals) and expressed in percentage. The maximum length of each fish species was determined from the literature. The degree to which the actual size distribution differs from the potential maximum length (literature values) was calculated using the following equation which will give an overall idea of growth potential for the fishes in the various zones:








- | | | |
|--|--|---|
|  Mangrove |  Intertidal flat with seagrass (<30%) |  Intertidal flat |
|  Mainland |  Subtidal seagrass (30 - 100%) | |

Fig.1. Distribution of different habitats and locations of sampling sites in Gazi bay, Kenya (A = 5, 8, 15, 20, 28 and B = 16, 21, 24, 26, 27, 38 NIOP; for details refer Appendix 1).

- - Netherlands Indian Ocean Programme
- - STD III Programme
- - Studies on annual occurrence, abundance and diversity

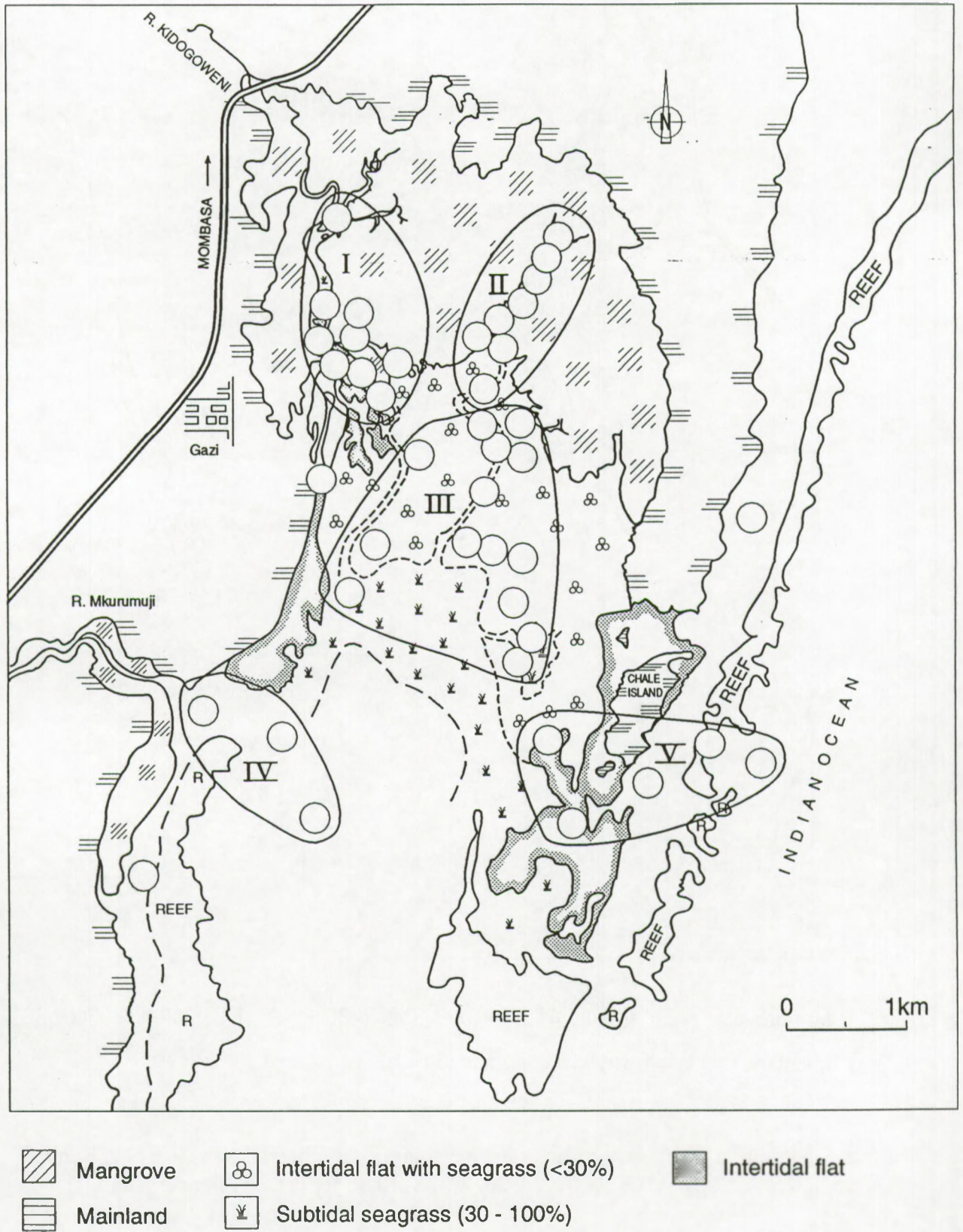


Fig.2. Map of Gazi bay showing the five zones, each representing a particular biotope.

$$Y = \frac{\sum_{t=0}^{t=n} vP}{\sum_{t=0}^{t=n} vR} \times 100$$

Where, vP is the potential abundance of size group x (x value in %), vR is the actual abundance of size group x (x value in %) and Y is the degree of difference from the actual size to the potential size.

In order to estimate the annual occurrence, abundance and diversity of fishes at Gazi bay, also 2 habitats (western mangrove creek and seagrasses) have been sampled (Fig. 1), during August 1993 - July 1994. Fishes were collected at fortnightly intervals using a seine net made of knotless netting with a stretched mesh size of 1.5 cm. Sampling was done for 10 - 15 minutes during the period of low tide. Samples were preserved in 10% formalin and all fishes were identified to species. Identified species were classified according to the trophic position based on examination of stomach contents and descriptions of their diet from the literature (Smith & Heemstra, 1986).

The data of the fish catches were processed using SAS (Statistical Analysing System). Computer programs like TWINSpan and FLEXCLUS were used for the clustering of the data. A number of ecological indices like Shannon-Wiener diversity (H') and Pielou's evenness index (J') were used to describe the structure of the fish community and also to enable comparisons between the zones.

Isotope analyses

For the stable isotope composition, several size classes of some fish species were investigated which were caught all over the Gazi bay. Dry muscle tissue of the fishes was lyophilized and ground to a fine powder. Samples were combusted using a CN analyser (NA1500) in on-line with a CT-NT Finnigan Mat Trapping Box, in which the CO_2 produced is submitted to a cryopurification treatment. The CO_2 is then analysed in the Delta E Finnigan Mat Isotope Ratio Mass Spectrometer. In order to get reproducible results and to avoid problems of air contamination a separate cryopurification method was set up for the measurement of $\delta^{15}N$. This is a stainless-steel system on-line with the CN analyser. The N_2 gas is trapped in a stainless steel tube filled with molecular sieve. This tube is then connected manually to the Mass Spectrometer to measure the $^{15}N/^{14}N$ ratio.

Results are expressed using the δ notation.

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \text{ (‰)}$$

where, $X = ^{13}C$ or ^{15}N and $R = ^{13}C/^{12}C$ or $^{15}N/^{14}N$

The National Bureau of standards (NBS) isotope standard NBS-19 was used as a working standard for carbon. The final values of $\delta^{13}C$ are expressed relative to the PDB (Pee Dee Belemnite) standard. The standard deviation on the average of ten measurements of the same gas sample is generally $< 0.04\text{‰}$. High-purity tank nitrogen gas was used as working standard for nitrogen during sample analysis. This working standard was calibrated against N1 and N2 ammonium sulphate (IAEA in Vienna) for $\delta^{15}N$ (Minagawa *et al.*, 1984, Nevins *et al.*, 1985). The values of $\delta^{15}N$ are reported relative to nitrogen in air. The standard deviation on the average of ten measurements of the same gas sample is generally $< 0.1\text{‰}$ and standard deviation of the analysis of ten aliquots of the same tissue sample is 0.2‰ .

RESULTS AND DISCUSSION

A total number of 3375 individuals representing 54 families and 162 species, was collected from Gazi bay, Kenya during NIOP and STD III programmes (Table 1). The highest number of 96 species was observed in Zone III and lowest number of species was recorded in Zone IV. Out of 162 species, *Leptoscarus vaigiensis* (Scaridae) was the only species common in all five zones.

The number of species collected from the Gazi bay (162) was very high when compared with other studies in tropical, subtropical and temperate regions (Table 2). The comparison of present results with the number of species collected in different studies is rather difficult, due to variations in the abiotic environment, habitat heterogeneity, sampling techniques and sampling efforts. However, the number of species in Gazi bay was found to be higher than nearby Tudor creek, Kenya (Little *et al.*, 1988).

Benthivores were dominant in the zone I (Fig. 3). High ratio of benthivores was mainly caused by the dominance of Gobiidae particularly *Gnatholepis cauerensis* and *Periophthalmus sobrinus* which are generally bottom dwelling fishes and feed at the bottom surface of the western mangrove creek. A higher percentage of zooplanktivores in zone I was due to *Atherinomorus lacunosus*. In eastern mangrove creek (zone II), high ratio of zooplanktivores resulted by the high presence of Apogonidae (*Sphaeramia orbicularis*). Almost half of the occurring fishes in zone III were herbivores (42%) such as Scaridae and Siganidae. Piscivores represented by Plotosidae (*Plotosus lineatus*) were more dominant in zone IV. Zone V was totally dominated by the benthivores (65%) and Labridae (*Cheilo inermis*) was the most dominant family. In comparison, a low occurrence of zooplanktivores (6%) and high presence of omnivores was recorded in zone V (see Fig. 3).

The length classes of the fishes observed in five zones indicate that most fishes collected during NIOP and STD III programmes were sub-adults or juveniles (Fig. 4). Such a high proportion of juveniles in the catches is typical of all other studies of mangrove and seagrass beds (Laegdsgaard and Johnson, 1995, and therein). The size group of 5-10 cm length class was most dominant in all zones except zone IV. This is possibly due to relatively lower number of individuals (35) in the zone IV. In addition, out of 35 individuals, 12 were represented by Apogonidae (*Siphamia mossambica*), a small species hiding between the spines of sea urchins like *Diadema* sp. which were generally grow smaller in size (maximum total length = 4 cm, Smith & Heemstra, 1986). From the actual length of fishes in each zone, the potential maximum length of fishes was calculated. The zone III recorded the maximum potential growth degree of 3.7 followed by zone V (3.0), zone I (2.9) and zone II (2.5). The lowest value (2.1) was accounted for zone IV which means that the most fishes caught in zone IV were already in adult stage and almost reached their maximum length.

The relative percentage abundance and weight of each family was calculated from the actual number and weight (wet weight) of each species. In order to get a clear view of the dominance of species at family level, the five highest abundant families in number (N%) and weight (W%) were listed for each zone (Table 3). Apogonidae, Scaridae (4 out of 5 zones), Lutjanidae and Labridae (2 out of 5) were most dominant families in the five zones. The families of Congridae (3 out of 5), Plotosidae, Scaridae and Serranidae (2 out of 5) were more dominant in biomass (W%). The results also shows that the high abundances (N%) of families were not resulted in high biomasses (W%). In general, the high biomass of each zone mainly contributed by the families with lower abundance except in zone III (Table 3). This is due to families with low abundance which have larger individuals and therefore a high weight. For example, Congridae (eels) was found to be low in abundance but high in biomass because of their large size.

The diversity indices H' and J' were found to be different for five zones (Table 4). A significant variation was recorded ($P < 0.01$) in the number of species and number of individuals ratios of total fish between these zones. The Shannon-Wiener diversity index ranged from 2.22 in zone II to 3.18 in zone III (Table 4). The highest number of individuals (2353), species (91) and families (35) were also recorded in zone III. The greater differences in the number of individuals of each species might be caused the maximum diversity index in zone III. For example, Scaridae accounted for 788 individuals out of 2353. The highest Pielou evenness indice (J') was observed in Zone IV (0.85) and lowest in zone II (0.65). This indicates that although zone IV supported fewer number of species, a higher proportion of species were evenly distributed than in other zones. The statistical analysis programmes such as TWINSpan and FLEXCLUS were used to group the fishes at the family and species levels (Fig. 5 and

Tables 5 & 6). Only the beam trawl data were used for this analysis.

Clustering the compositions of the fish catches at the family level yielded 3 distinguishable groups. The first group of samples (cluster A, Fig. 5) represents fish catches near the mangrove area. The second group of samples (cluster B, Fig. 5) consists of samples from sites in seagrass meadows in the bay. The third group (cluster C, Fig. 5) consists of two samples taken at sites with little or no vegetation. The site 12 was not considered for the analysis, because no fish were caught at this site. The average similarity between the groups created with TWINSpan is relatively low. The isolation (the average similarity of the samples within the groups divided by the average similarity between the groups, Table 3) of clusters A and B is low, implying a high similarity between the clusters. Despite this, the distinction between the clusters was maintained because of the occurrence of specific families in the clusters. Muraenidae, Teraponidae, Haemulidae, Blenniidae and Gobiidae were specific for cluster A, while Synodontidae and Lutjanidae were only present in cluster B. Monacanthidae and Ostraciidae were only found at the sites of cluster C, while Labridae and Diodontidae were also found with high frequencies. High frequencies of Syngnathidae and Platycephalidae were observed in the samples of clusters B and C, respectively. Plotosidae were more frequent in cluster D.

The clustering of the data at the species level showed a similar pattern. At the third level of the hierarchic clustering programme TWINSpan two groups were distinguished (Fig. 5). In contrast with the clustering at family level, the samples taken at sites 8 and 10 did not constitute a separate group. Furthermore, the sample of site 5 was joined with the samples of sites 2, 3 and 4 (cluster A of the clustering at family level). These samples were grouped together because *Apogon thermalis*, *Foa brachygramma*, *Plectorhinchus gaterinus*, *Lethrinus harak*, *Petroscirtus mitratus*, *Siganus stellatus*, *Bothus pantherinus* and *Arothron immaculatus* were only present in this cluster. The species of *Apogon nigripes* was found only in cluster A of the clustering at species level. In general, the distinction between the sampling sites from the seagrass meadows near the mangrove area and those from seagrass beds in the bay remained intact.

A total of 108 species belonging to 51 families have been collected during the period of August 1993 - July 1994 for studying the seasonal occurrence of different fish species in Gazi bay (Table 5). The western mangrove creek harboured 65 species and seagrass beds accounted for 90 species. In this mangrove creek, the Gerreidae and Clupeidae families were found more frequently and represented about 59% of the total number of individuals collected in the western mangrove creek (Table 6). Scaridae (16.5%) was the most common family in the seagrass beds.

The fish communities of Gazi bay were found to be similar in structure to that of Tudor creek situated north and west of Mombasa Island, Kenya (Little *et al.*, 1988). Gazi bay fish community was dominated by few species (*Geres oyena* and *Sardinella gibbosa*) which contribute more than 65% of the individuals recorded in the western mangrove creek. Like Gazi bay, Tudor creek has also dominated by few species (*Spratelloides delicatulus*, *Plotosus lineatus* and *G. oyena*) and accounted for approximately 70% of the total number of individuals (Little *et al.*, 1988). Stoner (1986) has also identified three types of species being dominant of the Western Atlantic mangrove creek near Puerto Rico. In Kenya, Gazi and Tudor creeks exhibits the same state of affair where Gobiidae, Gerreidae and Plotosidae families dominated the total population of fishes. Elsewhere, similar results have been also reported from the mangrove creeks (Austin, 1971; Arancibia *et al.*, 1980; Phillips, 1981; Blaber, 1980; Ntiba *et al.*, 1993).

The ecological diversity indices H' and J' of the community structure were similar for the western mangrove creek ($H' = 1.065$; $J' = 0.99$) and seagrass beds ($H' = 1.067$; $J' = 0.99$) (Table 7). This high similarity in community structure between the mangrove creek and seagrass beds reflects the high proportion of species common to both areas (42%). Out of 108 species, 45 species were mostly widespread in both mangrove creek and seagrass beds and dominate the catches in terms of individuals, thereby strongly influencing community structure. In the present study, the important overlapping families were Lutjanidae, Siganidae, Mugilidae, Scaridae, Carangidae and Teraponidae. These families are zooplanktivores, benthivores or herbivores. Thallot and Kulbit (1988) have reported the overlapping of fish species existing among the mangroves, coral reefs and soft bottoms with a similarity of 36 common species representing the trophic status of carnivores and piscivores.

During the NIOP programme, *Archamia mozambiquensis*, *A. fucata*, *Apogon guamensis*, *Conger cinereus cinereus*, *Fowleria aurita*, *Gazza minuta*, *Leptoscarus vaigiensis*, *Paramonacanthus barnardi*, *Plotosus lineatus*, *Parascorpaena mossambica* and *Siganus sutor* were analysed for their stable isotope composition. *Archamia mozambiquensis*, *A. fucata* and *Gazza minuta* were left out of

the scheme since these fishes were found in dead state and floating at the water surface and their origin is unknown. These species were also not caught alive within the area investigated. In addition during the STD III programme specimens of different size (juvenile to adults) of some other fish species were analysed for stable carbon and nitrogen isotope composition viz., *Siganus sutor* (herbivore) and *Sphyaena barracuda* (piscivore). The $\delta^{13}\text{C}$ values for *Siganus sutor* ranged between -14.36 to -21.58 ‰ and for *Sphyaena barracuda* ranged between -12.26 and -20.3 ‰ (Fig. 6). The $\delta^{13}\text{C}$ values of mangrove leaves range between -24.28 and -29.71 ‰ and the seagrasses range between -10.07 ‰ and -19.82 ‰ (Hemminga *et al.*, 1993; Rao *et al.*, 1993; Woitchik *et al.*, 1994). For *Siganus sutor* it appears that the smaller individuals (between 5 and 16 cm), have $\delta^{13}\text{C}$ values ranges between -14 and -21 ‰ (Fig. 7) and large individuals (20-25 cm) show a more narrow range of $\delta^{13}\text{C}$ values (-15 to -17 ‰). This suggests that smaller fishes grow up between seagrass beds near the mangrove area and seagrass meadows further away while larger ones are feeding mainly in the seagrass meadows. Specimens of *Sphyaena barracuda* showed less variability in $\delta^{13}\text{C}$ with size. Data for the 30 cm individuals, however showed larger unexplained variation.

As expected, the $\delta^{15}\text{N}$ values of the analysed fishes indicates a clear distinction between the piscivores and herbivores (Fig. 8) showing the higher trophical level of *Sphyaena barracuda* with respect to *Siganus sutor*. For *Sphyaena barracuda* no correlation is apparent between the $\delta^{15}\text{N}$ value and length. For *Siganus sutor* the data indicate higher $\delta^{15}\text{N}$ value for the larger specimens (Regression coefficient: $y = 6.55 + (0.097 \pm 0.025)x$; $r^2 = 0.43$; $P < 0.001$). The clustering of the stable radio isotope data with feeding characteristics of the fish species based on literature data shows that an overlap in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios of the various groups exists (Fig. 9, for details refer to Van der Velde *et al.*, 1994). However, three groups showed clear differences in stable isotope ratios viz., herbivores, piscivores and zooplanktivores/benthivores. With regards to the use of the sites as foraging grounds for the fish, it should be stressed that a higher proportion of piscivore/benthivore fish were present in or near channels and creeks. Since sites at a greater distance from the channel showed a somewhat lower relative occurrence of fish predators. This indicates that a number of fish species did not use the sites as a permanent habitat but only as foraging grounds.

Conclusions

- * A total of 3375 individuals representing 54 families and 162 species was collected from Gazi bay during the NIOP and STD Programmes.
- * The number of species collected from the Gazi bay (162) was very high when compared with other studies in tropical, sub-tropical and temperate regions.
- * Intertidal seagrass beds (zone III) harboured the highest number of species and showed the highest diversity.
- * The length classes of the fishes recorded in five zones indicate that most fishes in these zones were sub-adults and juveniles (approx. 90%).
- * The diversity indices H' and J' were found to be different for different zones in Gazi bay. The Shannon-Wiener diversity index (H') ranged from 2.22 in zone II to 3.18 in zone III. The highest Pielou evenness indice (J') was observed in zone IV (0.85) and lowest in zone II (0.65).
- * The values of $\delta^{15}\text{N}$ indicates a clear distinction between the piscivore and herbivore fishes in the case of *Sphyaena barracuda* and *Siganus sutor*.
- * $\delta^{13}\text{C}$ values indicate that seagrass beds are the main foraging grounds for the species analysed.
- * Clustering of the catch data showed that the fish assemblage of seagrass beds near the mangroves differed in species composition from those in the bay. This trend is accompanied with a change in the use of the seagrass beds as foraging grounds. This indicates that predator-prey relationships may play an important role in the structuring of the fish assemblages of seagrass beds.
- * Isotope analysis of muscle tissue of a selected number of fish species allowed the distinction of three groups with some overlap viz. herbivores, zooplanktivores and piscivores.

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Table 1. Abundance by numbers of species recorded in the samples collected from Gazi Bay, Kenya, during the Netherlands Indian Ocean Programme in June 1992 and the STD III Programme in October 1994.

Species (author)	Number of individuals					Total
	Zones					
	I	II	III	IV	V	
ACANTHURIDAE (herbivorous)						
<i>Acanthurus thompsonii</i> (Fowler, 1923)	0	0	1	0	0	1
<i>Naso brevirostris</i> (Valenciennes, 1835)	0	0	1	0	0	1
ANGUILLIDAE (piscivorous)						
✓ <i>Anguilla bicolor bicolor</i> (McClelland, 1844)	0	2	0	0	0	2
ANTENNARIIDAE (piscivorous)						
<i>Antennarius coccineus</i> (Lesson, 1831)*	-	-	-	-	-	-
<i>Antennarius pictus</i> (Latreille, 1804)	0	0	0	0	1	1
<i>Antennarius nummifer</i> (Cuvier, 1817)*	-	-	-	-	-	-
<i>Histrio histrio</i> (Linnaeus, 1758)	1	2	0	0	0	3
APOGONIDAE (zooplanktivorous)						
<i>Apogon cooki</i> (Macleay, 1881)	0	0	24	0	0	24
<i>Apogon fraenatus</i> (Valenciennes, 1832)	1	0	0	0	0	1
✓ <i>Apogon guamensis</i> (Valenciennes, 1832)	0	11	20	0	0	31
<i>Apogon lateralis</i> (Valenciennes, 1832)	2	3	0	0	0	5
<i>Apogon nigripes</i> (Playfair & Günther, 1866)	0	0	8	0	0	8
• <i>Apogon savayensis</i> (Günther, 1871)	0	3	8	0	0	11
• <i>Apogon thermalis</i> (Cuvier, 1829)	7	0	117	0	0	124
<i>Archamia fucata</i> (Cantor, 1850)*	-	-	-	-	-	-
<i>Archamia mozambiquensis</i> (Smith, 1961)*	-	-	-	-	-	-
• <i>Cheilodipterus quinquelineatus</i> (Cuvier, 1828)	0	0	19	0	0	19
<i>Foa brachygramma</i> (Jenkins, 1903)	1	0	17	0	4	22
✓ <i>Fowleria aurita</i> (Valenciennes, 1831)	0	0	105	0	2	107
<i>Siphamia mossambica</i> (Smith, 1955)	0	0	0	12	0	12
✓ <i>Sphaeramia orbicularis</i> (Kuhl & van Hassel, 1828)	4	80	2	0	0	86
ATHERINIDAE (zooplanktivorous)						
• <i>Atherinomorus lacunosus</i> (Forster, 1801)	135	0	0	0	0	135
BELONIDAE (piscivorous)						
✓ <i>Tylosurus crocodilus crocodilus</i> (Peron & LeSueur, 1821)	1	0	1	0	0	2
BLENNIIDAE (benthivorous)						
<i>Istiblennius andamensis</i> (Day, 1870)*	-	-	-	-	-	-
<i>Petroscirtes breviceps</i> (Valenciennes, 1836)	1	1	9	0	0	11
<i>Petroscirtes mitratus</i> (Rüppell, 1830)	1	2	42	0	1	45
BOTHIDAE (benthivorous)						
<i>Bothus panterinus</i> (Rüppell, 1830)	9	0	5	1	1	16
CARANGIDAE (zooplanktivorous)						
<i>Caranx papuensis</i> (Alleyne & Macleay, 1877)*	-	-	-	-	-	-
CARAPIDAE (benthivorous)						
<i>Carapus mourlani</i> (Petit, 1934)*	-	-	-	-	-	-
<i>Carapus parvipinnis</i> (Kaup, 1856)*	-	-	-	-	-	-

CENTRISCIDAE (zooplanktivorous)							
<i>Aeoliscus punctatus</i> (Bianconi, 1855)	0	0	2	1	0	3	
CHAETODONTIDAE (zooplanktivorous)							
<i>Chaetodon auriga</i> (Forsskål, 1775)*	-	-	-	-	-	-	
<i>Chaetodon lunula</i> (Lacépède, 1803)	3	0	0	0	0	3	
<i>Chaetodon xanthocephalus</i> (Bleeker, 1853)	0	0	4	0	0	4	
CLUPEIDAE (zooplanktivorous)							
<i>Herklotsichthys quadrimaculatus</i> (Rüppell, 1837)*	-	-	-	-	-	-	
CONGRIDAE (piscivorous)							
→ ✓ • <i>Conger cinereus cinereus</i> (Rüppell, 1830)	4	6	1	0	1	12	14
CONGROGADIDAE (benthivorous)							
<i>Halidesmus</i> sp.*	-	-	-	-	-	-	
CYNOGLOSSIDAE (benthivorous)							
<i>Cynoglossus gilchristi</i> (Ogilby, 1910)	1	0	0	0	0	1	
<i>Cynoglossus lachneri</i> (Menon, 1977)*	-	-	-	-	-	-	
ELEOTRIDAE (benthivorous)							
<i>Butis melanostigma</i> (Hamilton-Buchanan, 1822)	2	0	0	0	0	2	
<i>Eleotris melanostoma</i> (Bleeker, 1852)	1	0	0	0	0	1	
ENGRAULIDAE (zooplanktivorous)							
<i>Stolephorus holodon</i> (Boulenger, 1900)	17	0	0	0	0	17	
DACTYLOPTERIDAE (benthivorous)							
<i>Dactyloptena orientalis</i> (Cuvier, 1829)*	-	-	-	-	-	-	
<i>Dactyloptena peterseni</i> (Nyström, 1887)	1	0	0	0	0	1	
DASYATIDAE (benthivorous)							
→ • <i>Dasyatis kuhlii</i> (Müller & Henle, 1841)	0	0	0	0	2	2	4
✓ • <i>Taeniura lymma</i> (Forsskål, 1775)	0	2	2	0	0	4	3
DIODONTIDAE (omnivorous)							
<i>Diodon holocanthus</i> (Linnaeus, 1758)	0	0	6	0	1	7	
<i>Lophodiodon calori</i> (Bianconi, 1855)	0	0	6	0	0	6	
FISTULARIIDAE (piscivorous)							
<i>Fistularia commersoni</i> (Rüppell, 1838)	1	0	2	0	0	3	
GERREIDAE (benthivorous)							
→ <i>Gerres filamentosus</i> (Cuvier, 1829)	4	0	0	0	0	4	
✓ • <i>Gerres oyena</i> (Forsskål, 1775)	91	1	15	0	0	107	20
GOBIIDAE (benthivorous)							
→ <i>Amblygobius albimaculatus</i> (Rüppell, 1830)	0	0	4	0	1	5	
<i>Amblygobius sphynx</i> (Valenciennes, 1837)	0	0	1	0	0	1	
<i>Asterropteryx semipunctatus</i> (Rüppell, 1830)	0	0	5	0	0	5	
<i>Favonigobius reichei</i> (Bleeker, 1953)*	-	-	-	-	-	-	
<i>Gnatholepis cauerensis</i> (Smith, 1959)	131	0	20	0	0	151	
<i>Heteroleostis zonata</i> (Fowler, 1934)*	-	-	-	-	-	-	
<i>Oplopomus oplopomus</i> (Valenciennes, 1837)	4	0	0	0	0	4	
✓ • <i>Periophthalmus sobrinus</i> (Eggert, 1935)	24	0	0	0	0	24	3
<i>Gobiidae</i> sp.*	4	0	0	0	0	4	

HAEMULIDAE (omnivorous)

<i>Plectorhynchus gaterinus</i> (Forsskål, 1775)	0	1	15	0	0	16	
<i>Plectorhynchus gibbosus</i> (Lacépède, 1802)	0	1	0	0	0	1	4

HEMIRAMPHIDAE (herbivorous)

<i>Hemiramphus far</i> (Forsskål, 1775)	17	0	0	0	0	17	
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HOLOCENTRIDAE (benthivorous)

<i>Neoniphon sammara</i> (Forsskål, 1775)	0	0	1	0	0	1	
<i>Sargocentron diadema</i> (Lacépède, 1801)	0	0	1	0	0	1	
<i>Sargocentron ittodai</i> (Jordan & Fowler, 1903)	0	0	1	0	0	1	

LABRIDAE (benthivorous)

<i>Cheilinus bimaculatus</i> (Valenciennes, 1840)	0	0	4	0	6	10	
<i>Cheilinus chlorourus</i> (Bloch, 1791)	1	0	2	0	0	3	
<i>Cheilinus oxycephalus</i> (Bleeker, 1953)	0	0	3	1	2	6	
<i>Cheilinus trilobatus</i> (Lacépède, 1801)	0	2	16	0	4	22	2
<i>Cheilinus undulatus</i> (Rüppell, 1835)	0	1	0	0	0	1	
<i>Cheilo inermis</i> (Forsskål, 1775)	0	0	32	0	36	68	24
<i>Cymolutes praetextatus</i> (Quoy & Gaimard, 1834)	0	0	0	0	2	2	
<i>Epibulus insidiator</i> (Pallas, 1770)	0	0	3	0	0	3	
<i>Halichoeres dussumieri</i> (Valenciennes, 1839)*	-	-	-	-	-	-	
<i>Halichoeres scapularis</i> (Bennett, 1831)	0	0	2	0	0	2	
<i>Halichoeres</i> sp.	0	0	1	0	0	1	
<i>Novaculichthys macrolepidotus</i> (Bloch, 1791)	0	0	1	0	8	9	
<i>Pteragogus flagellifer</i> (Valenciennes, 1839)	0	0	5	0	0	5	
<i>Stethojulis albovittata</i> (Bonnaterre, 1788)	0	0	1	0	8	9	
<i>Stethojulis interrupta</i> (Bleeker, 1851)*	-	-	-	-	-	-	
<i>Stethojulis strigiventer</i> (Bennett, 1832)	0	1	106	0	2	109	8
<i>Thalassoma herbraicum</i> (Lacépède, 1801)	0	0	0	0	4	4	

LEIOGNATHIDAE (benthivorous)

<i>Gazza minuta</i> (Bloch, 1797)*	-	-	-	-	-	-	
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LETHRINIDAE (benthivorous)

<i>Lethrinus harak</i> (Forsskål, 1775)	9	0	18	0	0	27	6
<i>Lethrinus ramak</i> (Forsskål, 1775)	16	1	112	1	0	130	5
<i>Lethrinus variegatus</i> (Ehrenberg, 1830)	0	0	8	0	0	8	

LUTJANIDAE (benthivorous)

<i>Lutjanus argentimaculatus</i> (Forsskål, 1775)	3	0	0	0	0	3	
<i>Lutjanus ehrenbergii</i> (Peters, 1869)	21	8	0	0	0	29	11
<i>Lutjanus fulviflamma</i> (Forsskål, 1775)	2	1	119	0	4	126	34

MONACANTHIDAE (omnivorous)

<i>Paramonacanthus barnardi</i> (Fraser-Brunner, 1941)	0	0	49	0	0	49	
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MONODACTYLIDAE (zooplanktivorous)

<i>Monodactylus argenteus</i> (Linnaeus, 1758)	19	2	0	0	0	21	
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MORINGUIDAE (benthivorous)

<i>Moringua javanica</i> (Kaup, 1856)*	-	-	-	-	-	-	
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MUGILIDAE (herbivorous)

<i>Valamugil seheli</i> (Forsskål, 1775)	3	3	0	0	0	6	
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→ **MULLIDAE** (benthivorous)

• <i>Parupeneus barberinus</i> (Lacépède, 1801)	0	0	1	0	1	2	4
<i>Parupeneus cinnabarinus</i> (Cuvier, 1829)	0	0	4	0	0	4	
<i>Parupeneus macronema</i> (Lacépède, 1801)	1	0	0	0	0	1	
<i>Uperneus tragula</i> (Richardson, 1846)*	-	-	-	-	-	-	

→ **MURAENIDAE** (piscivorous)

<i>Echidna leucotaenia</i> (Schultz, 1943)	0	0	0	0	1	1	
<i>Echidna nebulosa</i> (Ahl, 1789)	0	0	0	0	1	1	
<i>Gymnothorax monochrous</i> (Bleeker, 1856)*	-	-	-	-	-	-	
• <i>Gymnothorax undulatus</i> (Lacépède, 1803)	0	0	4	0	6	10	6
<i>Gymnothorax</i> sp.	0	0	1	0	0	1	

OSTRACIIDAE (benthivorous)

<i>Lactoria cornuta</i> (Linnaeus, 1758)	0	0	1	2	0	3	
<i>Lactoria fornasini</i> (Bianconi, 1846)	0	0	7	0	5	12	

OPHICHTHIDAE (piscivorous)

<i>Myrichthys colubrinus</i> (Boddaert, 1781)*	-	-	-	-	-	-	
<i>Myrichthys maculosus</i> (Cuvier, 1816)*	-	-	-	-	-	-	
<i>Pisidonophis cancrivorus</i> (Richardson, 1844)*	-	-	-	-	-	-	

PLATYCEPHALIDAE (piscivorous)

<i>Onigocia oligolepis</i> (Regan, 1908)	0	0	0	0	1	1	
<i>Papilloculiceps longiceps</i> (Ehrenberg, 1829)	0	0	7	0	0	7	

→ **PLOTOSIDAE** (piscivorous)

• <i>Plotosus lineatus</i> (Thunberg, 1787)	0	0	135	2	0	137	11
• <i>Plotosus nkunga</i> (Gomon & Taylor, 1982)	0	0	14	2	0	16	2

→ **POMACENTRIDAE** (zooplanktivorous)

• <i>Abudefduf sexfasciatus</i> (Lacépède, 1801)	0	0	7	0	0	7	1
<i>Abudefduf vaigiensis</i> (Quoy & Gaimard, 1815)	1	0	2	0	1	4	
<i>Chromis dasygenys</i> (Fowler, 1935)*	-	-	-	-	-	-	
<i>Chrysiptera annulata</i> (Peters, 1855)	0	0	5	1	0	6	
<i>Chrysiptera unimaculata</i> (Cuvier, 1830)*	-	-	-	-	-	-	
<i>Dascyllus aruanus</i> (Linnaeus, 1758)	0	0	2	0	0	2	
<i>Neopomacentrus cyanomos</i> (Bleeker, 1876)	5	1	3	0	1	10	
<i>Neopomacentrus fuliginosus</i> (Smith, 1960)	56	0	1	0	0	57	
<i>Plectroglyphidodon lacrymatus</i> (Quoy & Gaimard, 1825)	0	2	1	0	0	3	
<i>Pomacentrus trilineatus</i> (Cuvier, 1830)	0	0	9	0	0	9	

RHINOBATIDAE (benthivorous)

<i>Rhinobatos holcorhynchus</i> (Norman, 1922)	0	0	0	1	0	1	
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→ **SCARIDAE** (herbivorous)

• <i>Calotomus spinidens</i> (Quoy & Gaimard, 1824)	0	0	33	0	16	49	2
<i>Hipposcarus harid</i> (Forsskål, 1775)	0	0	10	0	0	10	
• <i>Leptoscarus vaigiensis</i> (Quoy & Gaimard, 1824)	2	7	532	3	3	547	4 4
<i>Scarus collana</i> (Rüppell, 1835)	0	0	2	0	0	2	
<i>Scarus ghobban</i> (Forsskål, 1775)	4	4	21	0	2	31	
<i>Scarus psittacus</i> (Forsskål, 1775)	0	0	184	0	0	184	
<i>Scarus sordidus</i> (Forsskål, 1775)	0	0	1	0	0	1	
<i>Scarus</i> sp. 1	0	0	1	0	0	1	
<i>Scarus</i> sp. 2	0	0	4	0	0	4	

SCORPAENIDAE (benthivorous)

<i>Dendrochirus brachypterus</i> (Cuvier, 1829)	0	0	1	1	1	3	
<i>Parascorpaena mossambica</i> (Peters, 1855)	1	0	60	1	13	75	
<i>Pterois antennata</i> (Bloch, 1787)*	-	-	-	-	-	-	
<i>Pterois miles</i> (Bennett, 1828)	0	0	3	0	0	3	
<i>Synanceia verrucosa</i> (Bloch & Schneider, 1801)	0	0	1	0	0	1	

SERRANIDAE (piscivorous)

<i>Epinephelus caeruleopunctatus</i> (Bloch, 1780)	0	2	0	0	0	2	2
<i>Epinephelus malabaricus</i> (Schneider, 1801)	3	0	0	0	2	5	3
<i>Epinephelus microdon</i> (Bleeker, 1856)	0	0	1	0	0	1	1
<i>Epinephelus polypekadion</i> (Bleeker, 1849)	1	0	0	0	0	1	2
<i>Epinephelus tauvina</i> (Forsskål, 1775)*	-	-	-	-	-	-	
<i>Grammistes sexlineatus</i> (Thunberg, 1792)*	-	-	-	-	-	-	

SIGANIDAE (herbivorous)

<i>Siganus stellatus</i> (Forsskål, 1775)	0	4	7	0	0	11	
<i>Siganus sutor</i> (Valenciennes, 1835)	12	0	185	1	0	197	2 3

SILLAGINIDAE (benthivorous)

<i>Sillago chondrops</i> (Bleeker, 1849)*	-	-	-	-	-	-	
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SOLEIDAE (benthivorous)

<i>Pardachirus marmoratus</i> (Lacépède, 1802)	5	0	3	3	2	13	1
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SPHYRAENIDAE (piscivorous)

<i>Sphyrna barracuda</i> (Walbaum, 1792)	5	4	0	0	0	9	10
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SYNODONTIDAE (piscivorous)

<i>Saurida gracilis</i> (Quoy & Gaimard, 1848)	4	1	2	0	0	7	
<i>Synodus variegatus</i> (Lacépède, 1803)	0	0	1	2	1	4	

SYNGNATHIDAE (benthivorous)

<i>Hippichthys spicifer</i> (Rüppel, 1838)	2	0	0	0	0	2	
<i>Hippocampus histrix</i> (Kaup, 1853)*	-	-	-	-	-	-	
<i>Microphis brachyurus</i> (Bleeker, 1853)	0	0	0	0	1	1	
<i>Syngnathoides biaculeatus</i> (Bloch, 1785)	0	0	22	0	0	22	

TERAPONIDAE (benthivorous)

<i>Pelates quadrilineatus</i> (Cuvier, 1829)	0	1	87	0	1	89	6
<i>Terapon jarbua</i> (Forsskål, 1775)	2	0	0	0	0	2	

TETRAODONTIDAE (omnivorous)

<i>Arothron hispidus</i> (Linnaeus, 1758)	0	0	19	0	3	22	7
<i>Arothron immaculatus</i> (Bloch & Schneider, 1801)	1	0	7	0	1	9	4
<i>Arothron stellatus</i> (Bloch & Schneider, 1801)	0	0	2	0	0	2	2
<i>Canthigaster bennetti</i> (Bleeker, 1854)	0	0	0	0	5	5	
<i>Canthigaster solandri</i> (Richardson, 1844)	1	0	5	0	0	6	
<i>Canthigaster valentini</i> (Bleeker, 1853)	0	0	9	0	1	10	

TORPEDINIDAE (benthivorous)

<i>Torpedo fuscomaculata</i> (Peters, 1855)*	-	-	-	-	-	-	
Other fish species**	21	0	0	0	0	21	

*) Species collected from the sampling locations which are not included in the five zones.

**) Species to be identified.

Table 2. A selected data on the number of species reported from the mangrove ecosystem in tropical, subtropical and temperate regions in literature.

Place	Condition	Number of species	Reference
Mangrove creek, Western Puerto Rico	Tropical	59	Austin, 1971
Coastal lagoon system, Mexico	Tropical	44	Warburton, 1978
Trinity Inlet system, North Queensland, Australia	Tropical	55	Blaber, 1980
Serpentine creek, Queensland	Subtropical	45	Quinn, 1980
Seagrass meadows, Botany Bay, New South Wales, Australia	Subtropical	102	Middleton <i>et al.</i> , 1984
Labu estuary, Papua New Guinea	Tropical	48	Quinn & Kojis, 1985
Alligator creek, Queensland, Australia	Tropical	133	Robertson & Duke, 1987
Tudor creek, Kenya	Tropical	83	Little <i>et al.</i> , 1988
Embley estuary, Gulf of Carpentaria, Australia	Tropical	197	Blaber <i>et al.</i> , 1989
Klang-Langat delta of Selangor, Malaysia	Tropical	119	Chong <i>et al.</i> , 1990
Swan estuary, South Western Australia	Temperate	71	Loneragan & Potter, 1990
Moreton bay, Australia	Subtropical	46	Morton, 1990
Deception bay, South East Queensland, Australia	Subtropical	53	Laegdsgaard & Johnson, 1995
Gazi bay, Kenya	Tropical	162	Present study

Table 3. Most dominant families in relation with abundance (N%) and biomass (W%) for each zone.

	Zone I	Zone II	Zone III	Zone IV	Zone V
N%					
1	Gobiidae	Apogonidae	Scaridae	Apogonidae	Labridae
2	Atherinidae	Scaridae	Apogonidae	Plotosidae	Scaridae
3	Gerreidae	Lutjanidae	Siganidae	Scaridae	Scorpaenidae
4	Pomacentridae	Congridae	Labridae	Ostraciidae	Muraenidae
5	Lutjanidae	Sphyraenidae	Plotosidae	Scorpaenidae	Apogonidae
W%					
1	Congridae	Congridae	Scaridae	Soleidae	Muraenidae
2	Atherinidae	Dasyatidae	Plotosidae	Ostraciidae	Diodontidae
3	Gerreidae	Anguillidae	Siganidae	Plotosidae	Labridae
4	Lutjanidae	Apogonidae	Tetraodontidae	Rhinobatidae	Serranidae
5	Serranidae	Mugilidae	Lutjanidae	Scaridae	Congridae

Table 4. Ecological diversity indices for the five zones in the Gazi bay during NIOP and STD Programmes.

Zones	Ecological diversity indices		Most dominant family
	Shannon-Wiener H'	Pielou J'	
I	2.76	0.70	Gobiidae
II	2.22	0.65	Apogonidae
III	3.18	0.70	Scaridae
IV	2.36	0.85	Apogonidae
V	3.07	0.83	Labridae

Table 5. Resemblance of the samples of the clusters of the composition of the fish catches of the several locations at family level (FLEXCLUS).

Cluster	Size	Average resemblance	Most similar to	Resemblance	Isolation
E	1	1.0000	F	0.0345	29.0000
A	3	0.1065	B	0.6496	0.1639
B	5	0.5052	A	0.6496	0.7776
C	2	0.2169	B	0.1554	1.3956
F	1	1.0000	B	0.0397	25.1761

Table 6. Resemblance of the samples of the clusters of the composition of the fish catches of the several locations at species level (FLEXCLUS).

Cluster	Size	Average resemblance	Most similar to	Resemblance	Isolation
D	1	1.0000	C	0.0123	81.0000
B	4	0.3000	A	0.2173	1.3808
A	6	0.3191	B	0.2173	1.4686
C	1	1.0000	A	0.0193	51.6878

Table 7. Seasonal occurrence of families in western mangrove creek and seagrass ecosystems in Gazi Bay, Kenya during August 1993 - July 1994.

Family	No. of species	Western mangrove creek		Seagrass	
		N	N%	N	N%
DACTYLOPTERIDAE	1	0	0	2	1
BOTHEIDAE	2	0	0	8	0.6
MONOCANTHIDAE	1	1	0	0	0
CHANIIDAE	1	0	0	11	0.7
ACANTHURIDAE	3	7	0.2	2	0.1
FISTULARIIDAE	1	1	0	14	0.9
SYNGNATHIDAE	1	1	0	3	0.2
SYNODONTIDAE	1	4	0.1	4	0.3
ENGRAULIDAE	1	0	0	8	0.5
SILLANIDAE	1	20	0.5	24	1.6
GOBIIDAE	2	21	0.5	1	0.1
HAEMULIDAE	1	2	0.1	0	0
OSTRACIIDAE	1	8	0.2	0	0
SCOMBRIDAE	4	10	0.3	24	1.6
ARIIDAE	1	0	0	3	0.2
LABRIDAE	1	0	0	2	0.1
KYPHOSIDAE	1	0	0	1	0.1
ECHENIDAE	1	1	0	0	0
CHAETODONTIDAE	1	0	0	3	0.2
DRAPANIDAE	1	1	0	1	0.1
LOBOTHEIDAE	1	0	0	1	0.1
SCORPAENIDAE	3	15	0.4	1	0.1
GERREIDAE	4	1241	33.3	89	9.5
SCARIDAE	3	27	0.7	246	16.5
LETHRINIDAE	4	31	0.8	71	4.7
PLATYCEPHALIDAE	2	0	0	8	0.5
BELONIDAE	3	12	0.3	17	1.2
ACROPOMATIDAE	1	253	6.6	4	0.3
TERAPONIDAE	2	102	2.7	86	5.8
LUTJANIDAE	6	71	1.8	242	16.4
SIGANIDAE	2	155	4.1	163	11
HEMIRAMPHIDAE	1	3	0.1	16	1.1
MONODACTYLIDAE	2	54	1.5	26	1.8
LEIOGNATHIDAE	2	31	0.8	31	2.1
PLOTOSIDAE	2	120	3.1	3	0.2
CLUPEIDAE	3	1008	26.5	0	0
GATERINIDAE	1	1	0	18	1.2
CARANGIDAE	4	36	0.9	124	8.4
CHIROCENTRIDAE	1	1	0	34	2.3
EPHIPPIDAE	1	15	0.4	1	0.1
DASYATIDAE	2	0	0	11	0.7
HOLOCENTRIDAE	3	0	0	10	0.2
SERRANIDAE	3	0	0	18	1.5
MUGILIDAE	4	26	0.7	61	4.1
ATHERINIDAE	1	352	9.2	1	0.1
APOGONIDAE	4	23	0.7	1	0.1
TETRAODONTIDAE	4	10	0.3	10	0.7
MULLIDAE	7	61	1.6	47	3.1
SPHYRAENIDAE	2	78	2	28	1.9
CYNOGLOSSIDAE	2	1	0	3	0.2
SCATOPHAGIDAE	1	10	0.3	0	0

Table 8. Most dominant families of the western mangrove creek and seagrass ecosystems and their trophic status.

Family	Abundance (%)	Trophic status
Western mangrove creek		
Gerreidae	33.3	benthivore
Clupeidae	26.5	zooplanktivore
Atherinidae	9.2	zooplanktivore
Acropomatidae	6.6	zooplanktivore
Plotosidae	3.1	piscivore
Teraponidae	2.7	benthivore
Seagrass ecosystem		
Scaridae	16.5	herbivore
Lutjanidae	16.4	benthivore
Siganidae	11.0	herbivore
Gerreidae	9.5	benthivore
Carangidae	8.4	zooplanktivore
Teraponidae	5.8	benthivore

Table 9. Ecological diversity indices for the western mangrove creek and seagrass beds in Gazi bay during August 1993 - July 1994.

Ecosystem	Ecological diversity indices		Most dominant family
	Shannon-Wiener H'	Pielou J'	
Mangrove creek	1.065	0.99	Gerreidae
Seagrass beds	1.067	0.99	Scaridae

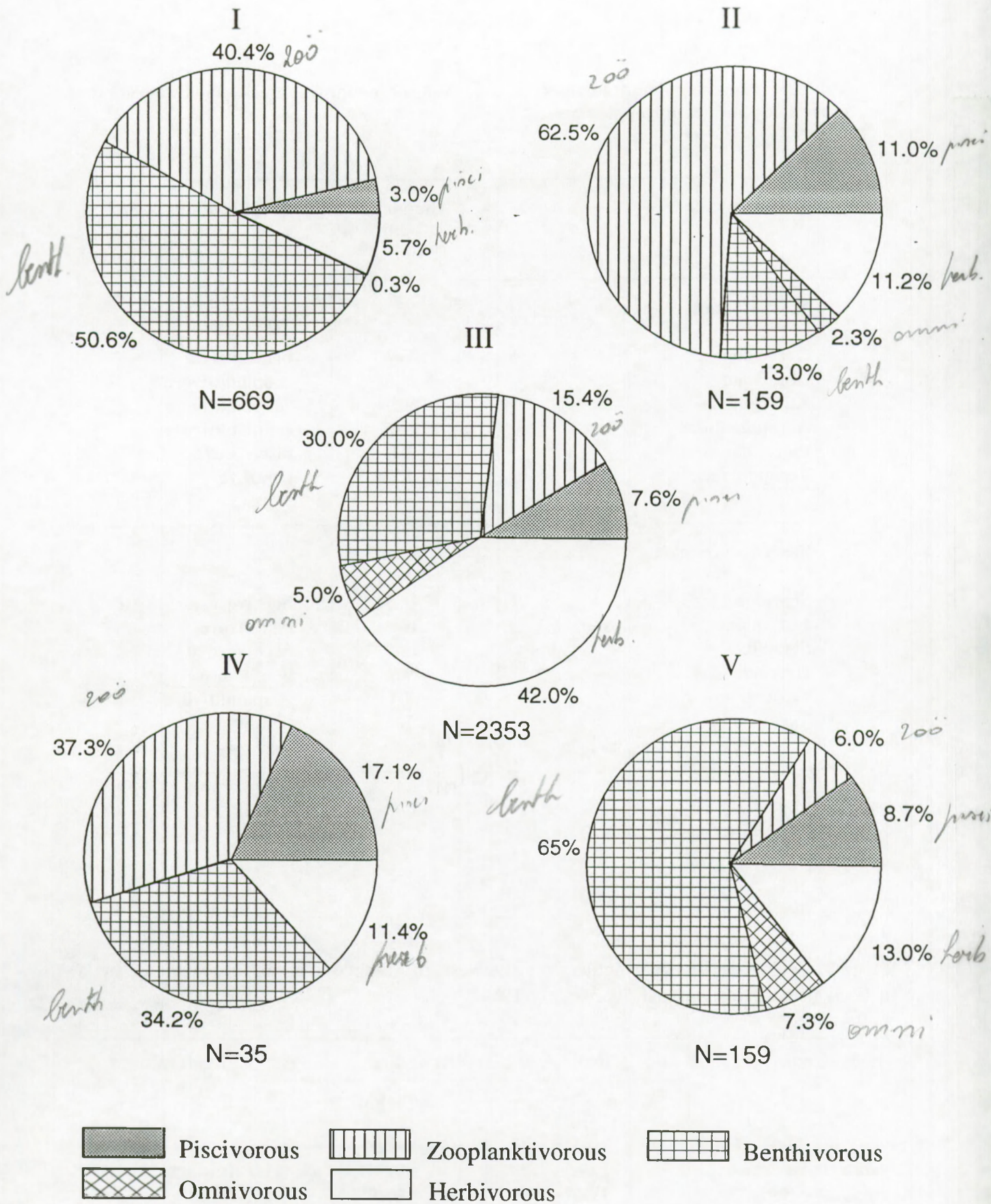


Fig.3: Shares of feeding guilds of fishes in five zones at Gazi Bay.

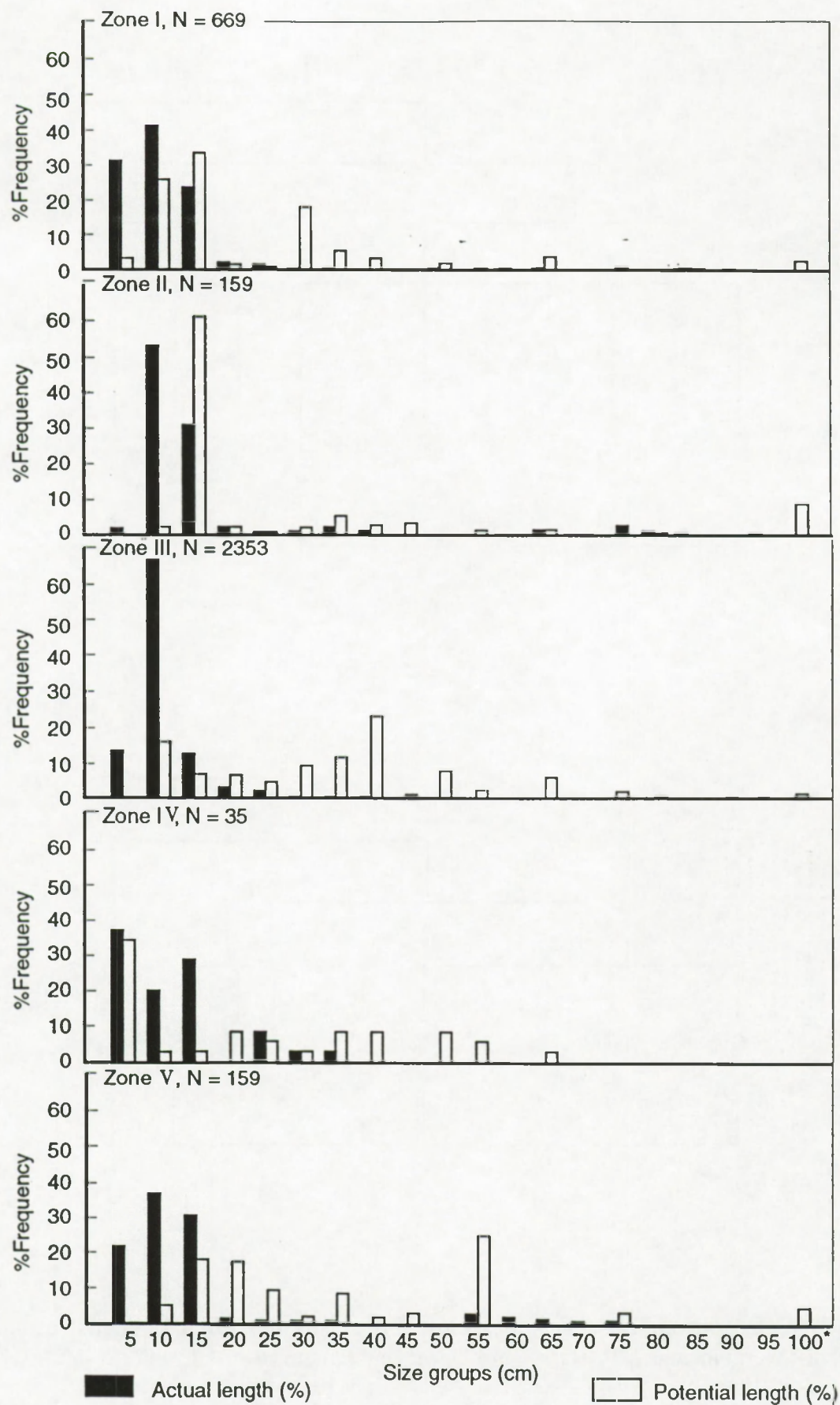


Fig.4: The percentage frequency of length classes of the fishes recorded in five zones during NIOP and STD III programmes (* included the fishes more than 100 cm length).

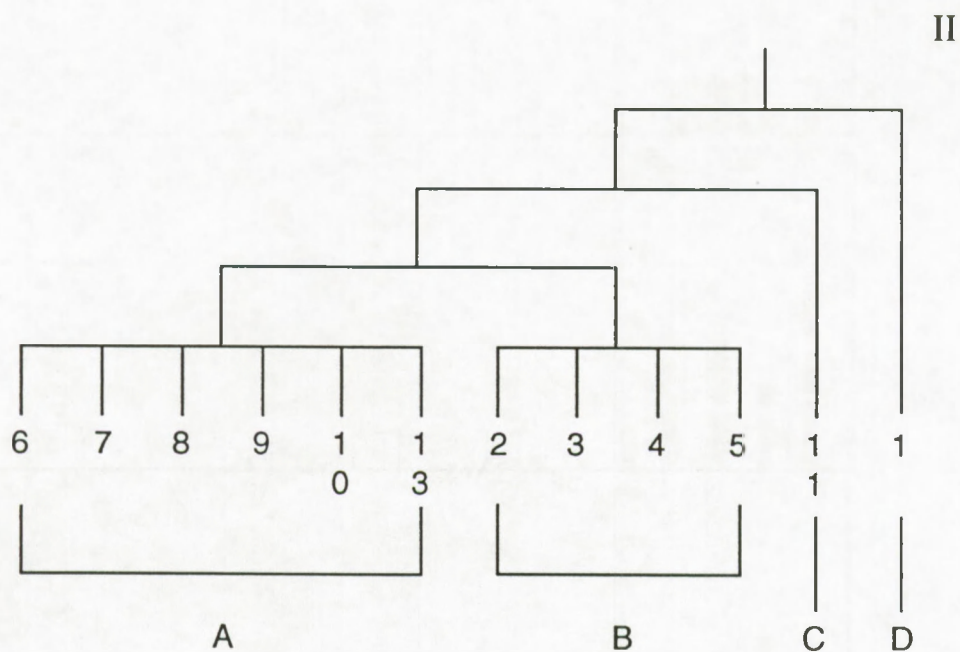
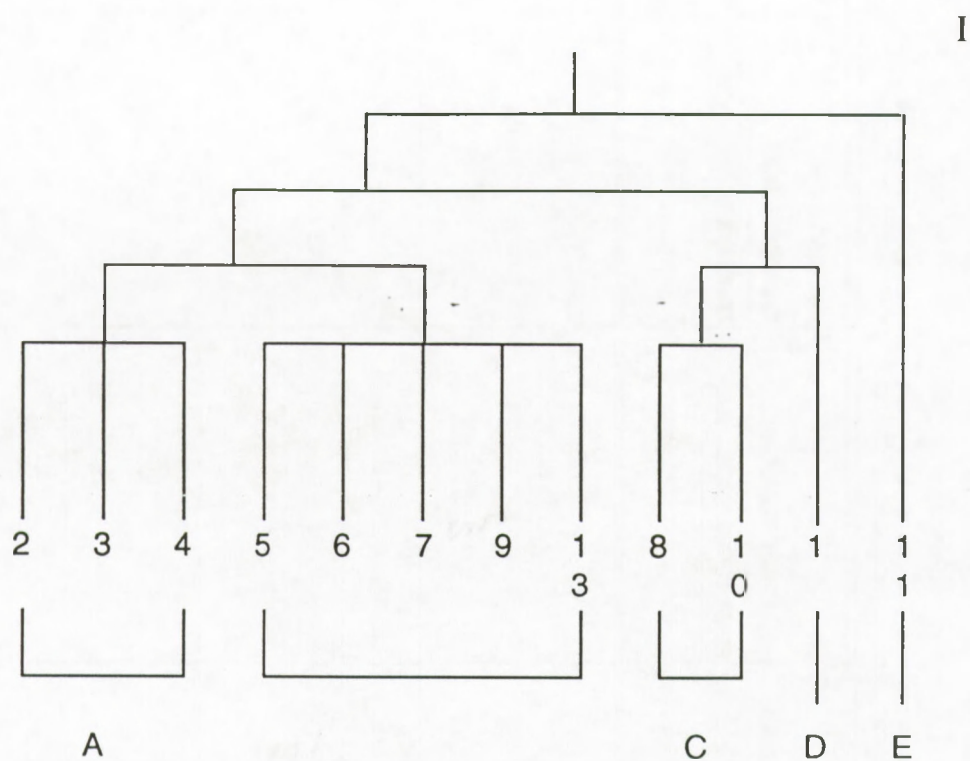


Fig.5. Dendrogram of the hierarchic clustering of the composition of the fish catches of several locations at (I) the family level, and (II) the species level (TWINSPAN).

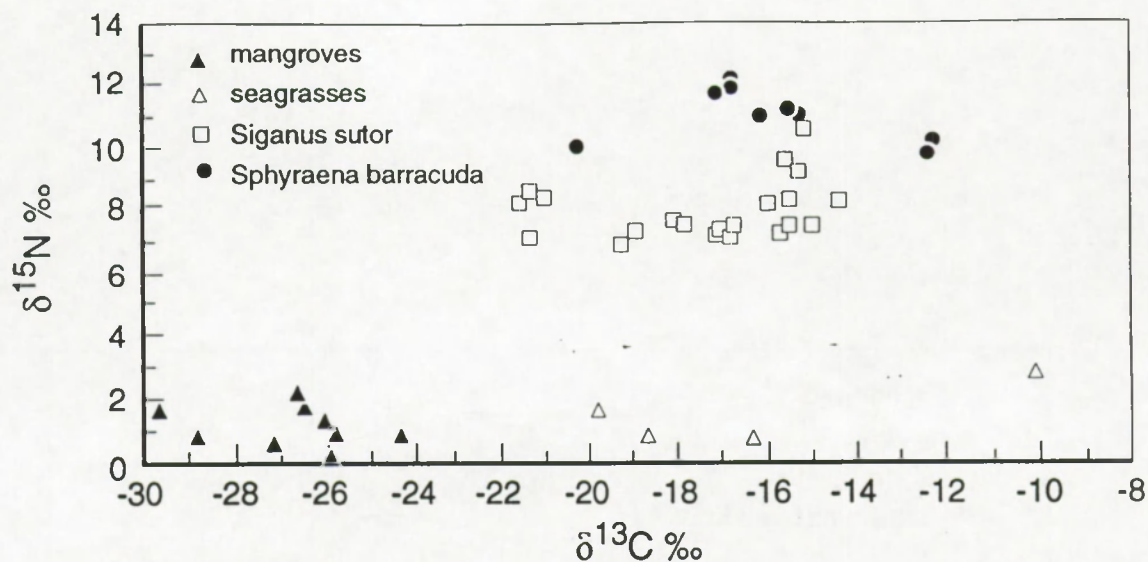


Fig.6: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the fishes *Siganus sutor* and *Sphyaena barracuda*

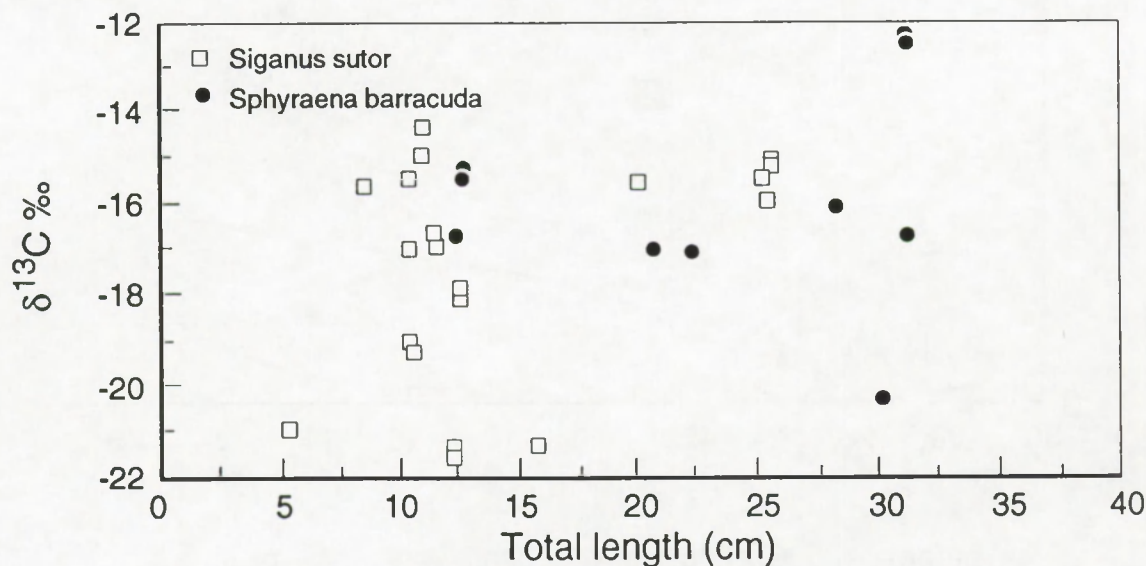


Fig.7: Relationship between length and $\delta^{13}\text{C}$ of *Siganus sutor* and *Sphyaena barracuda*

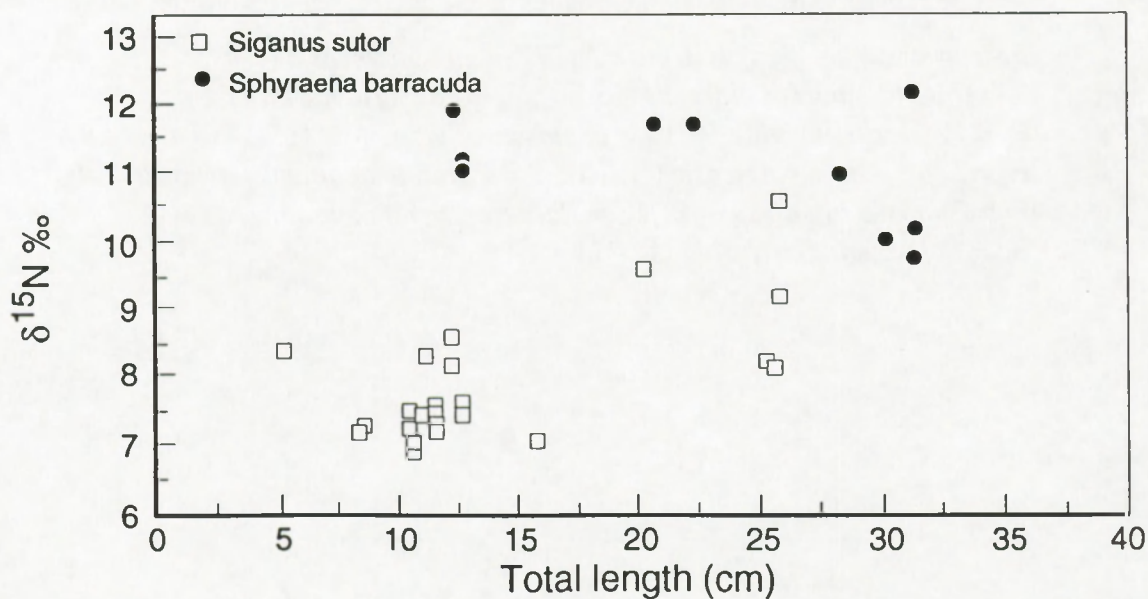


Fig.8: Relationship between length and $\delta^{15}\text{N}$ of *Siganus sutor* and *Sphyaena barracuda*

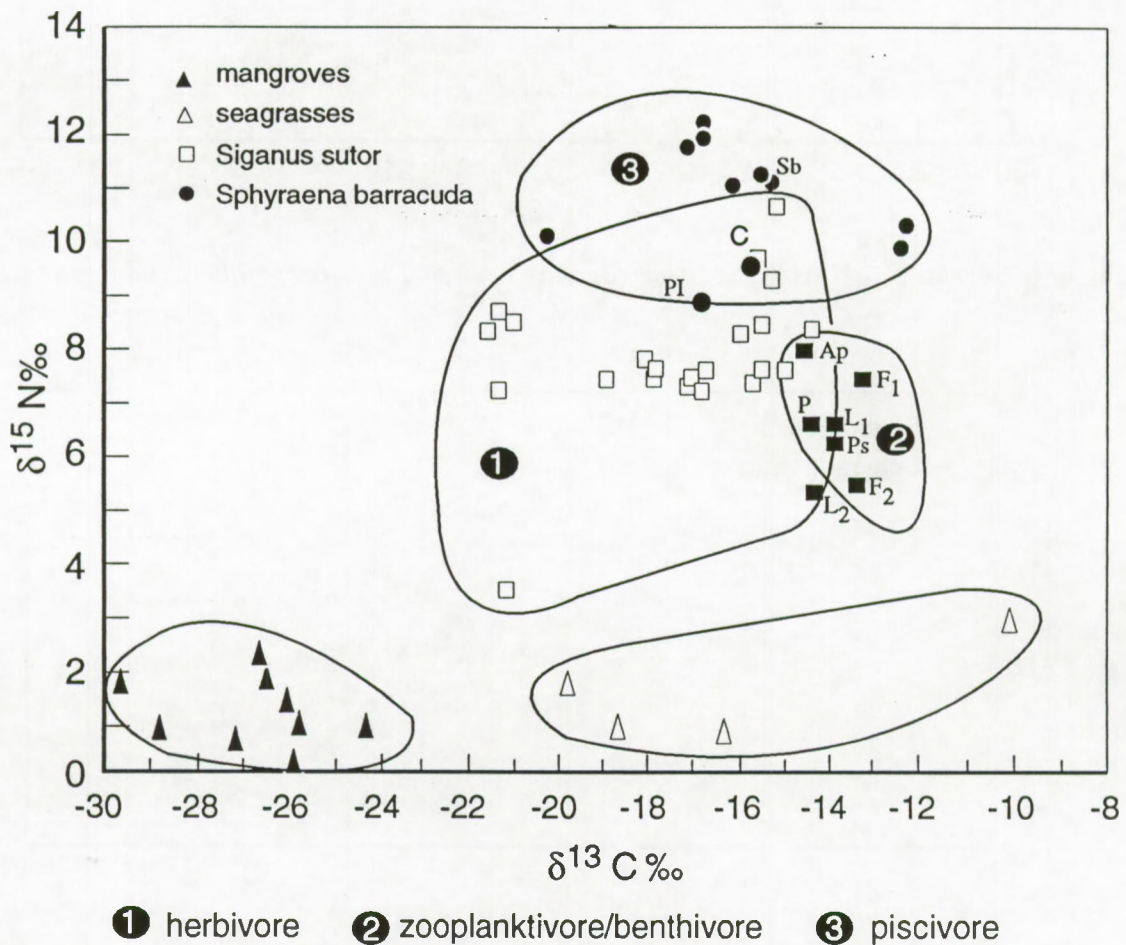


Fig.9: Stable isotope ratios ($\delta^{13}\text{C}/\delta^{15}\text{N}$) of fish muscle tissue. Combination of the isotope ratio and feeding characteristics of the fish species (literature data).

Fish species (total length in cm): Ap = *Apogon guamensis* (7-9), C = *Conger cinereus cinereus* (55-80), F₁ = *Fowleria aurita* (7-8), F₂ = *Fowleria aurita* (8-9), L₁ = *Leptoscarus vaigiensis* (15-18), L₂ = *Leptoscarus vaigiensis* (12-15), P = *Paramonacanthus barnardi* (8-10), PI = *Plotosus lineatus* (8-10), Ps = *Parascorpaena mossambica* (7-11), Sb = *Sphyaena barracuda* (12-32).

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- 21.92
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Appendix 1.

Sampling sites

During the Netherlands Indian Ocean Programme 44 sites were sampled, while during the STD III Programme 50 sites were sampled. The sampling sites were located all over the bay, in order to study as many biotopes as possible. The exact locations of the different sites are given in Fig.1.

The following numbers and codes given below, corresponds with the NIOP and STD III Programme codes used in Fig.1.

NIOP 1992

gill net: 1, 31
 beam trawl: 2, 3, 4, 6, 7, 9, 10, 13, 14, 17, 19, 23, 35, 42, 43, 44
 fike net (small): 5, 8, 15, 20, 28
 fike net (big): 16, 21, 24, 26, 27, 36
 hoop net (kubben): 11, 12, 18, 22, 25, 29, 33, 34
 dip net: 30, 40
 floating dead on water surface: 32
 fishermen's catch: 38
 sediment trap: 39
 light trap: 41

STD III Programme 1994

rotenone: rock pools, mangrove
 seine net: 1, 2, 3, 4, 5, 7, 15, 16, 26 (CS), 27 (CS), 28, 32, 37, 38, 39, 40, 41
 eel net: 6, 14
 standing fikes: 8, 9, 10, 11, 21, SF27, 31, 32, 43
 standing net: 17, 18, 25, 29, 36, 44, 47
 hoop nets (kubben): 33

The numbers of the STD III Programme, given in fig.1. are summarized in following way:

1: 8, 9, 10, 11, 12, 13
 2: 4, 19, 20, 21, 22, 23, 24
 3: 15, 16, 17, 18, 26
 4: 27, 37
 5: 25, 26 (CS), 27 (CS), 30, 32, 38, 39
 6: 24, 35, 36
 7: 42, 43, 44
 8: 40, 41, 45, 46, 47
 9: rotenone rock pools, bima trap, fishermen
 10: 28
 11: 7, 33
 12: 1, 2, 3, 4, 5, 6, 31(SF), 32 (SF)
 13: rotenone, mangroves

SPECIES COMPOSITION AND RELATIVE ABUNDANCE OF FISH AND MACRO-CRUSTACEA IN SEAGRASS BEDS, MANGROVES AND CORAL REEFS (ZANZIBAR, TANZANIA)

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INTRODUCTION

The nursery function of the main shallow water inter-linked coastal ecosystems, such as mangroves, seagrass beds and coral reefs have not been studied extensively in Tanzania. The distribution and relative abundance of larvae and juvenile fish and crustacea in the coastal waters and/or the function of the coastal ecosystems in fish recruitment have remained largely unknown, and more so in Zanzibar coastal waters. Information on recruitment in the shallow coastal waters is important in setting up management strategies for the fisheries resources.

The biological interlinkages between mangroves, seagrass beds and coral reefs can be explained by studying the temporal pattern and population structure of species in the different habitats. Some species are resident to coral reefs and use the mangrove creeks and seagrass beds as nursery grounds. From the fisheries point of view, the strength of a cohort in a given area is directly related to the distribution and abundance of juvenile stages (Smith and Richardson, 1977). The sustainability of a fishery will depend on conservation and management measures which are based on scientific information on the distribution and abundance of larvae and juveniles. There are certain advantages of using juvenile fish to monitor adult populations because early life stages are restricted to specific areas and seasons and can easily be sampled quantitatively (Smith and Richardson, 1977).

The three habitats, ie. mangrove, seagrass beds and coral reefs are known to offer a suitable environment for larvae and juvenile fish growth and have been indicated as important nursery grounds of both commercial and non-commercial fish species (Robertson & Duke, 1987; Weinstein & Brooks, 1983). This study attempts to describe and document the species utilizing these inter-linked coastal habitats and draw the patterns of the interlinkages.

MATERIALS AND METHODS

Study area

The study included Chwaka bay mangrove creeks (site A), Chwaka bay intertidal seagrass bed (site B) and in the Paje intertidal zone (site A). These areas are located on the eastern side of Unguja Island, Zanzibar (Fig. 1). While the Chwaka bay ecosystem is inter-linked with mangrove vegetation (seven species, Shunula, 1989), Paje coast is bordered by beautiful sandy beach on the landward and a barrier reef on the ocean side. Seaweed farms were near the sampling areas in Paje coast than in the seagrass beds of Chwaka Bay. Turbidity is higher in the mangrove creeks than in the seagrass beds. Salinity is known to vary considerably within the Chwaka Bay especially during the rainy season because of freshwater run-off and underground freshwater seepage dilution effects. Such changes have been observed to more pronounced in the mangrove creeks.

Sample collection.

Samples were collected in the intertidal and the subtidal areas where the depth does not exceed 2m and the bottom is without obstacles to prevent towing the net to the nearby shore (beach). Collection of samples was done during low water spring tides using a small beach seine net 10m long constructed by using a 19mm nylon net webbing. A variety of fish and macro-crustacean species were caught. Commercially important fish families caught by Chwaka and Paje fishermen were referred from the Fisheries Statistics department. The main fishing grounds are located in the mouth of the Chwaka bay and in the reef slope in Paje coast.

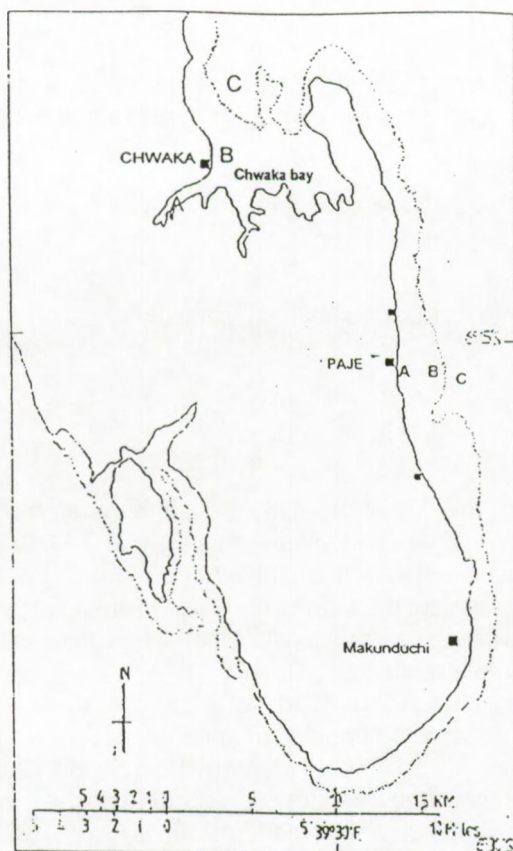


Fig.1. Map showing the study sites in Chwaka Bay and at the Paje coast.

Sample processing

Beach seine samples were sorted, identified and for each individual the length and weight was measured. Few representative specimens were preserved in formalin and stored pending identification or confirmation of identity. The rest of the catch was preserved by freezing pending dry-weight determination.

RESULTS

Total catch analysis

A total of 10,779 specimens representing 121 species of fish and 15 species of macro-crustaceans in 48 families of fish and 5 families of macro-crustaceans, were collected from the studied sites. Table 1 gives the species caught and their corresponding relative numerical contribution to the total catch for each site. The number of species recorded in the mangrove habitat was 62 from 29 Families while in the Chwaka seagrass beds and Paje seagrass beds the number of species were 74 in 35 families and 73 from 39 families, respectively. Twenty three (23) species were common to all sites. The number of species resident or recruiting only in the mangroves, Chwaka seagrass and Paje seagrass were 26, 31 and 34 respectively. Eight species were recorded only in the mangroves and in the adjacent seagrass bed in Chwaka Bay. Thirteen species were found only in the seagrass beds (Paje and Chwaka) while only five species were recorded in the mangroves as well as in Paje seagrass but not found in Chwaka seagrass beds. Fig. 2 (i, ii, & iii) shows the relative numerical contribution of the important species caught in this study. The minimum, maximum and mode length of important species caught are given in Table 2.

In Chwaka mangrove creek the Apogonidae species (*Apogon lateral**is*, *Apogon orbicularis*, *Apogon "silverband"*) dominated the catch except in July 1994 where most of the catch (86% or 1741 individuals) comprised of *Ambassis natalensis*. *Gerres oyena* was the dominant species in the seagrass beds of both Paje coast (65.4 %) and Chwaka seagrass beds (61.3 %).

Gerres oyena was the second in abundance in the mangroves, however if we exclude the catch of *Ambassis natalensis* in July, this species was numerically most abundant even in the mangroves. Prawns catch (or shrimps) contributed about 7.7 % of the total catch in the mangroves. *Monodactylus*

**Table 1: Species, families and the relative abundance of species caught
'in Chwaka bay (site A & B) and in Paje coast site A.**

Species	Family	Chwaka A		Chwaka B		Paje A	
		Total		Total		Total	
		60 Hauls	%N	81 Hauls	%N	50 Hauls	%N
<i>Acanthurus sp</i>	Acanthuridae	3	0.1		0.0	2	0.0
<i>Albula vulpes</i>	Albulidae		0.0		0.0	11	0.3
<i>Antennarius sp.</i>	Antennariidae	2	0.1		0.0		0.0
<i>Ambassis natalensis</i>	Ambassidae	1741	45.0		0.0		0.0
<i>Apogon lateralis</i>	Apogonidae	312	8.1	1	0.0	17	0.4
<i>Apogon "silver band"</i>	Apogonidae	223	5.8	16	0.6		0.0
<i>Apogon orbicularis</i>	Apogonidae	170	4.4	3	0.1		0.0
<i>Fowleria aurita</i>	Apogonidae		0.0		0.0	3	0.1
<i>Cheilodipterus quinquelineatus</i>	Apogonidae		0.0		0.0	10	0.2
<i>Apogon cooki</i>	Apogonidae		0.0	14	0.5		0.0
<i>Apogon nigripinnis</i>	Apogonidae		0.0	13	0.5		0.0
<i>Foa brachygramma</i>	Apogonidae		0.0	40	1.5		0.0
<i>Arius sp</i>	Ariidae		0.0	1	0.0		0.0
<i>Atherion africanus</i>	Atherinidae		0.0	3	0.1		0.0
<i>Hypoantherina temminkii</i>	Atherinidae		0.0	298	11.3	4	0.1
<i>Atherina sp</i>	Atherinidae		0.0	43	1.6		0.0
<i>Solenostomium cyanopterus</i>	Aulostomidae		0.0		0.0	2	0.0
<i>Abalistes stellatus</i>	Balistidae		0.0		0.0	2	0.0
<i>Tylosurus crocodilus</i>	Belonidae	12	0.3	10	0.4	4	0.1
<i>Tylosurus acus melanotus</i>	Belonidae		0.0	3	0.1		0.0
<i>Tylosurus sp.</i>	Belonidae		0.0		0.0	5	0.1
<i>Blennidae sp</i>	Blennidae		0.0	1	0.0		0.0
<i>Bothus sp</i>	Bothidae		0.0	14	0.5	15	0.4
<i>Bothus pantherinus</i>	Bothidae		0.0		0.0	1	0.0
<i>Caranx ignobilis</i>	Carangidae	15	0.4		0.0		0.0
<i>Caranx papuensis</i>	Carangidae	6	0.2	1	0.0		0.0
<i>Caranx sp</i>	Carangidae	2	0.1	1	0.0	8	0.2
<i>Trachinotus blochii</i>	Carangidae		0.0		0.0	82	1.9
<i>Scomberoides sp.</i>	Carangidae		0.0		0.0	1	0.0
<i>Cathigaster solandri</i>	Cathigasteridae		0.0	1	0.0		0.0
<i>Aeoliscus punctilatus</i>	Centriscidae		0.0		0.0	10	0.2
<i>Heniochus diphreus</i>	Chaetodontidae	10	0.3		0.0		0.0
<i>Sardinella gibbosa</i>	Clupeidae	1	0.0		0.0	237	5.5
<i>Conger cinereus</i>	Congridae		0.0		0.0	2	0.0
<i>Conger wilson</i>	Congridae		0.0	1	0.0		0.0
<i>Dactylopte orie</i>	Dactylopteridae	2	0.1		0.0		0.0
<i>Heteroleotris zanzibaiensis</i>	Eleotridae		0.0	1	0.0	2	0.0
<i>Stolephorus indicus</i>	Engrauridae	14	0.4		0.0		0.0
<i>Thrixa baelama</i>	Engrauridae	8	0.2		0.0	220	5.1
<i>Gerres oyena</i>	Gerreidae	620	16.0	1495	56.8	2720	63.6
<i>Gerres filamentosus</i>	Gerreidae	51	1.3	6	0.2		0.0
<i>Gerres acinaces</i>	Gerreidae		0.0	3	0.1		0.0
<i>Gobiidae sp</i>	Gobiidae	3	0.1	28	1.2	4	0.1
<i>Yongeichthys nebulosus</i>	Gobiidae	1	0.0		0.0		0.0
<i>Amblygobius albimaculatus</i>	Gobiidae	1	0.0	57	2.2	35	0.8
<i>Stenogobius criniger</i>	Gobiidae		0.0	6	0.2		0.0
<i>Pomadacy kaakan</i>	Haemulidae	61	1.6		0.0		0.0
<i>Plectorhynchus albivittatus</i>	Haemulidae	3	0.1		0.0		0.0
<i>Diagramma pictum</i>	Haemulidae	1	0.0	0	0	2	0.0
<i>Plectorhynchus sp.</i>	Haemulidae		0.0		0.0	8	0.2
<i>Hemiramphus sp</i>	Hemiramphidae	54	1.4	5	0.2	5	0.1
<i>Hemiramphus dussumieri</i>	Hemiramphidae	19	0.5		0.0		0.0
<i>Hyporhamphus dussumieri</i>	Hemiramphidae	4	0.1		0.0		0.0
<i>Neonipon sammara</i>	Holocentridae		0.0	23	0.9		0.0
<i>Neonipon opecularis</i>	Holocentridae		0.0	5	0.2		0.0
<i>Stethojulis albivittata</i>	Labridae		0.0		0.0	1	0.0
<i>Labridae</i>	Labridae		0.0	6	0.2	1	0.0
<i>Leiognathus sp</i>	Leiognathidae	157	4.1		0.0		0.0
<i>Gaza minuta</i>	Leiognathidae	14	0.4		0.0		0.0
<i>Leiognathus equulus</i>	Leiognathidae	1	0.0		0.0		0.0
<i>Lethrinus variegatus</i>	Lethrinidae	8	0.2	35	1.3	21	0.5
<i>Lethrinus harak</i>	Lethrinidae	6	0.2	44	1.7	226	5.3
<i>Lethrinus lentjan</i>	Lethrinidae	2	0.1	50	1.9	8	0.2

<i>Lethrinus mineatus</i>	Lethrinidae		0.0		0.0	1	0.0
<i>Lethrinus nebulosus</i>	Lethrinidae		0.0	2	0.1	42	1.0
<i>Lethrinus ramak</i>	Lethrinidae		0.0		0.0	18	0.4
<i>Lutjanus fulviflamma</i>	Lutjanidae	77	2.0	229	8.7	138	3.2
<i>Lutjanus argentimaculatus</i>	Lutjanidae	21	0.5		0.0		0.0
<i>Lutjanus russeli</i>	Lutjanidae	12	0.3	4	0.2		0.0
<i>Lutjanus fulvus</i>	Lutjanidae	2	0.1		0.0	1	0.0
<i>Lutjanus monostigma</i>	Lutjanidae	1	0.0		0.0		0.0
<i>Lutjanus kasmira</i>	Lutjanidae		0.0		0.0	14	0.3
<i>Lutjanus sanguines</i>	Lutjanidae		0.0		0.0	25	0.6
<i>Pristipoma nigri</i>	Lutjanidae		0.0	1	0.0		0.0
<i>Megalops cyprinoides</i>	Megalopidae	1	0.0		0.0		0.0
<i>Thamnaconus modestoides</i>	Monacathidae		0.0		0.0	1	0.0
<i>Monodactylus argenteus</i>	Monodactylidae	144	3.7	1	0.0		0.0
<i>Mugilidae sp</i>	Mugilidae	6	0.2		0.0		0.0
<i>Liza macrolepis</i>	Mugilidae		0.0		0.0	3	0.1
<i>Upeneus vittatus</i>	Mullidae	2	0.1		0.0		0.0
<i>Upeneus tragula</i>	Mullidae	1	0.0	1	0.0		0.0
<i>Parupeneus macronema</i>	Mullidae		0.0		0.0	5	0.1
<i>Parupeneus macronema</i>	Mullidae		0.0	16	0.6		0.0
<i>Parupeneus cinnabarinus</i>	Mullidae		0.0	1	0.0		0.0
<i>Mulloidis flavolineatus</i>	Mullidae		0.0		0.0	1	0.0
<i>Parupeneus barberinus</i>	Mullidae		0.0	1	0.0		0.0
<i>Siderea picta</i>	Muraenidae		0.0		0.0	2	0.0
<i>Scolopsis ghanam</i>	Nemipteridae		0.0	26	1.0		0.0
<i>Ophichthidae</i>	Ophichthidae		0.0		0.0	2	0.0
<i>Platax pinnatus</i>	Platacidae		0.0	4	0.2	3	0.1
<i>Platycephalus sp</i>	Platycephalidae		0.0	2	0.1		0.0
<i>Plotosus anguillaris</i>	Plotosidae		0.0	11	0.4		0.0
<i>Abudefduf sparoides</i>	Pomacentridae		0.0		0.0	6	0.1
<i>Abudefduf sexfasciatus</i>	Pomacentridae		0.0		0.0	3	0.1
<i>Leptoscarus vagiensis</i>	Scaridae		0.0	27	1.0	70	1.6
<i>Pterois antenattus</i>	Scorpaenidae		0.0	1	0.0		0.0
<i>Pterois mombasae</i>	Scorpaenidae		0.0	1	0.0		0.0
<i>Dendrochirus branchypterus</i>	Scorpaenidae		0.0	3	0.1		0.0
<i>Scorpaena sp</i>	Scorpaenidae		0.0	1	0.0	19	0.4
<i>Epinephelus malabaricus</i>	Serranidae	10	0.3	1	0.0		0.0
<i>Serranidae sp</i>	Serranidae		0.0	1	0.0		0.0
<i>Epinephelus merra</i>	Serranidae		0.0	1	0.0		0.0
<i>Grammistes sexlineatus</i>	Serranidae		0.0		0.0	1	0.0
<i>Siganus canaliculatus</i>	Siganidae	1	0.0	35	1.3	113	2.6
<i>Siganus stellatus</i>	Siganidae		0.0	1	0.0	13	0.3
<i>Sphyræna jello</i>	Sphyrænidae	26	0.7		0.0		0.0
<i>Sphyræna forsteri</i>	Sphyrænidae	16	0.4	2	0.1	8	0.2
<i>Sphyræna flavicauda</i>	Sphyrænidae	8	0.2	1	0.0		0.0
<i>Sphyræna Chrysotaenia</i>	Sphyrænidae	2	0.1		0.0		0.0
<i>Sphyræna putmaniae</i>	Sphyrænidae		0.0		0.0	1	0.0
<i>Sphyræna obtusata</i>	Sphyrænidae		0.0		0.0	35	0.8
<i>Syngnathus sp</i>	Syngnathidae	1	0.0	1	0.0	34	0.8
<i>Saurida gracilis</i>	Synodontidae	4	0.1	10	0.4	8	0.2
<i>Synodus variegatus</i>	Synodontidae		0.0	7	0.3		0.0
<i>Terapon quadrilineatus</i>	Teraponidae		0.0		0.0	1	0.0
<i>Terapon jabua</i>	Teraponidae		0.0	1	0.0	15	0.4
<i>Arothron immaculatus</i>	Tetraodontidae	6	0.2	1	0.0	6	0.1
<i>Arothron hispidus</i>	Tetraodontidae	2	0.1	2	0.1	13	0.3
<i>Torquigener hypselogenion</i>	Tetraodontidae		0.0		0.0	3	0.1
<i>Lactoria cornata</i>	Tetraodontidae	1	0.0	9	0.3	1	0.0
<i>Matuta lunaris</i>	Calappidae	1	0.0		0.0		0.0
<i>Calappa hepatica</i>	Calappidae		0.0	16	0.6	4	0.1
<i>Majidae sp</i>	Majidae		0.0	1	0.0		0.0
<i>Macrophthalmus latreillei</i>	Ocypodidae	2	0.1		0.0		0.0
<i>Ocypode ceratophthalmus</i>	Ocypodidae		0.0		0.0	1	0.0
<i>Prawns/Shrimps</i>	Panaeidae	329	8.5	4	0.2	58	1.4
<i>Thalamita crenata</i>	Portunidae	25	0.6	8	0.3	2	0.0
<i>Scylla serrata</i>	Portunidae	22	0.6		0.0	1	0.0
<i>Thalamita foresti</i>	Portunidae	17	0.4	19	0.7	33	0.8
<i>Portunus pelagicus</i>	Portunidae	2	0.1	23	0.9	20	0.5
<i>Thalamita pyrmna</i>	Portunidae	1	0.0		0.0		0.0
<i>Portunus orbitosinus</i>	Portunidae	1	0.0	4	0.2	13	0.3
<i>Thalamita admete</i>	Portunidae		0.0	2	0.1	3	0.1
<i>Thalamita sp</i>	Portunidae		0.0	7	0.3	1	0.0
		62		74		73	
136 species	53 Families	3871		2633		4275	

Fig. 2: Relative abundance of numerous species in sampled sites.

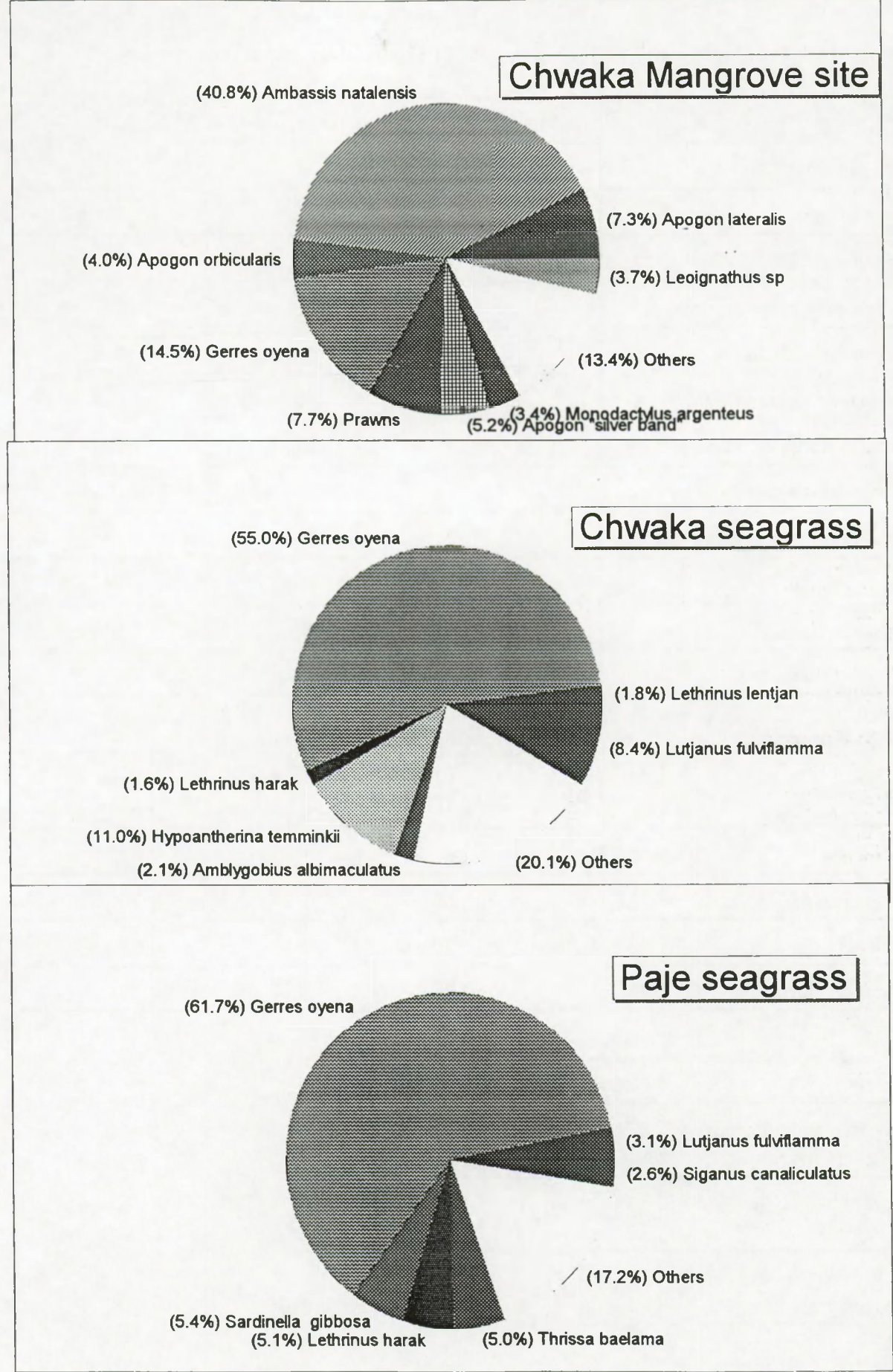


Table 2: Minimum, maximum and mode length of numerically important species

Species	Min (cm)	Max (cm)	Mode (cm)
<i>Ambassis natalensis</i>	5	9	7
<i>Gerres oyena</i>	4.5	14.5	7.5
<i>Apogon lateralis</i>	6	10	8
<i>Apogon orbicularis</i>	6	11	10
<i>Apogon "silverband"</i>	5	9	7.5
<i>Monodactylus argenteus</i>	4	10	7.5
<i>Lethrinus harak</i>	4	13	6.5
<i>Amblygobius albimaculatus</i>	4	9	6.5
<i>Hypoatherina temminckii</i>	5	11	7
<i>Sardinella gibbosa</i>	6	10	8
<i>Thryssa baelama</i>	5	8	6.5
<i>Lutjanus fulviflamma</i>	6	15	8.5

Table 3: Numerical comparison of Species, Families and their occurrence.

	All	Chwaka Mangroves	Chwaka Seagrass	Paje Seagrass
Specimen	10,779	3,871	2633	4275
Species	121 + 15	62	74	73
Families	48 + 4	29	35	39
Residence/Nursing	23	26	31	34

Habitats	Common species
Mangrove and adjacent seagrass (Chwaka)	8
Seagrass beds (Chwaka and Paje)	13
Mangrove (Chwaka) and Paje (Seagrass)	5

argenteus and *Leiognathus* species were also numerically important in the mangroves creeks of Chwaka. *Hypoatherina temminckii*, *Amblygobius albimaculatus* and *Lutjanus fulviflamma* were numerically important in Chwaka seagrass beds while *Sardinella gibbosa*, *Lethrinus harak* and *Thryssa baelama* were important in Paje coast.

Some species although not numerically important, they were frequently encountered in the different sites sampled, eg *Gerres filamentosus*, *Lutjanus argentimaculatus*, *Pomadacy kaakan* in the mangroves, *Lethrinus harak*, *Siganus canaliculatus* and *Leptoscarus vaigiensis* in the Chwaka seagrass beds and *Amblygobius albimaculatus*, *Leptoscarus vaigiensis*, *Arothron hispidus* and *Siganus canaliculatus* in Paje coast.

Temporal catch rates of selected species.

There is a seasonal pattern in the relative abundance of the species. In the mangroves for example, the cardinal fish *Apogon lateralis* seem to peak up in November, while *Apogon orbicularis* and *Apogon* "silverband" were numerous between October-January and in December respectively. *Leiognathus* species were found in the mangrove creeks in January and April. *Hypoatherina temminckii* was abundant in the Chwaka seagrass beds in March. *Lethrinus harak* was most abundant in Paje coast between April and July and *Lethrinus nebulosus* was found in Paje momentarily in January. Catches of *Lethrinus lentjan* were generally low in all areas. A small peak was observed in November in the seagrass beds of Chwaka. In general Lethrinidae species were not numerically important in Chwaka mangrove site. *Lutjanus fulviflamma* was found in all sites with peak abundance in December and March in the Chwaka seagrass, a smaller peak in April in the mangroves and in Paje coast. *Monodactylus argenteus* was found in Chwaka bay mostly in the mangrove creeks where higher catch rates were observed in December and April. Prawns were found in all sites, however, higher concentrations were found in the mangroves in September. *Pomadasy kaakan* juveniles are found in the mangrove environment mostly between October and December. *Sardinella gibbosa* was found mainly in the Paje coast with peak distribution in April and May. *Siganus canaliculatus* was found in the seagrass beds and was not well represented in mangroves. Peak distribution was in April in Paje and November in Chwaka. *Thryssa baelama* and *Trachinotus blochii* utilized the intertidal seagrass beds in Paje coast in January after which they migrated somewhere else.

DISCUSSION

Most of the catch in this study was composed of juvenile and small sized adult fish. The larval stages have probably filtered through the 19mm mesh net used. Higher representation of juveniles is not only a mesh size effect, but it also demonstrates that the tropical shallow coastal areas form an important nursery function for juvenile fish of many species. The function of shallow coastal habitats as nursery area have been demonstrated elsewhere (Little et al., 1988; Robertson & Duke, 1987; Weng, 1990). These studies, also show that only few (less than ten) species dominated the catch in the study sites investigated. The families Apogonidae, Ambassidae, Gerreidae, Leiognathidae were numerically dominant in the Chwaka Bay mangroves. A similar observation to that of Little et al. (1988) in Gazi bay mangrove creeks. The families Clupeidae and Blennidae were significant in Gazi Bay study (Little et al., 1988) and the non significant contribution of these species in Chwaka bay may be due to the large mesh size (19 mm) of the seine net used.

Fish species of commercial importance such as snappers, emperors, groupers, etc. were not numerically well represented in the mangrove creeks. Although the mangrove environment may seem to be less important in nursing juveniles of commercial importance, the bulk of species recruited in the mangroves are ecologically important as prey of nearby seagrass beds and coral reef fish species (Robertson & Duke, 1990). However, this fact remains to be confirmed by studies directed towards understanding migration patterns and predator prey relationships.

Gerres oyena was the dominant species in the seagrass bed and to a less extend in the mangroves. The limit of its distribution in the shallow coastal water seem to be dictated by the turbidity levels more than other factors. In this study *Gerres oyena* was caught in muddy-sandy parts of the mangroves and were not caught in soft muddy bottom and turbid environments in the mangrove. In the open coastal waters the species have been reported to occur abundantly in trawl catches (Iversen et al, 1984; Van Nierop, 1987).

The species that recruit in the seagrass beds include *Hypoatherina temminckii*, *Lutjanus*

fulviflamma, *Lethrinus harak*, *Siganus canaliculatus*, *Leptoscarus vaigiensis* and *Sardinella gibbosa*. Most of these species are of commercial importance, therefore, coastal management programs should take into consideration the function of the shallow coastal areas as nursery grounds of such species.

The recruitment of fish is a seasonal phenomenon both in mangroves and in the seagrass beds for most fish species. The result indicates that spawning is also seasonal. It is difficult at this stage to advance reasons for the seasonality in spawning in the studied areas, however factors such as food distribution, turbidity, salinity, predation, temperature, etc have been reported to affect the spatial and temporal distribution and abundance of fish larvae and juvenile.

In conclusion, this study has produced a list of the species utilizing the shallow intertidal habitats as resident or nursery areas. Some species favor the mangrove habitat while others prefer the seagrass beds. The number of species and families recruited in the mangroves were less compared to those in seagrass beds. This study has also shown that there is seasonal recruitment pattern. Information from this study will be useful in the formulation of management strategies.

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SPATIAL AND TEMPORAL DYNAMICS OF PHYTOPLANKTON BIOMASS AND SPECIES COMPOSITION IN CHWAKA BAY, ZANZIBAR.

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INTRODUCTION

To understand the working of the marine pelagic ecosystem one needs to study the logical frame of the complex food web. Phytoplankton which are predominantly autotrophic are primary producer of organic matter in the aquatic habitats. They comprise a major portion of primary production in the sea. They are like plants on land, the basic food in the sea for all consumers such as zooplankton and fish (Sournia, 1978). The phytoplankton thus stand on the baseline of many foodwebs in the aquatic environment and are in turn, dependent on the activities of other microbial organisms, mainly bacteria and fungi which convert organic material into the inorganic nutrients required by plants (Boney, 1975). Some phytoplankton genera especially those belonging to the Cyanophytes e.g. *Trichodesmium* sp. are able to fix nitrogen in water hence contribute to the rise in the level of nitrogenous nutrients in the marine environment (eg Bryceson, 1977; Lyimo, 1995). Sometimes blooms of toxic dinoflagellates occur, especially in coastal waters of tropical seas. These can lead to massive fish kills and contamination of shellfish with a consequent death of sea birds as well as human beings (Boney, 1975). The study of phytoplankton is therefore essential to the understanding of marine ecosystems and is relevant to environmental conservation at large. There have been no previous study on phytoplankton at Chwaka bay in particular. Related studies on phytoplankton which are relevant to this study have been done in Zanzibar waters and in the adjacent areas (e.g. Ballantine, 1961, Bryceson, 1977). In the Indian Ocean in general, different workers have reported low values of phytoplankton biomass of 0.1 mg/m³ in the Northern area and below 0.05 mg/m³ in the Southern area surface waters. Bryceson (1977) working on the coastal waters off Dar es Salaam, Tanzania, recorded values of phytoplankton biomass with a maximum of 1.4 mg/m³ in February and a minimum of 0.2 mg/m³ in June and August. Higher values of the phytoplankton in the tropical waters are reported in the richer zones characterized by coastal upwelling areas off Africa, with a biomass exceeding 500 mg/m³ (Zernova 1974).

METHODS

Study area

Zanzibar lies off the coast of Tanzania mainland between 5°40' and 6°30' south of the equator. The climate is warm and humid (tropical). The main rainy seasons are during the months of March to May (locally known as Masika) and October to November (Vuli) (Statistical abstract, 1991). Chwaka bay is located to the East coast of Zanzibar Island, about 40 km North-East of Zanzibar town. The area comprise of a shallow bay fringed by a coral reef offshore and by a dead coral reef now vegetated with mangroves at the southern end. The major ecosystems in the bay include the mangrove swamps, coral reefs and seagrass meadows. Two study sites were established in the bay. Station I was in the mangrove swamp at the centre of Mapopwe creek with and station II was at the mouth of the creek which is a seagrass ecosystem (see Figs. 1 & 2 in the contribution of Mohammed and Johnstone, this report, for site locations).

Determination of phytoplankton biomass

Samples for phytoplankton biomass determination were collected using 3 l glass bottles and filtered through membrane filters. The biomass was determined by the estimate of the amount of chlorophyll 'a'. The pigments were extracted from the filters using 90% acetone and their concentrations were determined spectrophotometrically as described by Parsons et al. (1989). Water samples for nanoplankton percentage biomass were collected after filtering off the microplankton composition

through a 20 µm pore size net. The retained water was collected and analysed for chlorophyll *a* as above.

Determination of phytoplankton cell numbers

Samples for determination of micro-plankton numbers were collected by filtering a known volume of seawater through a 20 µm mesh size phytoplankton net. The samples were then immediately fixed with 4% formalin and the cells were enumerated in a Sedgewick-Rafter cell (McAlice, 1971) by using a light microscope, Olympus system BHT.

Phytoplankton Identification

Samples for phytoplankton identification were collected by towing a plankton net (65 µm mesh size) at a low speed for about 5 minutes. The samples were then preserved with 4% formalin.

Identification of the phytoplankton was undertaken using a light microscope and the following references, Bryceson (1977), Sundstrom (1986), Cupp (1943), Hendey (1964) and Leewis (1985). Some photomicrographs of the phytoplankton were taken for future reference.

Temperature and salinity

Temperature and salinity were measured *in situ* by thermometer and refractometer respectively.

RESULTS

During this study 69 species of phytoplankton were identified. However, the plankton net used for towing had large pore size (65 µm), so the main taxa obtained were large species. We are certain that many species have remained unnoticed, partly because of their rarity and partly because of their smaller size. The many unidentified and undescribed taxa are not included in the present work and will be the subject of a later more detailed study with further experience, wider background knowledge of the flora and the availability of relevant literature and materials.

The values for the biomass of phytoplankton at the two study sites are shown in Table 2 and Figure 1 and 2. The phytoplankton biomass ranged from 0.123 mg/m³ (in May 1994) to 0.373 mg/m³ (September 1994) with a mean (\pm SD) number of 0.257 ± 0.087 mg/m³ at station I. Generally the biomass values at station I were higher during the months of August to March, lower during the months of April, May and June (Fig 1). At station II the biomass ranged from 0.021 mg/m³ (March 1994) to 0.346 mg/m³ (April 1994) with a mean value of 0.0817 ± 0.0865 mg/m³. In general there was a higher biomass at station II in April to June as compared to the rest of the months.

The values for biomass at the two stations and during monsoons are compared using "t" statistical test or Mann-Whitney 'U' test and the results revealed that there was a significant higher biomass at station I compared to station II, $t = 4.94$; $p < 0.001$. The biomass during southern monsoon (June - November) was not significantly different with that of northern monsoon (December -May) at station I and II, $t = 0.43$; $p > 0.50$ and 'U' = 19; $p > 0.20$ respectively. Also biomass trends were correlated with salinity and temperature trends. Results indicated that there is a significant positive correlation between biomass and salinity at station I, $r = 0.663$; $0.02 > p > 0.01$ while station II showed an insignificant negative correlation, $r = -0.541$; $0.01 > p > 0.05$. On comparison with temperature, biomass showed an insignificant correlation at both station I and II, $r = 0.095$; $p > 0.50$ and $r = -0.189$; $p > 0.50$ respectively.

The values for the number of trichomes of cyanophytes are shown in Table 2 and Fig. 3. At station I the values varied from 8 in (July 1994) to 82 trichomes/l in (October 1993) with a mean (\pm SD) of 39.67 ± 25.23 trichomes per liter. At station II the number of trichomes per liter varied from 4 (July 1994) to 5950 (January 1994) with a mean number of 583.17 ± 1691.90 trichomes per liter. A bloom of Trichomes (*Trichodesmium* sp) occurred in January at station II. The number of other phytoplankton (apart from cyanophytes) ranged from 71 (May 1994) to 9257 cells/litre (September 1993) with a mean (\pm SD) of 2473 ± 2969.74 at station I. At station II ranged from 89 (April) to 1530 cells per litre (January) with a mean number of 479.58 ± 425.55 cells per litre. In general there was a high number of phytoplankton cells at station I (with peaks in between) as compared to station II (Fig. 3). Also the general trend show that higher numbers of cells occurred during the period between the months of September and February while in April and May (during the period of heavy rainfall) the number was lower.

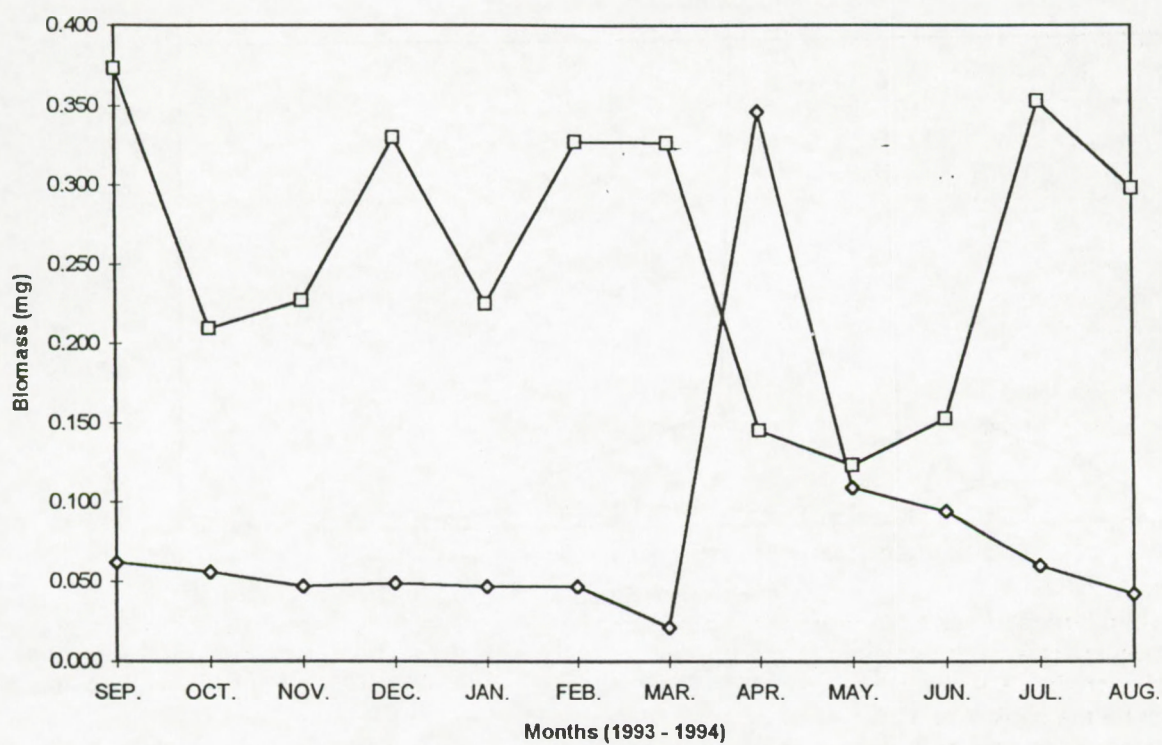


Fig.1 Monthly mean variations of phytoplankton biomass (mg/m³) at Chwaka Bay

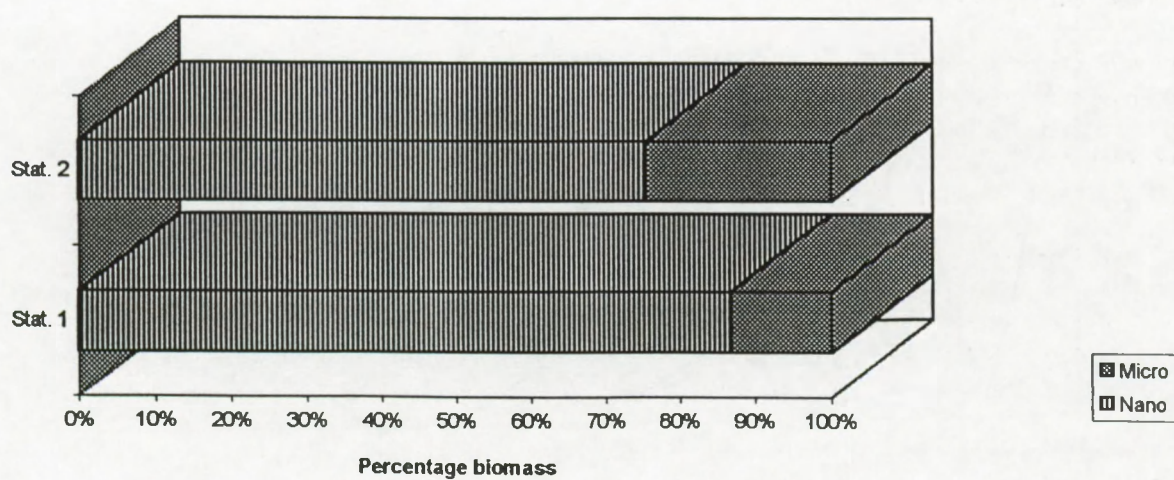


Fig. 2. Comparisons between the nano- and micro-plankton biomass in mg/m³ at Chwaka Bay.

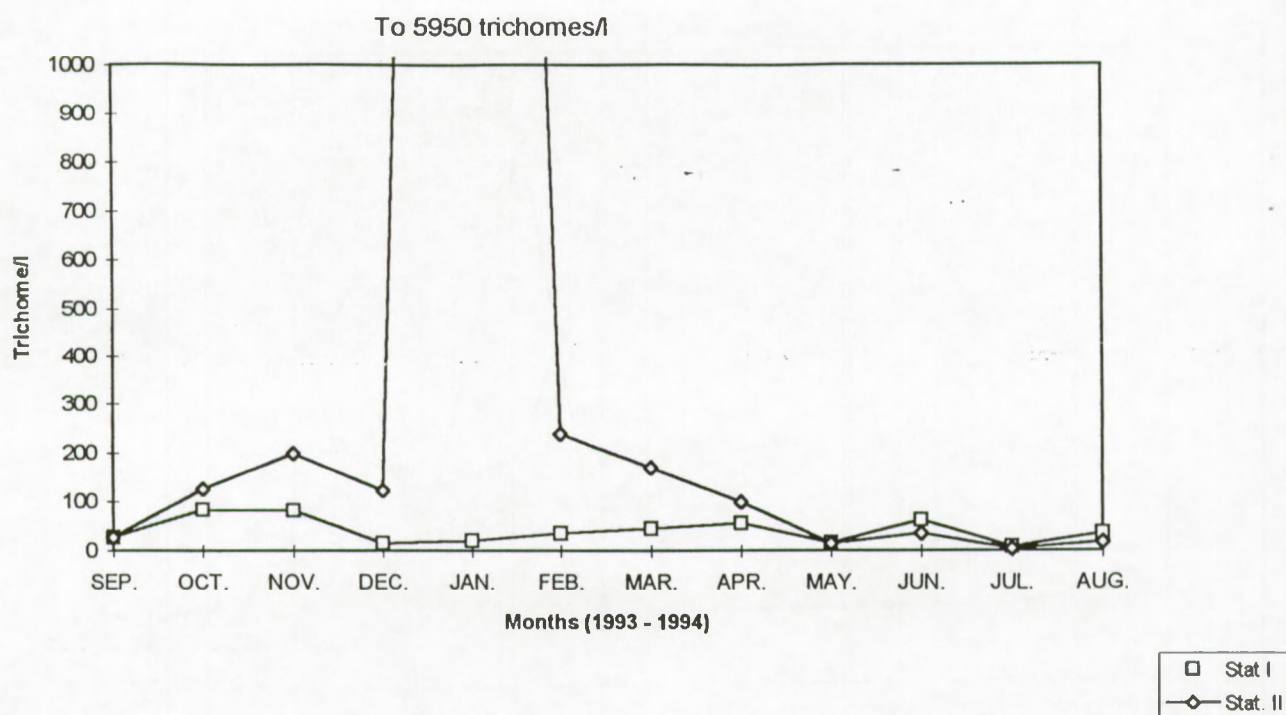


Fig. 3. Monthly mean variation of cyanobacteria trichome number at Chwaka Bay.

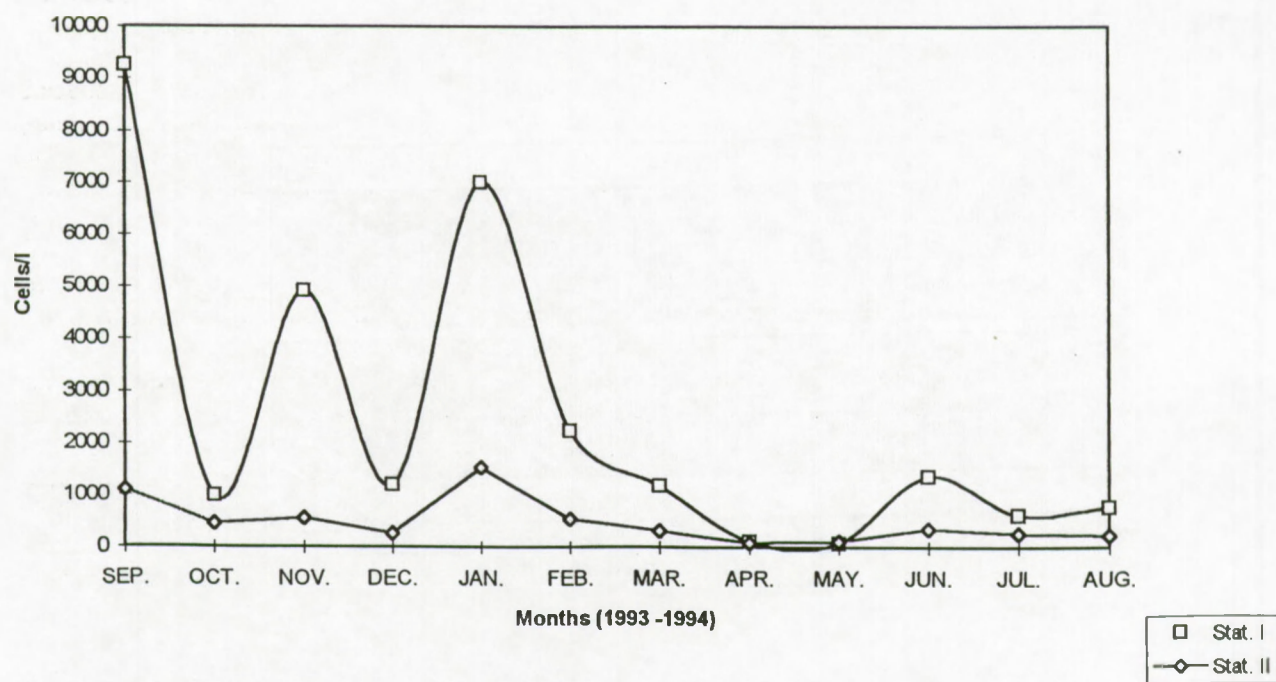


Fig. 4. Monthly mean variation of other phytoplankton (besides cyanophytes) cell numbers

The trichome number of cyanophytes and cell number of other phytoplankton (besides cyanobacteria) at station I were compared with that of station II using the Mann-Whitney 'U' test. It was revealed that the number of cyanobacteria trichomes was not significantly different between the two stations, 'U' = 99.5; $0.20 > p > 0.10$. Station II had a significantly higher number of cells of other phytoplankton when compared to station I, 'U' = 113; $p = 0.02$. The number of trichomes at station I was not significantly different between the monsoon, $t = 0.219$; $p \gg 0.50$. However at station II the trichome number was significantly higher during the northern monsoon, 'U' = 34; $p = 0.01$. There was no significant difference in the phytoplankton cell number between the monsoons at both station I and II, $t = 0.335$; $p \gg 0.50$ and $t = 0.531$; $p \gg 0.50$ respectively.

The cyanobacteria trichome number and the cell number of other phytoplankton from both station I and II were correlated with temperature and salinity trends. It was found that there was no any significant correlation between trichome number and salinity at both station I and II, $r = 0.35$; $p \gg 0.50$ and $r = 0.278$; $0.50 > p > 0.20$ respectively. There was also no significant correlation between trichome number and temperature at station I and II, $r = 0.1$; $p \gg 0.50$ and $r = 0.536$; $0.10 > p > 0.05$. The cell number of other phytoplankton indicated a significant correlation with salinity at station II, $r = 0.592$; $0.05 > p > 0.02$, but an insignificant correlation at station I, $r = 0.482$; $0.20 > p > 0.10$. On correlating with temperature the cell number did not show any significant correlation at both station I and II, $r = 0.30$; $0.50 > p > 0.20$ and $r = 0.353$; $0.50 > p > 0.20$ respectively.

The temperature and salinity values are shown in Table 2 and Fig. 5. Temperature ranged from 24.7°C (July 1994) to 32°C (January 1994) at station I and from 26.5°C (August 1994) to 31.4°C (January 1994) at station II. The temperature values were higher during the months of November to January and lower during the months of June to September. Salinity ranged from 5.5‰ (May 1994) to 35‰ (January 1994) at station I and from 22‰ (May 1994) to 35‰ in the months of September 1993 to February 1994 at station II. In general, salinity values were higher in the months of August to February and lower in May and June. Station II had higher salinity values than station I throughout the year.

DISCUSSION

The phytoplankton species composition was noted to vary with time and space. These variations were not quantified due to difficulties in identification. However, a general observation revealed that the predominant species varied greatly from time to time. For example during May to July 1994 the predominant species at station I were *Tropidoneis approximata*, *Nitzschia longissima* and *Climacosphenia moniligera*. During September 1993 to February 1994 the predominant species at station I were *Pleurosigma* and *Gyrosigma* sp. At station II the cyanobacterium *Microcoleus* sp. were predominant from September to December 1993 but in January - February 1994, *Trichodesmium* sp. dominated. As can be seen in table I, station II had a greater number of species than station I but lower biomass and phytoplankton counts. This may be due to the finding and the prediction by Margalef (1963) that biological diversity is inversely related to productivity or to the fact that the nanoplankton percentage biomass at station I was higher as compared to that of station II. The nanoplankton were poorly represented in the qualitative analysis samples as the net used had large pore size.

The biomass values obtained indicated that the two stations are poor in primary production with respect to phytoplankton production. However, the values were within the range of those obtained with other workers such as Saijo (1973) and Bryceson (1977). Station I had significantly greater biomass than that of station II. This could be due to the fact that station I has high nutrients concentration coming from mangrove as compared to station II. Thus, at station I the load of organic detrital matter was very high and the water had the yellowish tinge presumably containing large amounts of decomposition products and exudates from the mangrove and associated organisms with water soluble fulvo-humic acids or "Gelbstoff" (Kalle, 1966) which have been found to be stimulatory to the growth of some dinoflagellates (also Prakash and Rashid, 1968).

During a period of heavy rainfall, the environmental conditions at station I changed suddenly i.e. the salinities dropped to very low levels and water turbidity increased very drastically and temperature dropped as it rains. During that period the abundance of phytoplanktons dropped to very low number and as a consequence the biomass was very low showing a significant correlation with salinity $r = 0.663$, $0.02 > p > 0.01$. Also, the phytoplankton composition changed, thus during dry season the predominant species were *Pleurosigma* and *Gyrosigma* spp. while during the rain

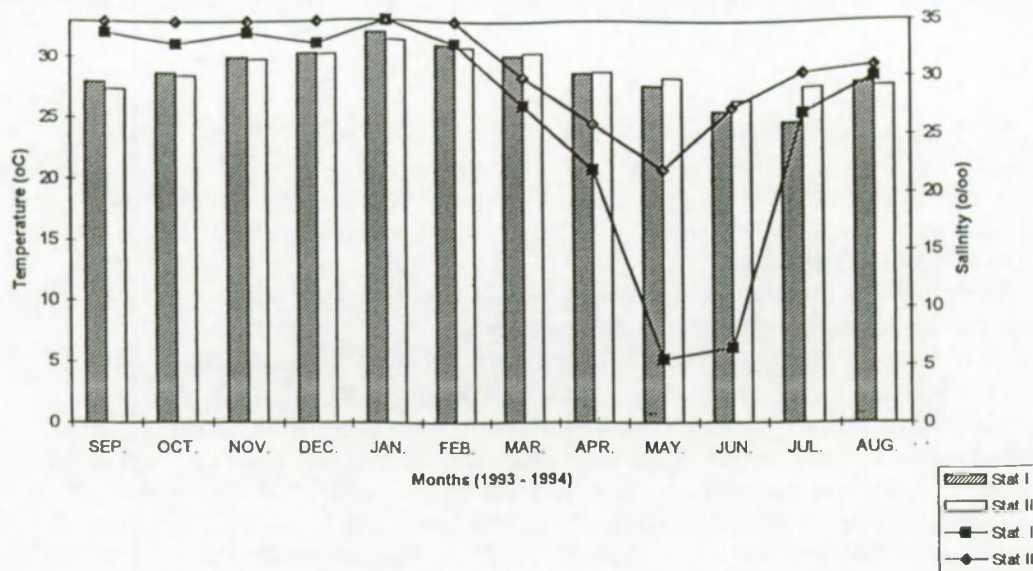


Fig. 5. Monthly mean variations of temperature (bar) and salinity (line) at Chwaka Bay.

season the predominant species were found to be *Nitzschia*, *Tropidoneis* and *Climacosphenia* spp. These fluctuations of biomass of phytoplankton may be due to drastic changes of environmental conditions which could have affected the physiological processes of organisms resulting into death. Also low production during this period could be due to light limitations as a result of high turbid waters.

At station II however, the changes of environmental parameters such as salinities were not drastic during the period of heavy rainfall as compared to station I, and salinities showed an insignificant negative correlation with the biomass, $r = -0.541$, $0.01 > p > 0.05$. This may be due to the fact that the changes of salinity was not big, so it did probably not affect the physiological processes of phytoplanktons but instead it promoted the introduction of biological active material such as humic acids which has been shown to stimulate algal cell metabolism and growth (Prakash et al., 1968). Also, Qasim et al., (1971) noted a marked increase of some tropical phytoplankton photosynthetic rates at low salinities. During the northern monsoon the rain may add nutrients through water runoff which also promote the growth of phytoplanktons. The nutrient could also have been added through biological nitrogen fixation by *Trichodesmium* species which occurs at high concentration during this period (Bryceson 1977, and Lyimo, 1994).

The annual number of trichomes of cyanophytes were not significantly different between station I and II. At station I the number of trichomes of cyanophytes were not significantly different between the northern and southern monsoon. However, there was a significant differences in the number of trichomes of cyanophytes at station II between the northern and southern monsoon ($U = 34$; $p = 0.01$). It must be pointed out that the cyanophytes trichomes constituted mainly *Oscillatoria* and *Microcoleus* species at station I. These species seem to occur throughout the year and variations with seasons were not very high. During northern monsoon, blooms of *Trichodesmium* sp. do occur in coast waters of Tanzania (Bryceson, 1977 and Lyimo, 1995) and the cyanophytes numbers were very high at station II during this period. The *Trichodesmium* sp. which are mainly found in open ocean, very poor in nutrients (Goering et al., 1966; Marumo et al., 1974 and Carpenter et al., 1975) were probably brought to the station II by water tides from open ocean but did not reach station I. These observation generally agree with those of Bryceson (1977) and Teixeira et al., (1969) who found *Trichodesmium* to be absent at mangrove stations. The occurrence of *Trichodesmium* during Northern monsoon have also been reported by several Authors in Indian Ocean (eg. Bryceson, 1977; Lyimo, 1995; Nagablushanam, 1967, Prabhu et al., 1978; Ramamurthy, 1980, Devassy et al., 1978). At this time wind are calm and conditions are favourable for blooms (Bryceson, 1977). The environmental parameters measured i.e. salinity and temperature seem to influence phytoplankton abundance, but these are not the only factors to be taken into consideration. Other factors such as nutrients, water clarity, light intensity, pH, diseases intra- and interspecific interactions should be considered. An attempt to measure the rate of photosynthesis in light and dark bottles by measuring changes in the concentration of dissolved oxygen (Strickland and Parson 1972) was done but the results obtained were unsatisfactory. A use of ^{14}C method in future is recommended.

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MACROBENTHIC COMMUNITIES OF SANDY BEACHES OF THE INHACA ISLAND (MOZAMBIQUE)

By

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Abbreviated title: Macrobenthic communities of sandy beaches

ABSTRACT

This paper deals with the composition of endobenthic macroinvertebrate communities in the sandy beaches of Inhaca Island, Mozambique. The study is based on sampling stations located along levelled transects, taking samples for macroinvertebrate, grain-size distribution, organic matter and phytopigments. Highly mobile macrofauna was video recorded. Results indicate that in west coast the beach has a dissipative profile with low gradients, within the large intertidal sand flats, and a grain-size characterised by fine to medium sands, with a coarser fraction at the upper level. The east coast beaches otherwise, are reflective type with a gradient characteristic of an instable beach, with a step, and the sediments dominated by medium to coarse sands with a finer fraction at the upper level.

Macrofauna abundance and diversity is related not only with grain-size distribution but also with the profile, % OM, chlorophyll *a* and phaeopigments. Thus major values of abundance and diversity are found on the west coast (96 species) while the lowest values were recorded on east coast (8 species). Macrofauna zonation seems to match Salvat (1964) scheme on the west coast, while at the east coast the only clear zonation is between air and water breathers.

INTRODUCTION

Inhaca Island with an extension of 12.5Km nearby Maputo bay, is part of an extent littoral fringe developing from South to North in the SW coast of southern

Africa. Although located in a subtropical area (26° S) Macnae & Kalk (1969) and Moreira Lopes (1973) consider the climate as tropical as a consequence of both the warm current of the Mozambique channel, and of the atmospheric circulation from the East always present and dominant the most of the year. According to Moura (1969) this atmospheric influence induces the water mixture between the Mozambique warm current and the cooler waters coming from South, thus originating the processes of sedimentation which are the origin of the several north-pointing spits on the east coast of Africa, as the Inhaca island.

Consequently, the soils of the Inhaca Island are sandy and while the East coast is exposed to Indian Ocean the West coast, facing Maputo Bay, is protected with large sand flats. In fact, only the eastern sandy beaches are exposed to heavy wave action with clear reflective profiles, while the west coast, with three shallow bays, is characterised by large intertidal sand flats extending up to 1 Km when exposed to low water. Also in West coast developing from Inhaca Channel develops a reef of living coral (Barreira Vermelha), referred as the most southern reef (Macnae & Kalk, 1969), reinforcing the idea that Inhaca Island is in a biological point of view a case to study, where geographically confine the austral limit of tropical eastern Africa fauna and flora, and the septentrional limit of occurrence of coastal fauna and flora from Natal and Southeast Africa.

The aim of this study was to describe with a quantitative approach the endobenthic macrofaunal communities of the intertidal sandy beaches of Inhaca Island, and its relationship with environmental parameters such as grain-size distribution, organic matter and phytobenthos. Both exposed and sheltered beaches were studied.

MATERIAL AND METHODS

Field techniques

During the low tides of June and July 1993 an intensive survey was made in two transects established on the sandy beaches of the West coast, one nearby the Marine Biology Station (MIP/I) and the other facing the coral reef at Barreira Vermelha (MIP/II). A third transect was studied during the low tides of January 1994, this one located on the East coast (MIP/III) (Fig. 1). On each of those transects were located sampling stations according to macroscopic evaluation of sediments, biological communities and tidal levels. Sampling was made on the intertidal area from High Water (0m) to the upper limit of Low Water level (LW) (Fig. 2a, b, c)).

For the study of macrobenthos ($\geq 1\text{mm}$) in each of the stations an area of 0.25m^2 (subdivided in four replicates) was sampled with a PVC core or with a spade,

the material sieved through a 1mm mesh-sieve, fixed in 10% formaldehyde-seawater solution and returned to the laboratory for sorting. The presence of epibenthic species non sampled by these techniques was video recorded for further identification/counting. A 50 g sediment sample was also taken and frozen for the study of grain-size distribution, organic matter and pigments. Salinity and temperature of superficial sediment were recorded with a refractometer and thermometer. The profiles and slopes of the beaches were measured using water levels and graduated scales, and the extension of intertidal sand flats were measured.

Laboratory analysis

For grain-size purposes mud ($<62\mu\text{m}$, $>4\phi$), sand ($62\mu\text{m}$ - $2000\mu\text{m}$, 4ϕ - 1ϕ) and gravel ($>2000\mu\text{m}$, $<10\phi$) were measured using a video camera attached to a binocular microscope and using the image analysis programme JAVA (Jandel Scientific). The system was calibrated using an object of known dimensions and then measured the maximum width of each grain (400 by sample), which equals the critical dimension of retention in a wet sieve system as proposed by Buller & McManus (1979). Sand grain-size distribution (phi-level) was also analysed. The sediment organic matter content (OM g/m^2) was estimated by loss on ignition ($\pm 500^\circ\text{C}$, 24h period) after the estimation of sediment water contents (%H₂O) by 24h drying at $\pm 70^\circ\text{C}$.

The concentration of the sediment phytopigments was evaluated by spectrophotometry, after 24h cool extraction in 90% acetone. Concentrations ($\mu\text{g/g}$ dry sediment) of chlorophyll a (Chl. a), phaeopigments (Phaeop.), carotenoids (Car.), and chlorophyll b and c, were calculated by modified Lorenzen (Chl. a, Phaeop.), Parsons and Strickland (Car) and Jeffrey and Humphrey equations (in Plante-Cuny, 1974). The Margalef index and the Chl a % degradation were used (Plante-Cuny, 1978) and the Moss index was calculated (Moss, 1967). To obtain phytopigment values per unit area (mg/m^2) from phytopigment values per weight ($\mu\text{g/g}$), a sediment specific weight was used (Cancela da Fonseca et al. 1987).

Analysis tools

Data analysis was achieved on the basis of the fitness of the $0.25/\text{m}^2$ sample area, being the community species adequately represented whereas upon an species curve/area, following the criteria of Hartnoll (1983). Shannon-Weaver diversity index and evenness were calculated (Daget, 1979). Community dominance index (McNaughton, 1968 in Fonseca, 1989) was calculated. General matrices of values of sediment parameters and distribution of individuals per station including values from MIP/I and MIP/II were built. Cluster analysis (correlation coefficient of Bravais-Pearson) was used to group biological and sediments characteristics (Pielou, 1984). In

order to summarise the information, principal component analysis (PCA - Sneath & Sokal, 1973) was used. Cluster analysis and PCA were only performed on the matrixes of MIP/I and MIP/II, once the extremely low values of density and diversity at MIP/III were not compatible with the theoretical principles of those methods.

RESULTS

Sediment parameters

The analysis of Fig. 3a), b) and c) and Table 1 shows that MIP/I (Biologia Marinha) presented a higher percentage of medium and fine sands, MIP/II (Barreira Vermelha) was dominated by fine sands while MIP/III (East coast) had higher percentages of medium sand and an important fraction of coarse sand. There is also in MIP/I and MIP/II a clear gradient from medium and fine sands to fine and very fine sands from High water to Low water level. At the East coast (MIP/III) was recorded an opposite gradient with a greater percentage of medium and fine sands at the upper level while at the lower level, although medium sands dominate, the percentage of coarse sands more than doubles the percentage of fine sands. Considering those results together with the profiles drawn in Fig. 2 and according to criteria of Short (1983) we can consider MIP/I and MIP/II as dissipative beaches typified by low gradients with large intertidal flats and fine to medium sands. Also present are small current ripples and associated with cross-bedding, as a consequence of an highly dynamic current, parallel to the coast, and the sequence of low and high tides. Both at MIP/I and in MIP/II three vertical layers were distinguished respectively, at #-1.35m and #ADT: 1) a clean (oxygenated) sand; 2) a gray (RPD) transition zone and a 3) black (reduced) zone. Otherwise, MIP/III is considered as reflective type with an high gradient and the presence of a "step", at its upper level of the tidal flat (characteristic of an instable beach) and the sediments dominated by clean medium and coarse sands.

Analysing Table 2 becomes evident that both transects (MIP/I and MIP/II) present similar results both to water content and organic matter, with the first parameter increasing from high water to low water level as a consequence of the grain size gradient, the higher values of organic matter at #ADT and # -1.20m seem to be related with the percentages of finer sediments. Water percentage is also related at MIP/I and MIP/II with the higher values of phytopigments ($R = 0.811$ and $R = 0.749$ to Chl *a*, respectively). The values of Moss index are similar in both beaches indicating an identical deposition of alien material along the intertidal sand flats. At MIP/III the higher concentrations of phytopigments are related to coarser sediments; stations MW and LW are the only ones that indicate the occurrence of detritic deposition, thus justifying the higher values of organic matter.

Macrobenthic communities

On transects MIP/I and MIP/II were identified 96 species, being 25 common to both transects. The analysis of Fig. 4a), b) and c) reveals that those transects are clearly dominated by polychaetae and, in a minor fraction crustacea. Exceptions are stations 0m, where only insecta were sampled, DX and -0.5m where *Bivalvia* is the dominant taxa, as a consequence of high densities of *Donax faba* (considering a density of 469 ind./m² 443 correspond to *D. faba*). At the beach on the East coast were recorded only 8 species, also dominated by polychaetae and crustacea, all sampled at low water level (#LW), with the exception of the decapode *Ocypode kuhli* recorded at #MW.

Table 3, where are presented the values of density, diversity and evenness, shows that the higher values of abundance, diversity and evenness, correspond to Stations -1m, -1.35m; -1.20m and LW on transect MIP/I and HMW, MW, LW and ADT on transect MIP/II while the community dominance index of McNaughton (Dc) presents its lower values, thus revealing a large number of species and individuals distributing in an identical way for those species. On the other hand, Dc index is higher at stations 0m, -0.5m and DX, where Insecta and Bivalvia, respectively, clearly dominate. The diversity increases towards finer sediments from high water to low water level, and that characteristic associated with the dissipative profile of these beaches permits the formation of half-permanent holes, where polychaetes and crustaceans are found. Although the total number of individuals and species are superior at MIP/I, the distribution of those individuals and the dominance in both transects present identical values on the corresponding stations. So, it may be considered that the communities present in both beaches are similar. As to MIP/III presents a density of 202 ind./m² at #LW while the indexes indicate a relatively uniform distribution of individuals by species.

Principal component analysis (PCA) was performed on 36% of identified species of Biologia Marinha (MIP/I) and Barreira Vermelha (MIP/II) transects, accounting for 90% of total abundance. The analysis of Table 4 reveals that the third factor accounts 56.5% of total information, while first and second factors (25.2% and 41.9%) are mainly due to grain size distribution of sands (Fig. 5), the third factor accounts mainly to clay (coarse silt) distribution (Fig.8), thus considering grain size distribution as the main factor affecting macrobenthos distribution and distinguishing stations. Fig. 5 clearly shows four distinct sections corresponding respectively to medium and coarse sand (first sector), very fine sand to coarse silt (sector 2); a

transition zone (sector 3) and, finally a fourth sector corresponding to fine sands. These sections also integrate species associated not only with grain size distribution but also with, %OM, %H₂O and phytopigments (mainly Chl *a* and phaeopigments).

In fact, analysing the results of hierarchic classification (Fig. 7), it becomes evident that four distinct clusters arise: the first one formed by the bivalve *Donax faba* and Isopoda sp.1 (Sphaeromidae) with a *Spion* sp.1 corresponding to coarse and very coarse sand. This association corresponds to the stations in the upper level of the beach, as shown in Fig.9 by the group formed by stations 0m; -0.5m; -1m (MIP/I); 0m; DX (MIP/II) thus confirming identity between transects I and II on the west coast. The second cluster corresponds to sector 4 and fine sands dominated by the decapode *Dotilla fenestrata* and the polychaetes *Spion* sp3, *Magelona cincta*, *Nephtys tulearensis*, *Glycera alba* and *Gravierella multiannulata*, although the late two extend their occurrence to low water level (Annex 1). The third group matches the third sector, a transition area between fine and very fine sands mainly defined by *Glycera convoluta* (#-1.35m), *Scoloplos madagascarensis*, *Eulalia sanguinea* and *Dendronereis arborifera*, the occurrence of the bivalve *Loripes clausus*, and related to the higher values of Moss index, corresponding mainly to stations -1.35m and LW in MIP/I, an area marked by dead coral. Also must be recorded that the opposition between stations -1.20m and -1.35m (MIP/I) is visible on factor 3 (Fig.8) resulting from the opposition between fine and coarse silt.

The last cluster corresponds to fine and very fine sands undoubtedly linked with the higher values of %OM; %H₂O, Chlorophyll *a* and phaeopigments where the polychaets *Armandia intermedia*, *Glycera capensis*, *Mediomastus capensis* and the amphipoda sp1 clearly dominate. This association corresponds to the stations near low water level, where diversity is higher as far as grain size becomes smaller and the %OM increases.

At east coast (MIP/III) as referred, the community was composed only by eight species concentrated at low water level where %OM, % H₂O are higher, and dominated by the polychaetes *Pisionidens indica* and *Pisione africana*. These characteristics together with the values of the diversity index ($H' = 2.303$) evenness ($J = 0.768$) and dominance ($D_c = 63.4\%$) configured a situation characteristic of beaches with reflective profiles as in present case.

DISCUSSION

According to the classification of sandy beaches by Short & Wright (1983) both beaches studied on west coast of Inhaca Island can be considered as dissipative type, characterised by low gradients, large intertidal sand flats; fine to medium sands

with a coarser fraction towards its upper level and presenting an uniform beach face alongshore. These are common beaches in regions exposed to high breakers as those of southern Africa and Australia. The East coast beach is considered of reflective type with a gradient characteristic of an instable beach, with a berm or step at the upper level of the intertidal platform. Sediments are dominated by medium to coarse sand with a finer fraction at its upper level. The higher percentage of fine sands seems to be mainly a consequence of eolic deposition, derived from the strong southern winds during winter.

As stated by McLachlan (1983) grain size, shape and sorting are most important in fixing porosity and permeability which influence drainage. Drainage is critical in determining the moisture content and increases on stepper beaches as the permeability increases with coarser substrate and better sorting. Accordingly the higher concentrations of phytopigments occurred where were recorded the highest values of % OM and the finest sediments. One possible explanation is given by Tietjen (1968) suggesting that the low dynamics of these beaches may favour the deposition of autochthonous material as well as the retention of alien material, which is associated with the increase of the finest fraction of sediment. Jonge (1985) refers the colloidal characteristic of finer sediments gathering nutrients and organic compounds, thus creating a substrate favourable to the growth of microphytobenthos. The strong correlation found between water content and phytopigments concentration according to Riaux (1982) can be attributed to the retention of water by the mucus produced by microphytobenthos or, otherwise, that high water percentage infavours the development of microphytobenthos, which is in fact limited by the water content of sediments.

The east coast beach (MIP/III) presents the highest concentrations of phytopigments associated to coarser sediments. This however is explained by the reflective characteristic of the beach and the instability of sediments which do not favour a substrate to primary producers. Thus, in high energy beaches organic matter is mainly "imported" from surf zone and retained by sediments that act as sieves draining large water volumes at each tide (McLachlan, 1983; Carter, 1989).

As stated by McLachlan (1983) the macrofauna of these sandy beaches is mainly dominated by molluscs, crustaceans and polychaetes, however the dominant group in the less exposed beaches here considered (MIP/I and MIP/II) are the polychaetes as suggested by Dexter (1983), while the reflective beach of east coast is dominated by crustaceans.

If it is well known that grain size and /or organic content influence distribution and abundance of organisms on sandy beaches (McLachlan, 1983) in present case PCA analysis suggested that the defined sectors integrate species not only associated

with those factors but also with phytopigments, mainly chlorophyll a and phaeopigments. As it would be expectable diversity and abundance are higher in the low gradient dissipative beaches of the west coast, with increasing values following the grain size gradient from medium to fine sand at the lower level. Eleftheriou & Nicholson (1975) however showed that grain size alone can not characterise a beach, and in fact, McLachlan et al. (1981 b) obtained significant correlation between macrofauna diversity and abundance with both grain size and slope, considering the latest as the crucial factor once the flatter the slope is the more evenly the wave energy is dissipated.

One of the hardest tasks on studying macrofaunal distribution of sandy beaches, is trying to establish a zonation scheme in the classic sense of the word, and accordingly consider the several and conflicting points of view, as McLachlan (1983) accurately exposed. The present work was mainly concerned with endomacrobenthos, nevertheless the high mobile fauna of these sandy beaches, mainly crabs and sometimes isopods, must be considered even in a qualitative approach, based on remarking the presence of the mobile fauna as in present work. Thus, if a quantitative approach is desirable on endobenthos, these studies must be complemented with different approaches, including video census of the highly mobile macrofauna, sediment parameters and water dynamics (unfortunately impossible to accomplish at this phase of present work), towards a more holistic approach.

Nevertheless, the crossed information between the quantitative analysis of endobenthos, sediment parameters and previous work of Macnae & Kalk (1969), allows to highlight some of the structure of macrobenthos zonation of sandy beaches of Inhaca Island. The upper level of the west coast beach is marked by the coarser sediment and the presence of the ocypodid crab Ocypes ceratophthalmus and insecta larvae, just below the level of mean high neap tide, using Macnae and Kalk's terminology, the bivalve Donax faba together, with the Spharomidae isopods make the boundaries of this area. Another cluster matches what those authors classified as the wetter areas of mixed sand, where the decapod Macrophthalmus grandidieri together with the polychaetes Armandia intermedia, Glycera capensis and Mediomastus capensis appear associated to the higher values % OM, % H₂O and concentration of chlorophyll a and phaeopigments. The cluster identified as a transition zone between those late two where Glycera convoluta, Scoloplos madagascarensis, Eulalia sanguinea, Dendronereis arborifera and the bivalve Loripes clausus occur, can be considered as the upper limit of the late zone, being the separation mainly attributed to the opposition between fine and coarse silt.

The second sector identified by PCA analysis has its correspondence on Macnae & Kalk (1969) work as the drier patches of mixed cleaner sand resulting from

the irregular drainage of sand flats of the west shore allow some areas to be drier than others. In this sector the crustacean Dotilla fenestrata and the polychaetes Spion sp3., Magelona cincta, Nephtys tulearensis, Glycera alba and Gravierella multiannulata appear associated, although the late two species extend to lower areas.

Although there are some different or absent records between present work and Macnae & Kalk (1969) reference, the main divergence is in what concerns to gastropods, once the major key species as Nassa arcularia, Nassa coronata or Bullia natalensis were found only as empty shells (with enormous concentrations) or at very low numbers escaping the sample. However, without following the extreme zonation scheme of Brown (in McLachlan, 1983) considering only a division between air breathers and water breathers areas, Salvat's zones (Salvat, 1967) of drying, retention and resurgence seem to match the three main areas previously considered, as well as the Zostera /Halodule and Cymodocea serrulata / C. rotundata associations merge Salvat's saturation zone. The Dotilla fenestrata patches clearly illustrate what Bally (1983, 1987) called the irregular distribution of macrobenthos on sandy beaches environments and the patchiness of its distribution, and this is the main factor apparently separating (in what regards the presence of some species) transects MIP/I and MIP/II, that must be considered representative of the same environment, being the differences the consequence of patchiness.

East coast and its reflective beaches represents, on the other hand, a case where only two areas can be clearly defined, and those correspond to the area occupied by the air breathers and that occupied by the water breathers, mainly polychaetes, amphipods and sometimes (not sampled) the bivalve Donax incarnata. Thus, the attempts to clarify the zonation of sandy beaches must be carried using crossed information between species occurrence and distribution, sediments parameters, hydrodynamics studies and the understanding that it is hardly possible to define or adopt a unique zonation scheme, even within the same geographical area.

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CAPTIONS FOR FIGURES AND TABLES

Fig. 1 - Location of transects MIP/I (Biologia Marinha), MIP/II (Barreira Vermelha) and MIP/III (East Coast) at Inhaca Island (Mozambique).

Fig. 2 - Location of stations and profiles at MIP/I (Biologia Marinha), MIP/II (Barreira Vermelha) and MIP/III (East Coast).

Fig. 3 a) - Grain-size distribution at MIP/I (Biologia Marinha).

Fig. 3 b) - Grain-size distribution at MIP/II (Barreira Vermelha).

Fig. 3 c) - Grain-size distribution at MIP/III (East Coast).

Fig. 4 a) - Variation of relative frequencies of taxa in each station at MIP/I (Biologia Marinha).

Fig. 4 b) - Variation of relative frequencies of taxa in each station at MIP/II (Barreira Vermelha).

Fig. 4 c) - Variation of relative frequencies of taxa in each station at MIP/III (East Coast).

Fig. 5 - Principal Component Analysis (PCA) on sediment and biological parameters of MIP/I and MIP/II - factors 1 and 2.

Fig. 6 - Principal Component Analysis (PCA) on sediment and biological parameters of MIP/I and MIP/II - factors 1 and 3.

Fig. 7 - Classification by hierarchic analysis based on sediment and biological parameters of MIP/I and MIP/II .

Fig. 8 - Principal Components Analysis (PCA) - representation of stations (MIP/I and MIP/II) based on factor 1 and factor 3.

Fig. 9 - Hierarchic Analysis - representation of stations (MIP/I and MIP/II) .

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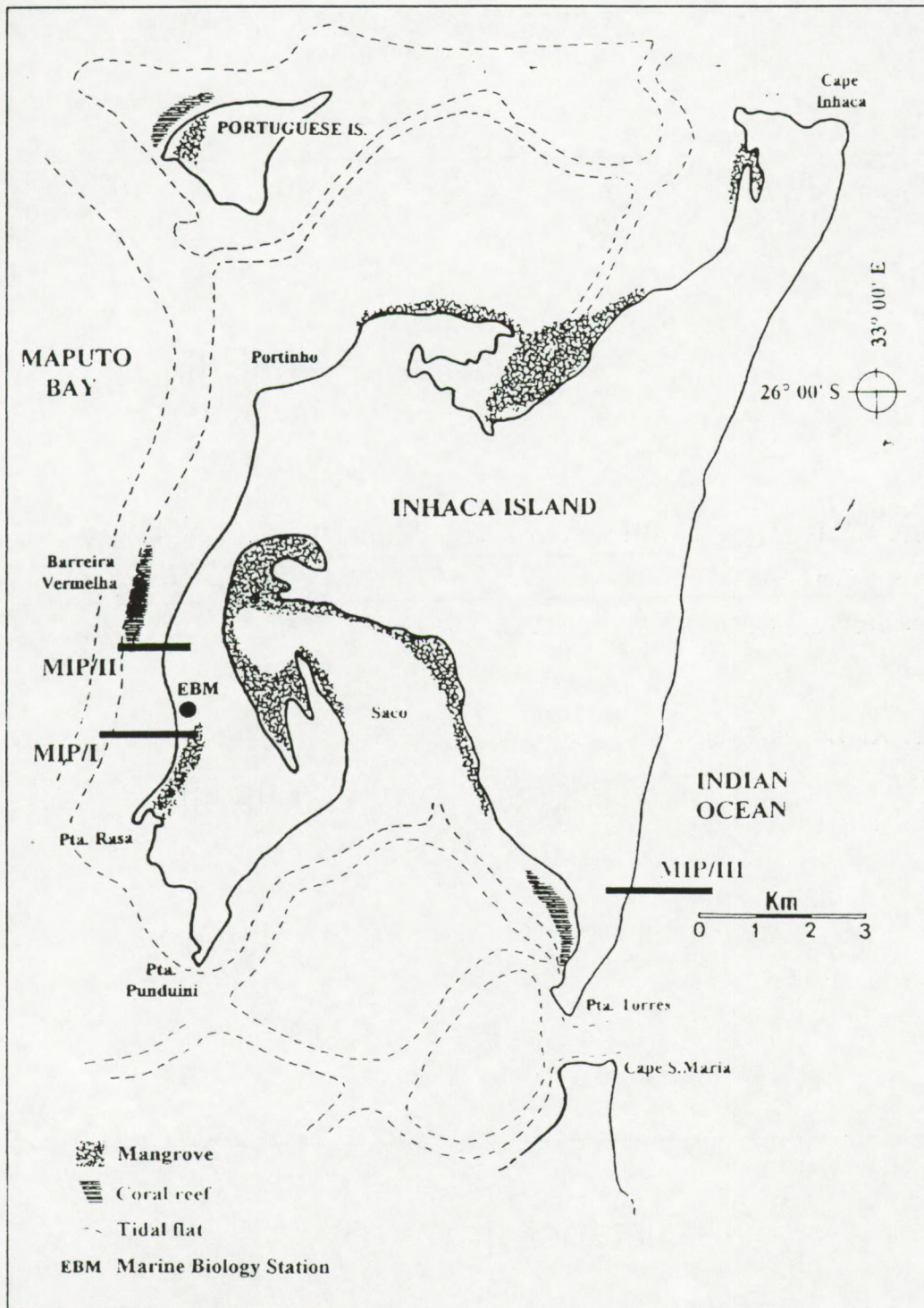


Fig.1 - Location of transects MIP/I (Biologia Marinha), MIP/II (Barreira Vermelha) and MIP/III (East Coast) at Inhaca Island (Mozambique).

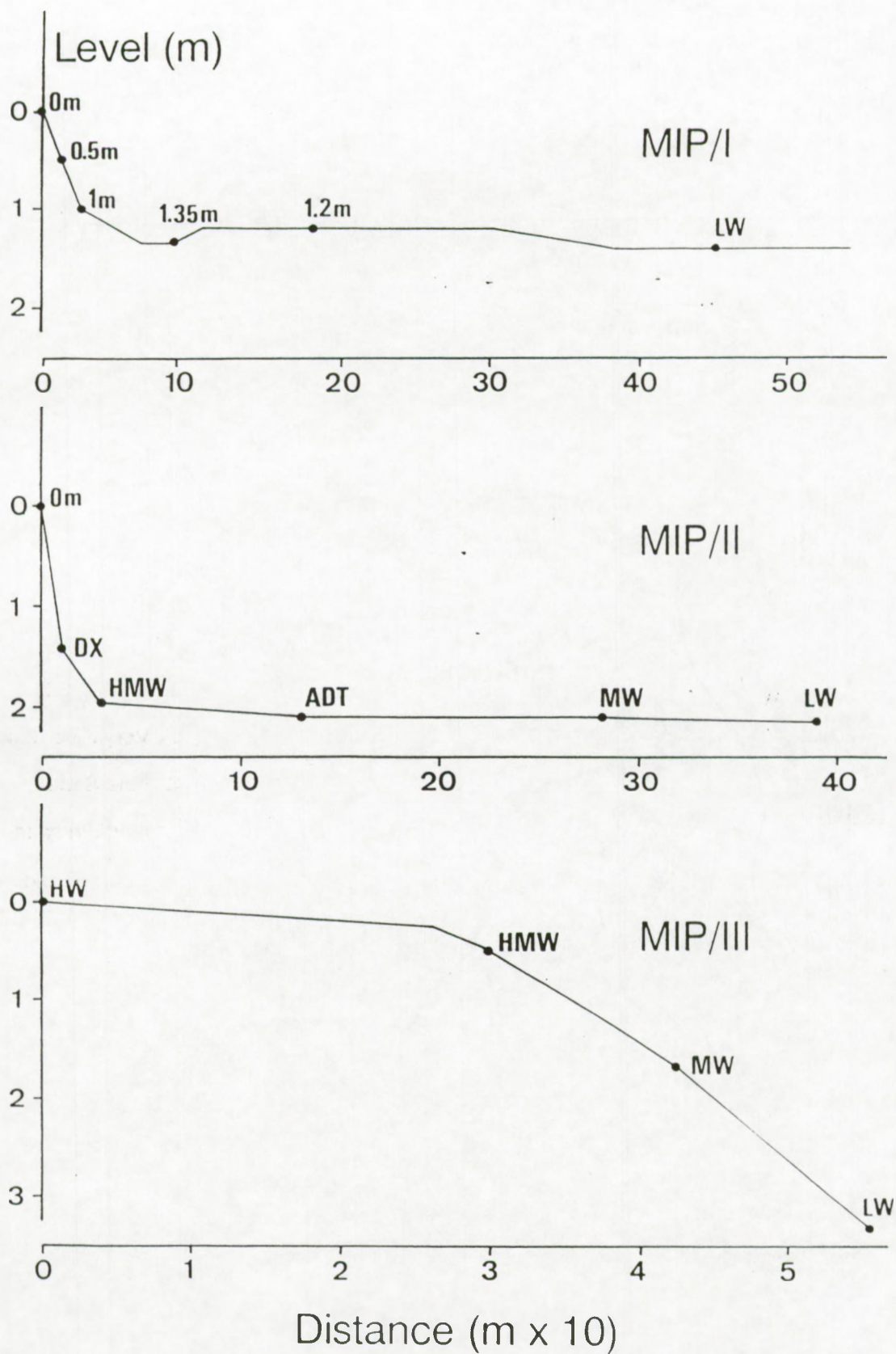


Fig.2 - Location of stations and profiles at MIP/I (Biologia Marinha), MIP/II (Barreira Vermelha) and MIP/III (East Coast).

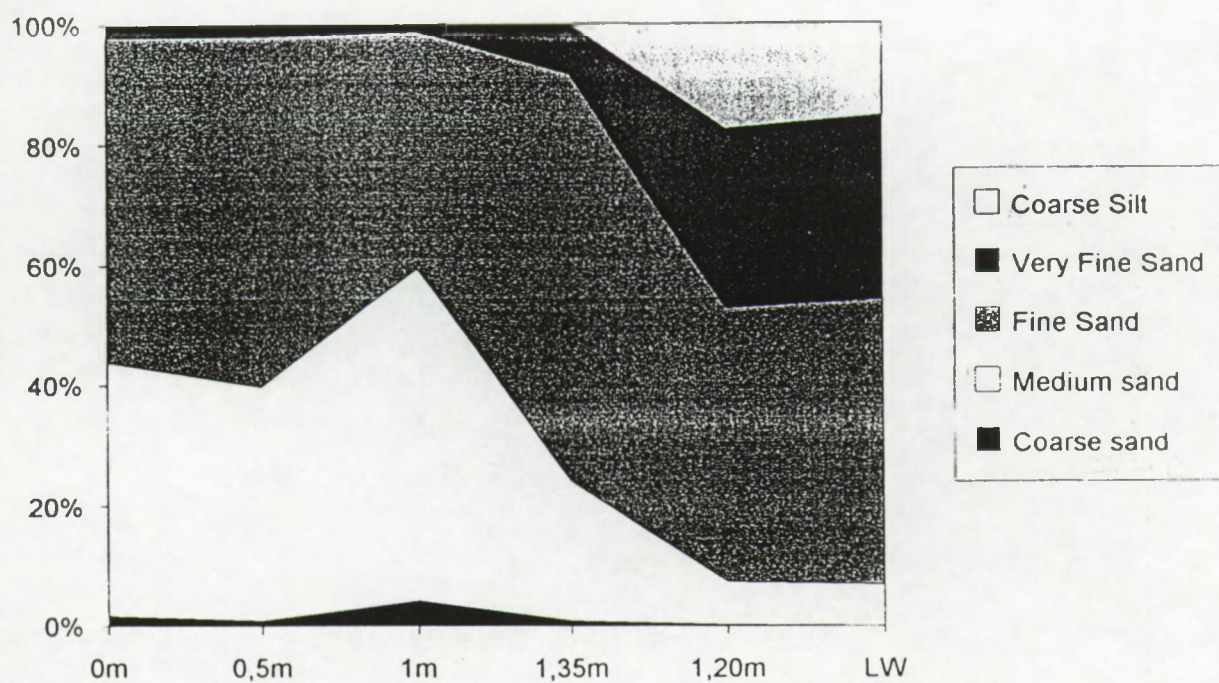


Fig.3 a) - Grain-size distribution at MIP/I (Biologia Marinha).

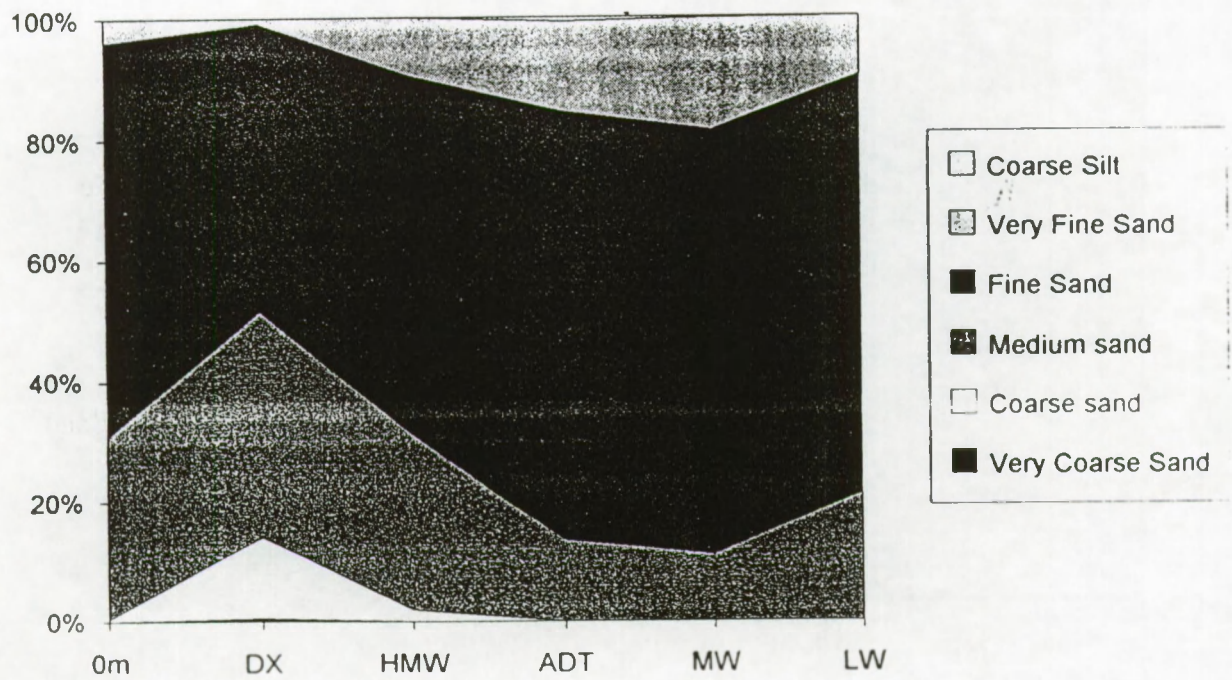


Fig. 3 b) - Grain-size distribution at MIP/II (Barreira Vermelha).

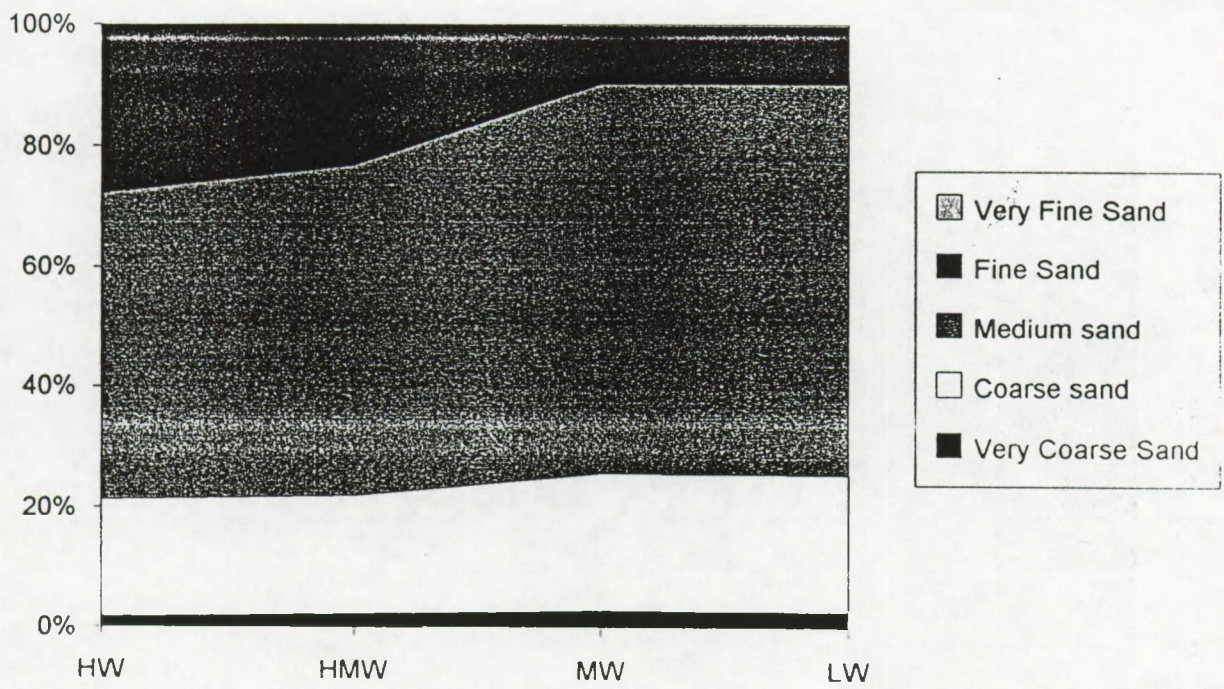


Fig. 3 c) - Grain-size distribution at MIP/III (East Coast).

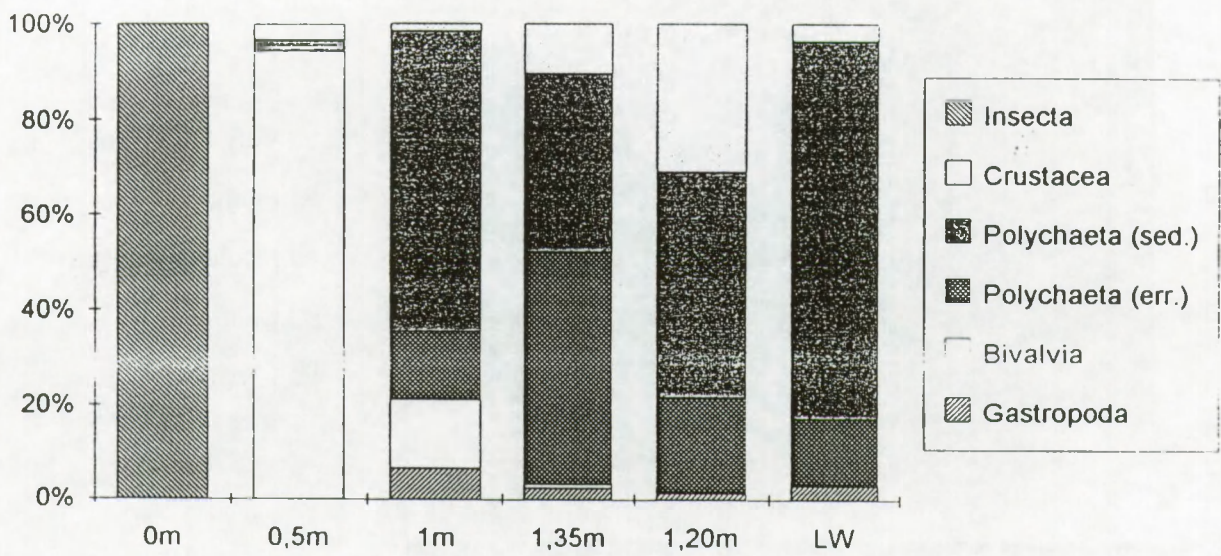


Fig.4 a) - Variation of relative frequencies of taxa in each station at MIP/I (Biologia Marinha).

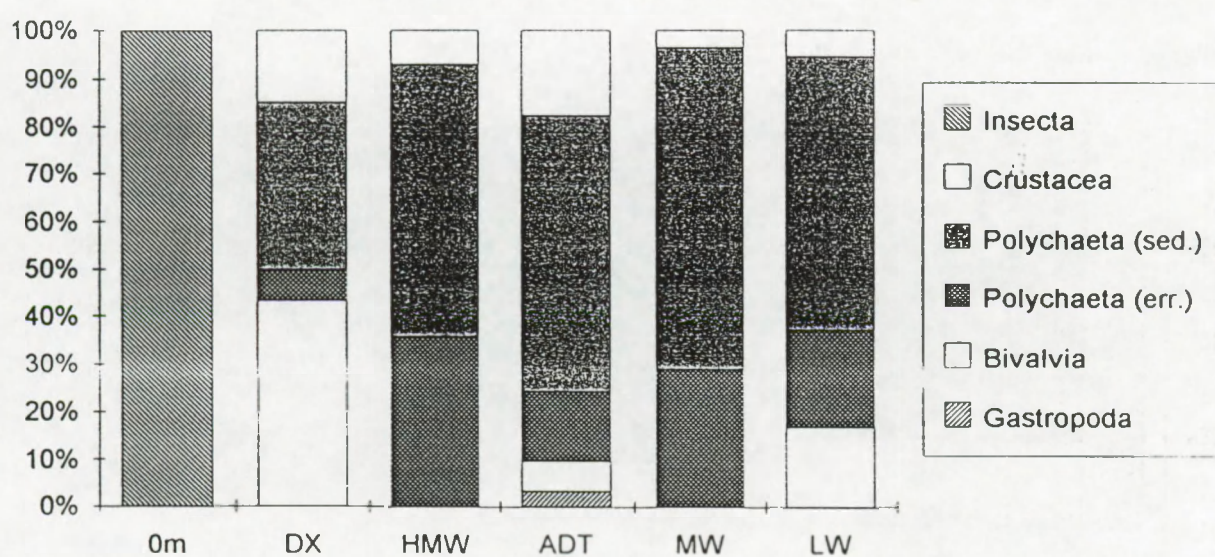


Fig. 4 b) - Variation of relative frequencies of taxa in each station at MIP/II (Barreira Vermelha).

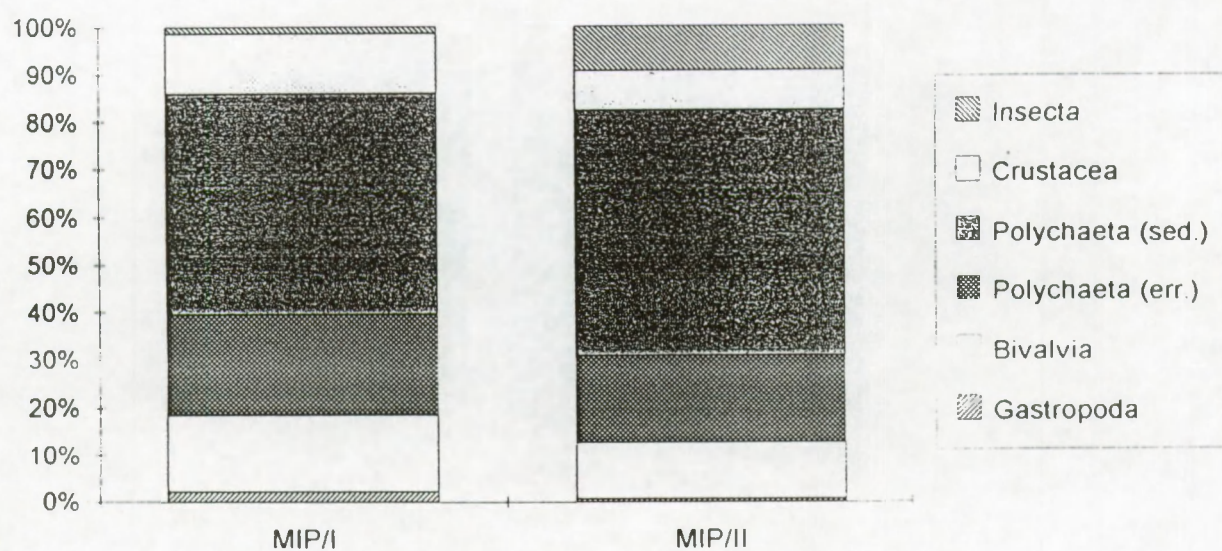


Fig.4 c) - Variation of relative frequencies of taxa in each station at MIP/III (East Coast).

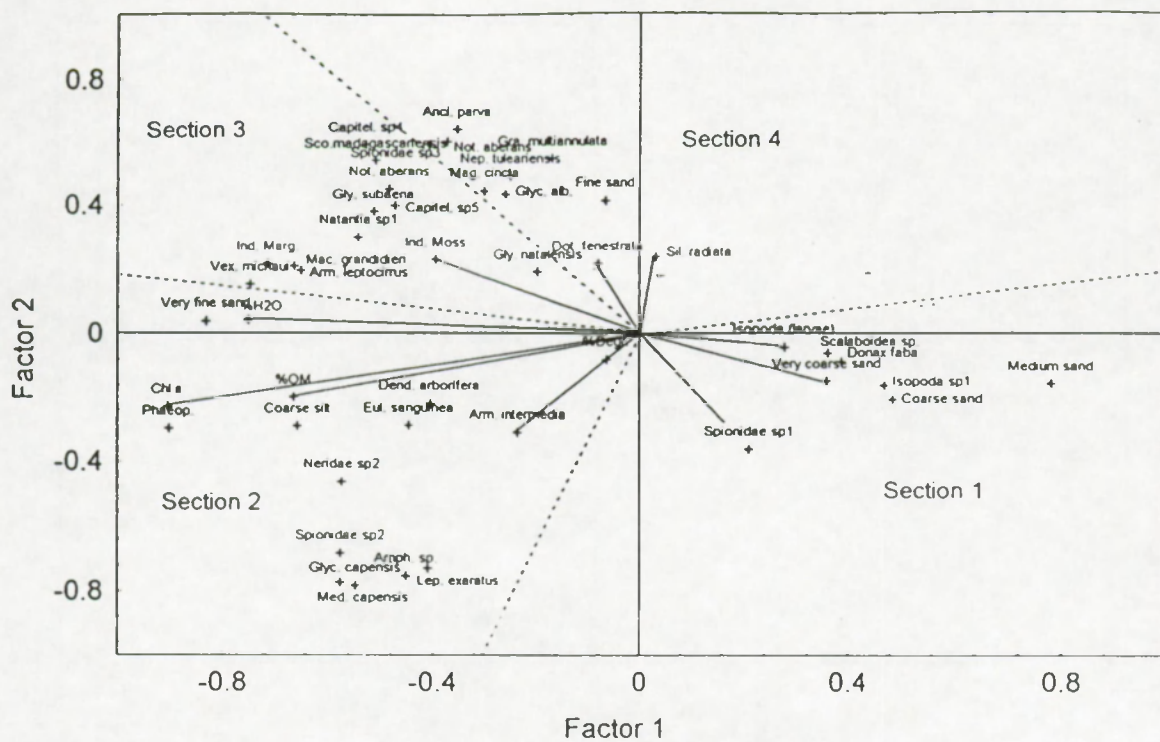


Fig.5 - Principal Component Analysis (PCA) on sediment and biological parameters of MIP/I and MIP/II - factors 1 and 2.

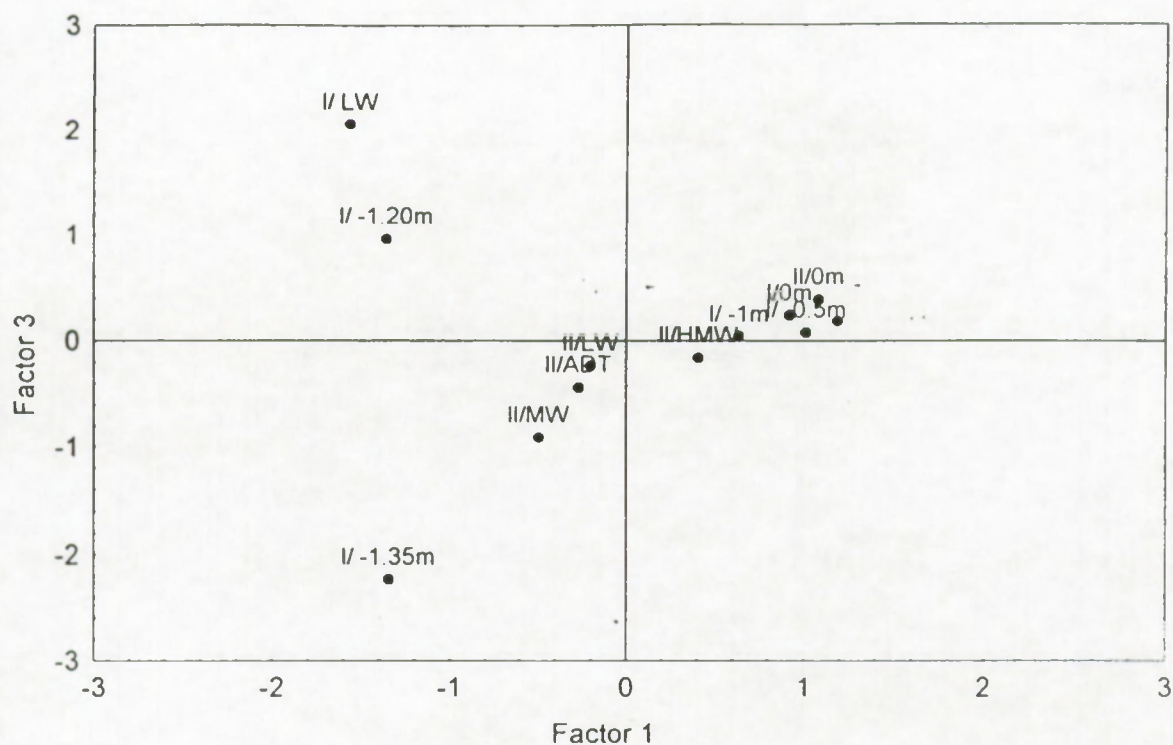


Fig. 6 - Principal Component Analysis (PCA) on sediment and biological parameters of MIP/I and MIP/II - factors 1 and 3.

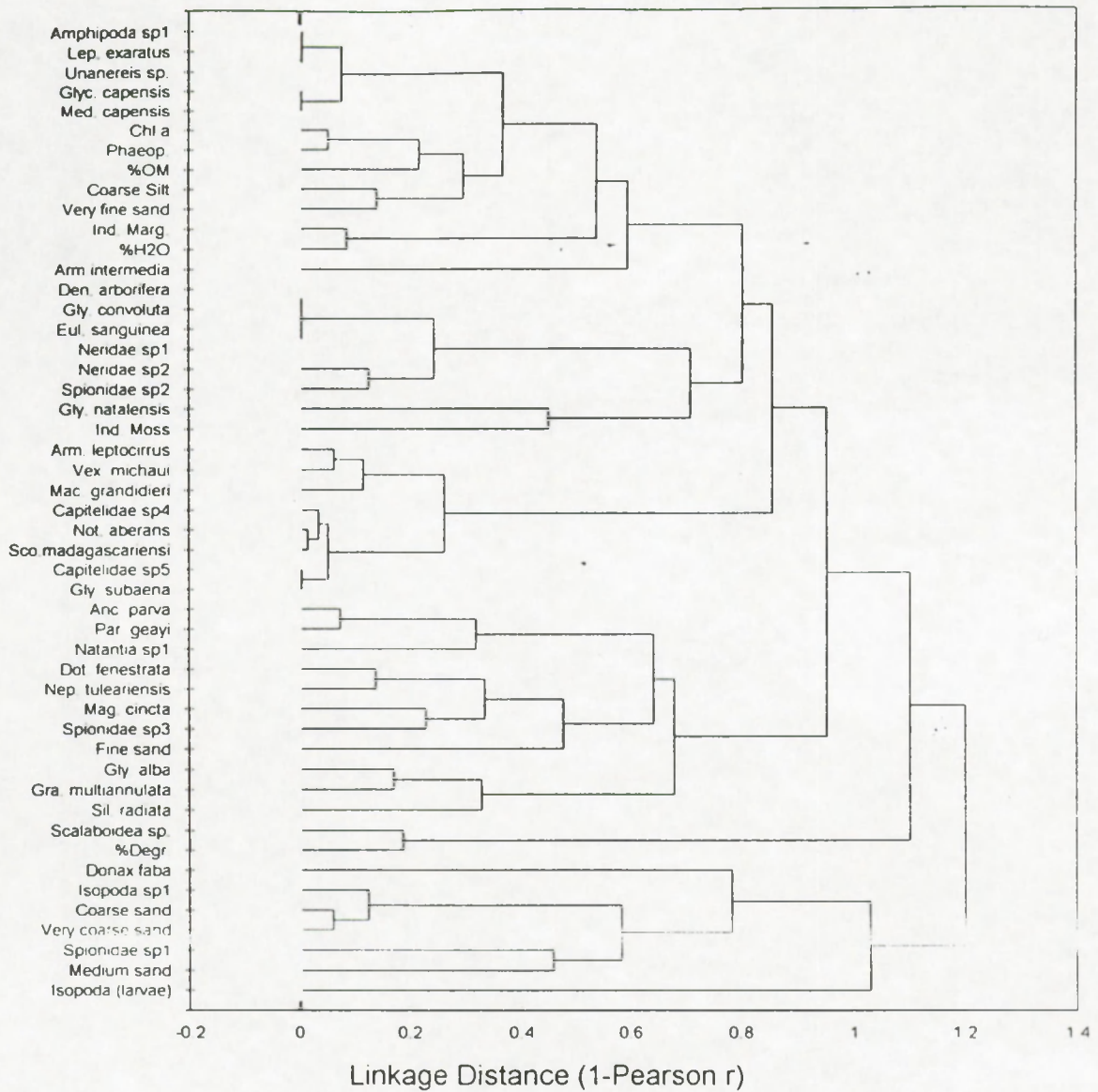


Fig. 7 - Classification by hierarchic analysis based on sediment and biological parameters of MIP/I and MIP/II.

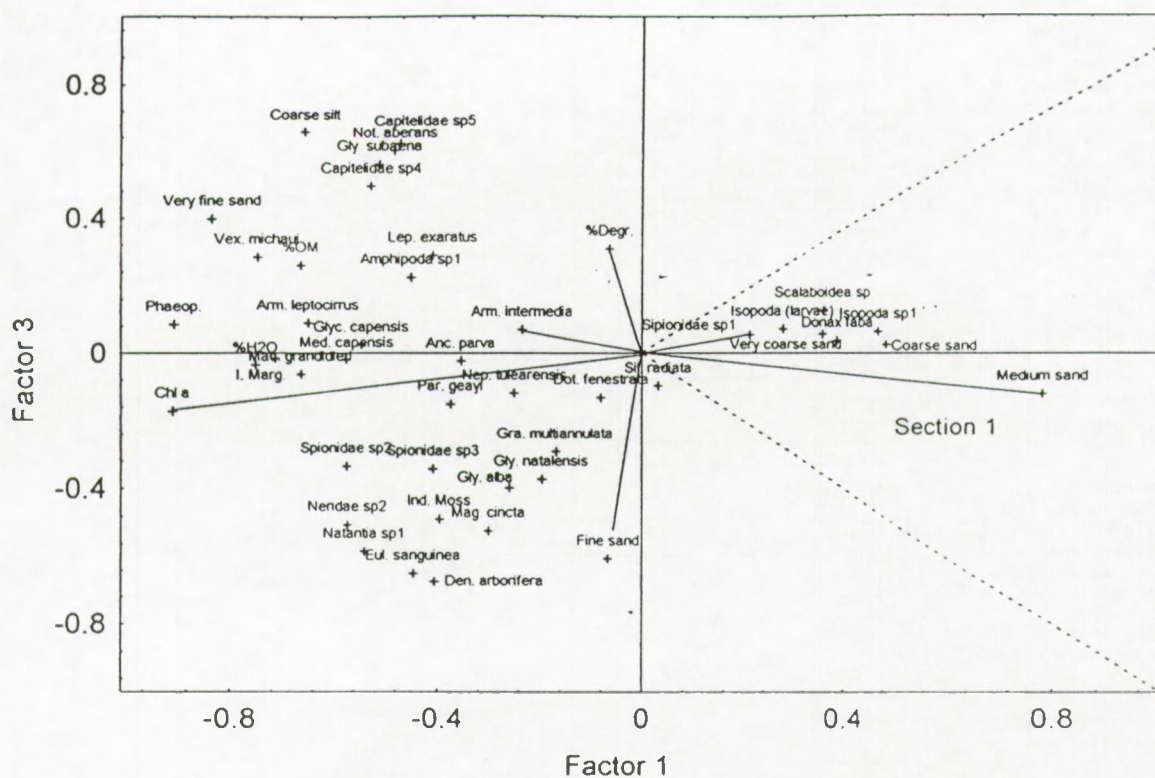


Fig 8 - Principal Components Analysis (PCA) - representation of stations (MIP-I and MIP-II) based on factor1 and factor 3.

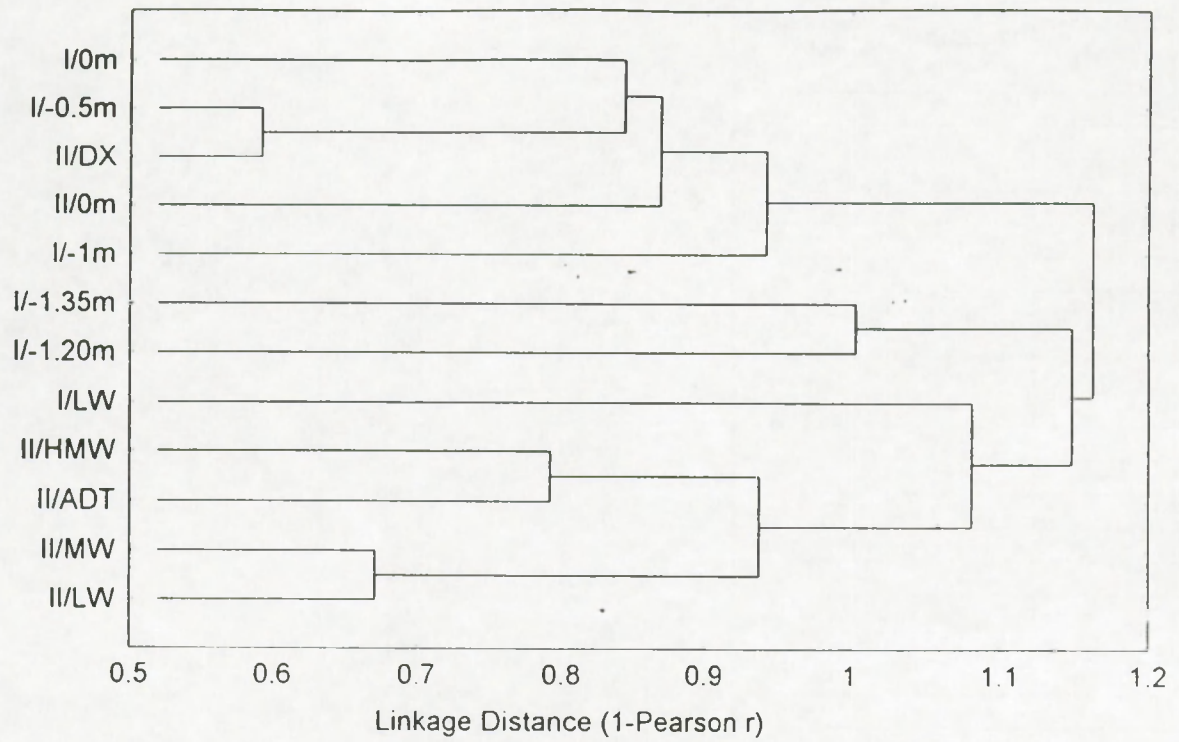


Fig.9 - Hierarchic Analysis - representation of stations (MIP/I and MIP/II) .

	Well Sorted Sands	Moderately Well Sorted Sands	Moderately Sorted Sands
MIP/I			
#0m	+		
#0,5m	+		
#1m		+	
#1,35m		+	
#1,20m			+
#LW			+
MIP/II			
#0m	+		
#DX		+	
#HMW		+	
#ADT	+		
#MW	+		
#LW	+		
MIP/III			
#HW		+	
#HMW		+	
#MW			+
#LW			+

Table 1. - Grain-size classification at MIP/I, MIP/II and MIP/III.

	%OM	%H2O	Chl a	Phaeop.	Marg. index	Moss index
MIP/I						
#0m	0.14	19.83	3.49	0.98	1.63	0.98
#0,5m	0.11	6.68	9.35	2.76	1.28	1.10
#1m	0.86	16.56	39.11	13.61	2.01	1.14
#1,35m	0.48	20.83	115.47	43.37	2.10	1.22
#1,20m	1.53	27.34	106.54	64.33	2.27	1.08
#LW	0.92	22.62	76.20	42.58	2.64	1.12
MIP/II						
#0m	0.21	0.23	4.14	4.88	0.00	0.98
#DX	0.38	5.95	12.20	5.02	1.22	1.14
#HMW	0.27	17.57	19.51	7.51	2.04	1.19
#ADT	1.06	21.11	68.47	26.52	2.22	1.23
#MW	0.57	21.22	44.42	18.75	2.23	1.18
#LW	0.88	24.34	53.07	29.51	2.34	1.10
MIP/III						
#HW	0.43	1.22	0.03	0.06	0.00	1.05
#HMW	0.41	2.70	0.09	0.20	0.00	1.13
#MW	1.02	1.79	0.20	0.38	1.36	1.26
#LW	0.47	8.44	0.17	0.26	1.22	1.08

Table 2. - Values of sediment parameters at MIP/I, MIP/II and MIP/III.

	Ind./m2	S	H	J	Dc
MIP/I					
0m	44	4	1.68	0.84	81.8
0,5m	469	5	0.42	0.18	96.8
1m	248	9	2.18	0.69	69.4
1,35m	667	33	4.32	0.86	27.3
1,20m	843	33	3.66	0.73	50.0
LW	720	24	3.02	0.66	62.2
MIP/II					
0m2	164	7	1.20	0.43	85.4
DX	240	5	1.86	0.80	78.3
HMW	75	7	2.61	0.93	49.3
ADT	331	18	3.57	0.86	35.4
MW	443	13	3.28	0.89	38.6
LW2	475	22	3.53	0.79	43.8
MIP/III					
HW	0	0	0	0	0
HMW	0	0	0	0	0
MW	0	0	0	0	0
LW	202	8	2.30	0.77	63.37

Table 3. - Values of abundance; diversity (H'), evenness (J) and community dominance (D_c) indexes at MIP/I, MIP/II and MIP/III.

		% of total	Cumul.	Cumul.
	Eigenvalues	Variance	Eigenvalues	%
1	12.35	25.21	12.35	25.21
2	8.19	16.72	20.55	41.93
3	6.67	13.61	27.22	55.54

Table 4. - Principal component analysis (PCA) - results on MIP/I and MIP/II.

	MIP/I						MIP/II					
	0m	0,5m	1m	1,35m	1,20m	LW	0m	DX	HMW	ADT	MW	LW
Classe Gastropoda												
<i>Strombina heptagonalis</i>	0	0	0	5	0	0	0	0	0	0	0	0
<i>Littoridinaria fictilis</i>	0	0	0	0	0	0	0	0	0	5	0	0
<i>Littoridinaria sp1</i>	0	0	12	0	0	0	0	0	0	0	0	0
<i>Littoridinaria sp1</i>	0	0	4	0	5	0	0	0	0	0	0	0
<i>Littoridinaria michauxi</i>	0	0	0	11	5	21	0	0	0	5	0	0
Classe Bivalvia												
<i>Littoridinaria meridionalis</i>	0	0	0	0	0	0	0	0	0	0	0	5
<i>Littoridinaria faba</i>	0	443	0	0	0	0	0	104	0	0	0	0
<i>Littoridinaria clausus</i>	0	0	0	5	0	0	0	0	0	0	0	0
<i>Littoridinaria lilacea</i>	0	0	0	0	0	0	0	0	0	0	0	11
<i>Littoridinaria radiata</i>	0	0	0	0	0	0	0	0	0	0	0	11
<i>Littoridinaria radiata</i>	0	0	36	0	0	0	0	0	0	21	0	53
Classe Polychaeta (Errantia)												
<i>Littoridinaria parva</i>	0	0	0	0	0	5	0	0	0	0	11	5
<i>Littoridinaria iricolor iricolor</i>	0	0	4	5	5	0	0	0	0	0	0	0
<i>Littoridinaria iricolor caerulea</i>	0	0	0	0	0	0	0	0	0	5	0	0
<i>Littoridinaria arborifera</i>	0	0	0	59	0	0	0	0	0	0	0	0
<i>Littoridinaria sanguinea</i>	0	0	0	53	5	0	0	0	0	0	0	0
<i>Littoridinaria siciliensis</i>	0	0	0	5	0	0	0	0	0	0	0	0
<i>Littoridinaria alba</i>	0	0	20	16	0	5	0	0	0	11	27	43
<i>Littoridinaria convoluta</i>	0	0	0	21	0	0	0	0	0	0	0	0
<i>Littoridinaria gigantea</i>	0	0	0	0	0	5	0	0	0	0	0	0
<i>Littoridinaria natalensis</i>	0	0	12	11	0	5	0	0	16	0	11	0
<i>Littoridinaria prashadi</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Littoridinaria subaenea</i>	0	0	0	5	0	53	0	0	0	0	0	0
<i>Littoridinaria capensis</i>	0	0	0	27	69	0	0	0	0	0	0	0
<i>Littoridinaria coccinea</i>	0	0	0	0	0	0	0	0	0	0	0	16
<i>Littoridinaria meteorana</i>	0	0	0	0	0	5	0	0	0	0	0	0
<i>Littoridinaria capensis</i>	0	0	0	0	0	0	0	0	5	0	0	0
<i>Littoridinaria tulearensis</i>	0	0	0	0	0	5	0	0	0	21	11	0
<i>Littoridinaria sphaerocirrata</i>	0	0	0	0	0	0	0	0	0	5	0	0
<i>Littoridinaria sp1</i>	0	0	0	59	5	0	0	0	0	0	0	0
<i>Littoridinaria sp2</i>	0	0	0	53	37	0	0	16	0	0	21	16
<i>Littoridinaria geayi</i>	0	0	0	5	0	16	0	0	5	5	43	5
<i>Littoridinaria ehlersiaeformis</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Littoridinaria capensis</i>	0	0	0	0	0	0	0	0	0	0	0	5
<i>Littoridinaria capense</i>	0	0	0	0	0	0	0	0	0	0	0	5
<i>Littoridinaria hyalina</i>	0	0	0	5	0	0	0	0	0	0	5	0
<i>Littoridinaria benguellana</i>	0	0	0	0	16	0	0	0	0	0	0	0
<i>Littoridinaria sp.</i>	0	0	0	0	21	0	0	0	0	0	0	0
Classe Polychaeta (Sedentaria)												
<i>Littoridinaria accraensis</i>	0	0	0	0	0	5	0	0	0	0	0	0
<i>Littoridinaria intermedia</i>	0	0	0	0	11	0	0	0	11	11	0	0
<i>Littoridinaria leptocirrus</i>	0	0	0	16	0	21	0	0	0	0	0	0
<i>Littoridinaria sp1</i>	0	0	0	0	16	0	0	0	0	0	0	0
<i>Littoridinaria sp2</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Littoridinaria sp3</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Littoridinaria sp4</i>	0	0	0	0	0	128	0	0	0	5	43	32
<i>Littoridinaria sp5</i>	0	0	0	0	0	21	0	0	0	0	0	0
<i>Littoridinaria sp6</i>	0	0	0	0	0	11	0	0	0	5	0	0
<i>Littoridinaria africanus</i>	0	0	0	0	5	0	0	0	0	5	0	5
<i>Littoridinaria sp1</i>	0	0	0	5	0	0	0	0	0	0	0	0
<i>Littoridinaria multiannulata</i>	0	0	0	0	0	0	0	0	11	64	107	128
<i>Littoridinaria cincta</i>	0	0	0	21	0	0	0	0	0	37	64	5
<i>Littoridinaria capensis</i>	0	0	0	123	256	5	0	0	0	0	0	0
<i>Littoridinaria aberans</i>	0	0	0	0	0	21	0	0	0	0	0	5
<i>Littoridinaria fusiformis</i>	0	0	0	0	0	5	0	0	0	0	0	0
<i>Littoridinaria tenuis</i>	0	0	0	0	0	16	0	0	0	0	0	0
<i>Littoridinaria sexoculata</i>	0	5	0	5	0	0	0	0	0	0	0	0
<i>Littoridinaria brevibranchia</i>	0	0	0	5	11	0	0	0	0	0	0	0
<i>Littoridinaria serpens</i>	0	0	0	5	0	0	0	0	0	0	0	0
<i>Littoridinaria kraussii</i>	0	0	0	0	11	0	0	0	0	0	0	0

ANNEX 1 - Original matrix of densities (ind./m²) in transects MIP/I, MIP/II and MIP/III. The species marked with *, are new records to Inhaca Island.

<i>Spion.sp2</i>	0	5	0	37	32	0	0	0	0	0	0	
<i>Spion.sp3</i>	0	0	0	16	0	16	0	0	21	43	32	16
<i>Streblossoma persica</i>	0	0	0	0	5	0	0	0	0	0	0	0
Classe Cirripedia												
<i>Balanus amphitrite</i>	0	0	0	5	0	0	0	0	0	0	0	0
<i>Chthamalus dentatus</i>	0	0	4	0	0	0	0	0	0	0	0	0
Classe Malacostraca												
<i>Alpheus sp</i>	0	0	0	0	11	0	0	0	0	0	0	0
<i>Amph.sp1</i>	0	0	0	16	165	0	0	0	0	0	0	0
<i>Amph.sp2</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Amph.sp3</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cumacea sp1</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Ootilla fenestrata</i>	0	0	0	0	0	0	0	0	0	53	0	0
<i>sop.sp1</i>	0	11	0	0	0	0	0	24	0	0	0	0
<i>sop.sp2</i>	0	5	0	0	0	0	0	12	0	0	0	0
<i>Leptodius exaratus</i>	0	0	0	0	37	0	0	0	0	0	0	0
<i>Macrophthalmus grandidieri</i>	0	0	0	11	0	11	0	0	0	0	0	5
<i>Matuta lunaris</i>	0	0	0	0	0	0	0	0	5	0	0	0
<i>Natantia sp1</i>	0	0	0	16	0	5	0	0	0	0	16	5
<i>Natantia sp2</i>	0	0	0	11	0	0	0	0	0	0	0	0
<i>Natantia sp3</i>	0	0	0	0	0	5	0	0	0	0	0	0
<i>Natantia sp4</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Natantia sp5</i>	0	0	0	5	5	0	0	0	0	0	0	0
<i>Nanaid.sp1</i>	0	0	0	0	5	0	0	0	0	5	0	5
<i>Nanaid.sp2</i>	0	0	0	0	0	0	0	0	0	0	0	11
<i>Nanaid.sp3</i>	0	0	0	5	5	0	0	0	0	0	0	0
<i>Nanaid.sp4</i>	0	0	0	0	5	0	0	0	0	0	0	0
<i>Thalamita admete</i>	0	0	0	0	11	5	0	0	0	0	0	0
Classe Insecta												
<i>larva Coleoptero sp1</i>	0	0	0	0	0	0	8	0	0	0	0	0
<i>larva Coleoptero sp2</i>	0	0	0	0	0	0	8	0	0	0	0	0
<i>larva Coleoptero sp3</i>	4	0	0	0	0	0	0	0	0	0	0	0
<i>larva Coleoptero sp4</i>	0	0	0	0	0	0	4	0	0	0	0	0
<i>Crysomelidae sp1</i>	0	0	0	0	0	0	4	0	0	0	0	0
<i>ninfa Heteroptera sp1</i>	0	0	0	0	0	0	4	0	0	0	0	0
<i>limenoptero sp1</i>	0	0	0	0	0	0	4	0	0	0	0	0
<i>larva Isoptera sp1</i>	20	0	0	0	0	0	0	0	0	0	0	0
<i>Scalaboidea sp1</i>	16	0	0	0	0	0	132	0	0	0	0	0
<i>Onebrionidae sp1</i>	4	0	0	0	0	0	0	0	0	0	0	0

	MIP/III			
	HW	HMW	MW	LW
<i>Amphipoda spa</i>	0	0	0	37
<i>Amphipoda spb</i>	0	0	0	5
<i>Amphipoda spc</i>	0	0	0	11
<i>Equinoderme n.d.</i>	0	0	0	5
<i>Oligochaeta n.d.</i>	0	0	0	11
<i>Pisionidens indica</i>	0	0	0	85
<i>Pisione africana</i>	0	0	0	43
<i>Pilargidae n.d.</i>	0	0	0	5

**MACROBENTHIC COMMUNITIES OF MANGROVES IN AN EASTERN
AFRICAN ECOSYSTEM (INHACA ISLAND, MOZAMBIQUE)**

By

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Abbreviated title: Macrobenthic communities of mangroves

ABSTRACT

In this paper we analyse the composition of endobenthic macroinvertebrate communities in the mangroves of Inhaca island, Mozambique. The study is based on sampling stations placed along leveled transects, taking samples for macroinvertebrates, grain-size distribution, organic matter and phytopigments. Results indicate that there is a dominance of medium and fine sands, instead of colloidal sedimentation, which is due to the sedimentary origin of the island. There is a clear zonation of organisms as a function of several combined environmental factors, which contribute to define mangrove communities. Grain-size was found the major factor affecting macrobenthos distribution. The Saco mangrove constitutes a southern example of a sub-tropical mangrove with high diversity and production, while Ponta Rasa mangrove may be considered as an atypical mangrove, or an extreme situation of

sub-tropical mangroves where diversity is very low. The differences between the two mangroves seem to indicate that microenvironmental conditions are determinant to the richness of these ecosystems.

INTRODUCTION

Both Eastern and Western African mangroves have lately received a good deal of descriptive attention in literature, focusing several important aspects of economical, ecological and scientific relevance. As highly productive ecosystems their role as breeding and "nursery" areas, their linkage with the adjacent marine ecosystems, namely in what concerns the stabilisation of coast line and coral reefs, is well known (Howell & Semesi, 1982; John & Lawson, 1990).

Although mangroves are mainly tropical ecosystems, sometimes they can occur outside these areas, associated with warm oceanic streams and suggesting that water temperature has a determinant role on the limits of mangrove occurrence. Thus, as stated by Berjak *et al.* (1982), eastern African mangroves between Inhaca Island (Mozambique) and Port Elizabeth (South Africa) are atypical as they are sub-tropical lacking the richness and diversity of tropical mangroves. Inhaca Island, by its geographical location near the austral limit of tropical eastern African fauna and flora and at the same time the septentrional limit of occurrence of coastal fauna and flora from Natal and Southeast Africa, is particularly relevant to the knowledge and understanding of eastern African ecosystems.

The present work is part of the European Community programme studying relationships between mangroves, tidal flats and seagrass bed communities in Mozambique, Tanzania and Kenya, which is one of the aspects that has received less attention both in eastern as in western Africa (John & Lawson, 1990). This paper describes quantitatively the structure and composition of macrobenthic communities of mangroves at Inhaca Island, and their relationship with sediment parameters such as its

nature, composition, pigments and organic matter. Also emphasised is the comparison with Macnae & Kalk (1962) previous work on the mangroves benthic epifauna.

MATERIAL AND METHODS

Field techniques and sampling areas

At Inhaca Island the mangrove is restricted to protected bays in the north and south (basically identical) and along a water stream on the West coast (Kalk, 1954; Freitas, 1960; Macnae & Kalk, 1962). During low tides of June and July 1993 an intensive survey was made in two transects established on the mangroves of "Saco da Inhaca" (MIM/I) and "Ponta Rasa" (MIM/II) (Fig. 1).

In each of the transects (Fig. 2) were defined seven sampling points, according to macroscopic biological and sediment characteristics. At Ponta Rasa mangrove the transect could not be levelled due to the dense vegetation. At "Saco" mangrove the sampling points were 0m= upper level near terrestrial vegetation; RO= presence of *Avicenia marina* and *Cassostrea 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. At "Ponta Rasa" sampling points were: 1= upper limit of *Avicenia* sp.; 2= presence of *Rizophora 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 *Rizophora/Avicenia* association within a sandy area; 6 and 7= sandy platform towards sea, respectively middle water and low water.

For the study of macrobenthos ($\geq 1\text{mm}$) in each of the stations an area of 0.25m^2 (subdivided in four replicates) was sampled with a PVC core or with a spade. the material sieved through a 1mm mesh-sieve, fixed in 10% formaldehyde-seawater solution and returned to the laboratory for sorting. The presence of epibenthic species non sampled by these techniques was video recorded for further

identification/counting. A 50 g sediment sample was also taken and frozen for the study of grain-size distribution, organic matter and pigments. Salinity and temperature of superficial sediment were recorded with a refractometer and thermometer.

Laboratory analysis

For grain-size purposes mud ($<62\mu\text{m}$, $>4\phi$), sand ($62\mu\text{m}$ - $2000\mu\text{m}$, 4ϕ - 1ϕ) and gravel ($>2000\mu\text{m}$, $<10\phi$) were separated by wet sieving (Buller & McManus, 1979). Sand grain-size distribution (phi-level) was also analysed. The sediment organic matter content (OM g/m^2) was estimated by loss on ignition ($\pm 500^\circ\text{C}$, 24h period) after the estimation of sediment water contents ($\%\text{H}_2\text{O}$) by 24h drying at $\pm 70^\circ\text{C}$.

The concentration of the sediment phytopigments was evaluated by spectrophotometry, after 24h cool extraction in 90% acetone. Concentrations ($\mu\text{g/g}$ dry sediment) of chlorophyll a (Chl. a), phaeopigments (Phaeop.), carotenoids (Car.), and chlorophyll b and c, were calculated by modified Lorenzen (Chl. a, Phaeop.), Parsons and Strickland (Car) and Jeffrey and Humphrey equations (Plante-Cuny, 1974). The Margalef index and the Chl a % degradation were used (Plante-Cuny, 1978) and the Moss index was calculated (Moss, 1967). To obtain phytopigment values per unit area (mg/m^2) from phytopigment values per weight ($\mu\text{g/g}$), a sediment specific weight was used (Cancela da Fonseca *et al.*, 1987).

Analysis tools

Data analysis was achieved on the basis of the fitness of the $0.25/\text{m}^2$ sample area, being the community species adequately represented whereas upon an species curve/area, the slope becomes nearly horizontal (Barbour *et al.*, 1980).

Shannon-Wiener diversity index and evenness were calculated (Daget, 1979). General matrices of values of sediment parameters, distribution of individuals per station, and a global one with sediment and biological information were built. Cluster analysis (correlation coefficient of Bravais-Pearson) was used to group biological and sediments characteristics (Pielou, 1984). Central value analysis (CVA) was also carried

out, trying to represent the distribution of species along environmental gradients (Salen-Picard, 1987). In order to summarize the information, principal component analysis (PCA - Sneath & Sokal, 1973) was used.

RESULTS

Sediment parameters

The analysis of grain-size distribution in "Saco" Mangrove - MIM/I (Table 1) indicates that all the stations of this transect are mainly composed by medium and fine sands. Although relatively similar between stations the grain size increases towards the #LW, where gravel presents its higher value (11.96%). Values of organic matter are higher in stations RO, R and 0m, where very fine sand and mud dominate the grain size distribution, resulting also in higher percentages of water content. Values of microphytobenthos together with Moss index seem to indicate an highly productive area, as the percentage of degraded Chlorophyll a is always under 50%. The presence of chlorophyll a, b and carotenoids together in stations 0m, R, RO, indicates the presence of superior plants as A. marina and R. mucronata probably with green algae (Prézelin, 1981).

Transect MIM/II (Table 2) has a more homogeneous grain size distribution than MIM/I but is also dominated by medium and fine sands, with an increasing grain size towards sea and clearly a superior gravel fraction in stations 6 and 7, where the lowest values of organic matter and %H₂O were recorded. Phytopigment analysis indicates a lower productivity in stations 1 and 4. Margalef index in stations 3, 4 and 5 is >2.5 indicating a stability in microphytobenthos while at the same time the Chl. a degradation (%) reaches the highest values in this transect, which suggests a limitation in nutrients.

Faunal Composition and Sample Area

Fig.3 (a and b) indicates that in both mangroves the species/area curve reaches a slope nearly horizontal at 0.19m^2 , showing that the 0.25m^2 area was adequate for the purpose of present work, following the concept of Barbour *et al.* (1980).

The analysis of Fig.4, Table3 and Annex 1 shows that station LW on transect MIM/I presents high values of density and diversity although largely dominated by polychaeta. The low value of evenness reflects the fact that 60% of individuals are the sum of 3 taxa, namely Ceratonereis erytraeensis, Parheteromastus tenuis (polychaeta) and Balanus amphitrite (Cirripedia). Lowest diversity occurs at station R where Balanus amphitrite (very abundant on R. mucronata roots) represents 95% of all individuals. Stations ADT, RO and VA present decreasing values of abundance although the diversity index is higher in #RO, where Cassostrea cucullata (Bivalvia) and Terebrallia palustris (Gastropoda) dominate. Polychaeta dominate in stations VA and LW while oligochaeta are confined to #0m, characterising together with the decapod Uca annulipes this upper level. Station ADT is dominated by Dotilla fenestrata while the polychaeta Prionospio sexoculata is the most abundant taxon in #VA, followed by the bivalve Loripes clausus and the decapod Macrophthalmus grandidieri. Gastropods and bivalves, namely Seta sp.1 and Pseudophytina africana are dominant at #MW.

The Ponta Rasa mangrove (MIM/II) is clearly distinguished from the Saco mangrove (MIM/I) by its low values of diversity, where gastropods are the dominant group, followed by decapods, polychaets and bivalves. In fact at stations 3 and 7 were only recorded two taxa, respectively, Terebrallia palustris and Setia sp1, the latter reaching a density of 656 ind./m^2 . Also #6 is dominated by Setia sp1 that represents 96% of total individuals. Higher diversity was recorded at #4 where the decapod Uca annulipes dominates.

PCA and Cluster analysis

Principal components analysis (Figs. 6, 7 and Table 3) indicates on MIM/I (Saco Mangal) a clear separation on first factor between coarse sediment (gravel, very coarse sand and medium sand) and finest sediments (fine sands, very fine sand and silt+clay). Stations 0m and RO, containing the higher percentages of fine sediments separate from station LW, where coarser sediments dominate thus confirming the dominance of grain size distribution. On second factor, Chl a degradation % separates from Chl. a, Chl.c, phaeopigments and carotenoids, also stations MW and ADT form a group related to coarser sediments and higher abundances, opposing to finest sediments, with lower abundances and higher values of diversity (#0m, #R and #RO). These two first factors concentrate of 62.4% variability. Cluster analysis (Fig.8) confirms the previous results relating higher abundance with coarser sediments, higher values of abundance and Moss Index, while finest sediments form a group with higher values of diversity and Chl. a %Degradation.

The PCA on transect MIM/II (Ponta Rasa) (Figs.9, 10 and Table 3), also indicates at the first factor a separation between coarse sands, gravel (associated with higher abundance and Moss index) and fine sands to silt+clay, which are associated with higher values of %H₂O, organic matter, carotenoids, Chl a degradation %, phaeopigments, Chlorophyll a, b and c. The first two factors represent 66.5% of variability. Stations 1, 2 and 5 although in opposite ends of transect MIM/II, are grouped together on second factor as they represent both ends of mangrove, being the first the dunar area, and the latest the end of mangrove by the beach, and so revealing the symmetric characteristic of grain size distribution on this mangrove. Cluster analysis (Fig.11) relates the first group of variables at the level 0.4, and approximately at the same level another major group including Margalef index together with the finest sediments and carotenoids, Chl. a degradation (%), phaeopigments, Chlorophyll a, b and c.

Central Values Analysis

Central values were calculated using the values of factor 1 of PCA as the gradient profile. This approach allows the ordination of species in relation to a gradient that is more informative, since it integrates the information of several variables. In present case it became evident that grain-size distribution was the major factor influencing faunal distribution. Variation coefficient was used instead of standard deviation in order to eliminate the effect of largely different densities between stations and species. All taxa represented on central axis (variation coefficient =0), are species sampled only at a single point, or at several stations but with identical values. The results of this analysis are presented in Figs. 12 ,13 and Table 4, relating the affinity of species to different sediment types.

DISCUSSION

There is not much bibliography concerning endobenthic macrofauna of mangroves, and much of the work which has been developed in this field (in Eastern Africa, as in other parts of the world), has a qualitative rather than quantitative basis, as it is in present case the previous work of MacNae & Kalk (1969) at Inhaca Island. In the present study the 0.25m² sampling area seems to represent adequately the macrobenthic community, at least as far as endobenthos is concerned, and referring to the criteria expressed by Barbour et al. (1980). As to epibenthos, a quantitative approach must have different techniques, as emphasized by Daniel & Robertson (1990).

Considering Pérès (1961) general description of mangroves, the most outstanding results in this study are the clear dominance of medium and fine sands, instead of colloidal sedimentation (silt+clay); in fact there is no station exclusively constituted by silt+clay, as it should be expectable in a mangrove community. This fact, which influences all the infaunal distribution following grain-size distribution (with increasing grain size from low water level to upper levels) is probably a direct

reflex of the sub-tropical condition of the Inhaca island, which has a sedimentary origin (Lopes, 1973), together with the currents regime, mainly the warm current of Mozambique channel.

Moss index showing little variation between stations and with values of Chl.a % degradation always under 50%, indicates relatively high values of primary production (Moss, 1967). Otherwise the values of Margalef index together with Chl.a % degradation considered a good estimate of physiological condition of microphytobentic populations (Plante-Cuny, 1974), indicate a steady state in celular division at Stations 3, 4 and 5 (MIM/II), may be understood as the beggining of limitation in nutrients. It is in this context relevant to emphasise that the mangrove of Ponta Rasa, considerably smaller than Saco mangrove, may be much less resistant to human pressure of past 15-20 years, where population of the island triplicate.

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 of mangrove closely paralleled by associations of animals". In fact, whether considering flora or fauna there is a clear zonation as a function of several combined environmental factors, which contribute to define mangrove communities as several authors pointed out (Kiener, 1965; MacNae, 1968; Weiss & Kiener, 1971; Daniel & Robertson, 1990). The results of present work agree with that characteristic, taking into account the benthic species of large abundance but restricted distribution in mangrove flats, which was clearly reavealed by central values analysis, considering grain-size as the main factor affecting macrobenthos distribution.

Considering the Saco mangrove and the upper limit at high spring tides (#0m) near the halophyte vegetation, the substratum is mainly constituted by fine and very fine sands, oligochaeta and the crustacean Cardisoma carnifex dominate. The upper edge of mangrove flat bordered by Avicenia marina (#R/#RO), where the silt+clay fraction is higher, is dominated by Cassostrea cucullata fixed on the roots of A. marina, also characterized by the presence of the gastropods Terebrallia palustris.

Cerithium caeruleum and Littorina scabra, also recorded the presence of Uca annulipes.

The barnacle Balanus amphitrite although occurring on the trunks of A. marina has a wider dispersion reaching the level of low water on gastropod and bivalve shell debris. Although Macnae & Kalk (1969) sustained that polychaete are rare, mainly in mangrove mud, present results show the opposite, being polychaetes the major group, which is understandable accounting to the qualitative nature of their work. In fact, together with C. cucullata occur the polychaetes Perinereis cultrifera, Perinereis nigropunctata and Capitella capitata.

At the lower end of the mangrove and after the fringe of Rizophora mucronata, that boards the mangrove channels where Periophtalmus spp. occurs, the sediment varies from medium to fine sands (#VA to #LW), and macrofauna is dominated by the bivalves Loripes clausus and Pseudophytina africana, the crabs Dotilla fenestrata (that seems nevertheless to prefer medium sands = #ADT) and Macrophtalmus grandidieri, together with polychaetes (Phylodoce castanea, Prionospio sexoculata and Dendronereis arborifera).

The Ponta Rasa mangrove developing on a relatively narrow fringe along both sides of a central channel and ending at a sandy beach, presents a much lower diversity. Nevertheless, although lacking several of the species recorded at Saco mangrove, mainly the polychaetes, it seems to have the same basic community structure. Nevertheless, the absence of Cassostrea cucullata which is somehow "substituted" by Siliqua radiata, the clear interpenetration between the A. marina and R. mucronata fringes and the low values of phytopygments, contribute to considerer this as an atypical mangrove, or an extreme situation of sub-tropical mangroves where diversity is very low.

If as Berjak et al (1982) sustained, the occurrence of mangroves beyond tropical limits depends mainly of warm water currents, Saco mangrove of Inhaca Island constitutes a southern example of a sub-tropical mangrove of high diversity and production, as well as Ponta Rasa mangrove is probably an example of extremely low

diversity in mangroves. Thus, it is legitimate to reinforce the belief that also microenvironmental conditions, as local patterns of water circulation and consequently sediment deposition and type, are determinant to the richness of these ecosystems.

Bell & Westboy (1986), as several other authors, sustained that the positive relationships between plant biomass or productivity and faunal density of epibenthos of mangroves should be understood as the result of the combination of three main factors, (1) increased food availability, (2) reduction of predation, (3) and increased living space. In what concerns endobenthos the grain-size distribution pattern must be added, as a factor determinant to the structure and composition of these communities.

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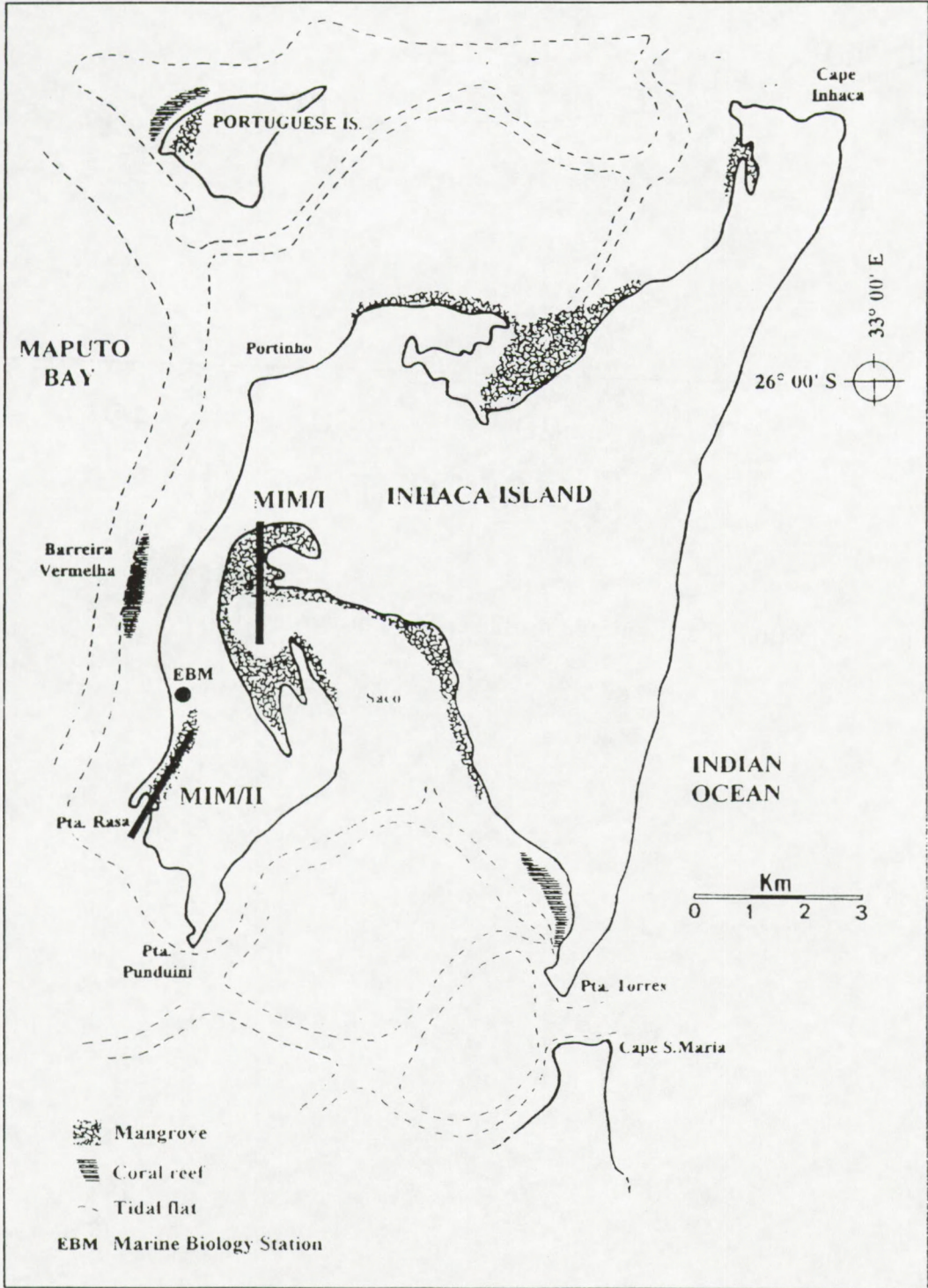


Fig.1 - Location of transects MIM/I (Saco mangrove) and MIM/II (Ponta Rasa mangrove) at Inhaca Island (Mozambique).

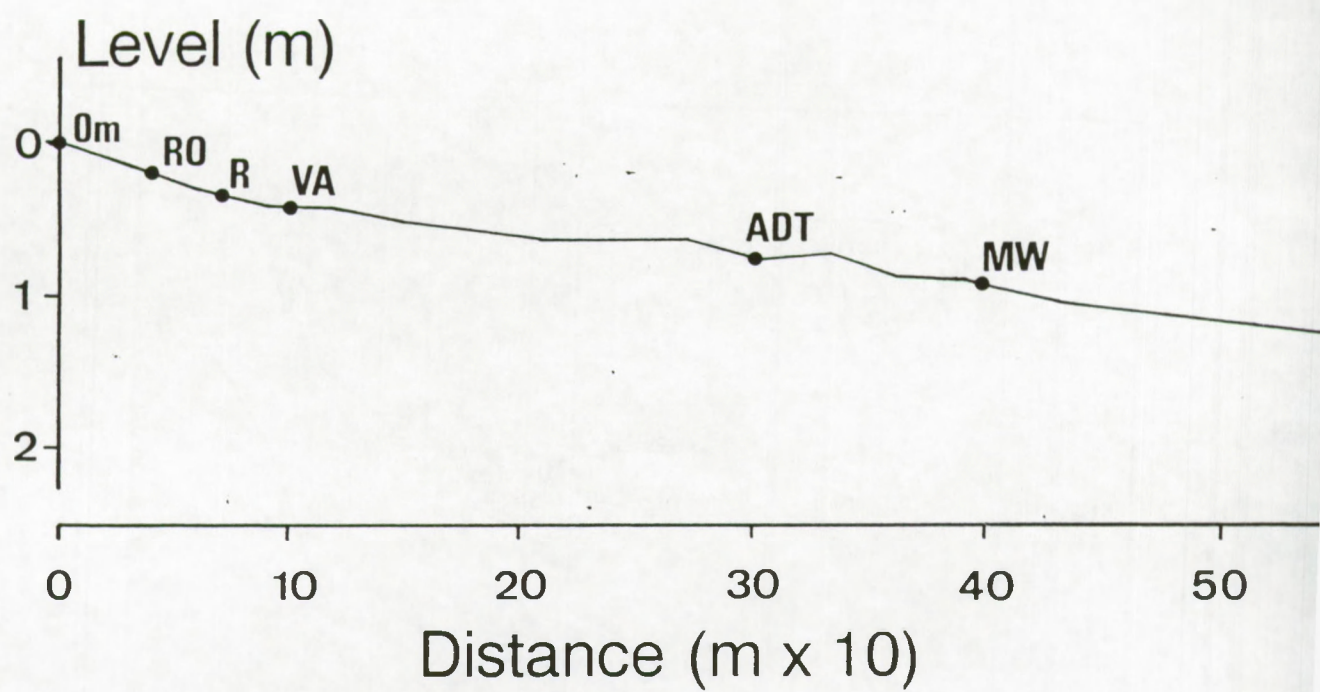


Fig. 2 - Location of stations and profile at Saco mangrove (MIM/I).

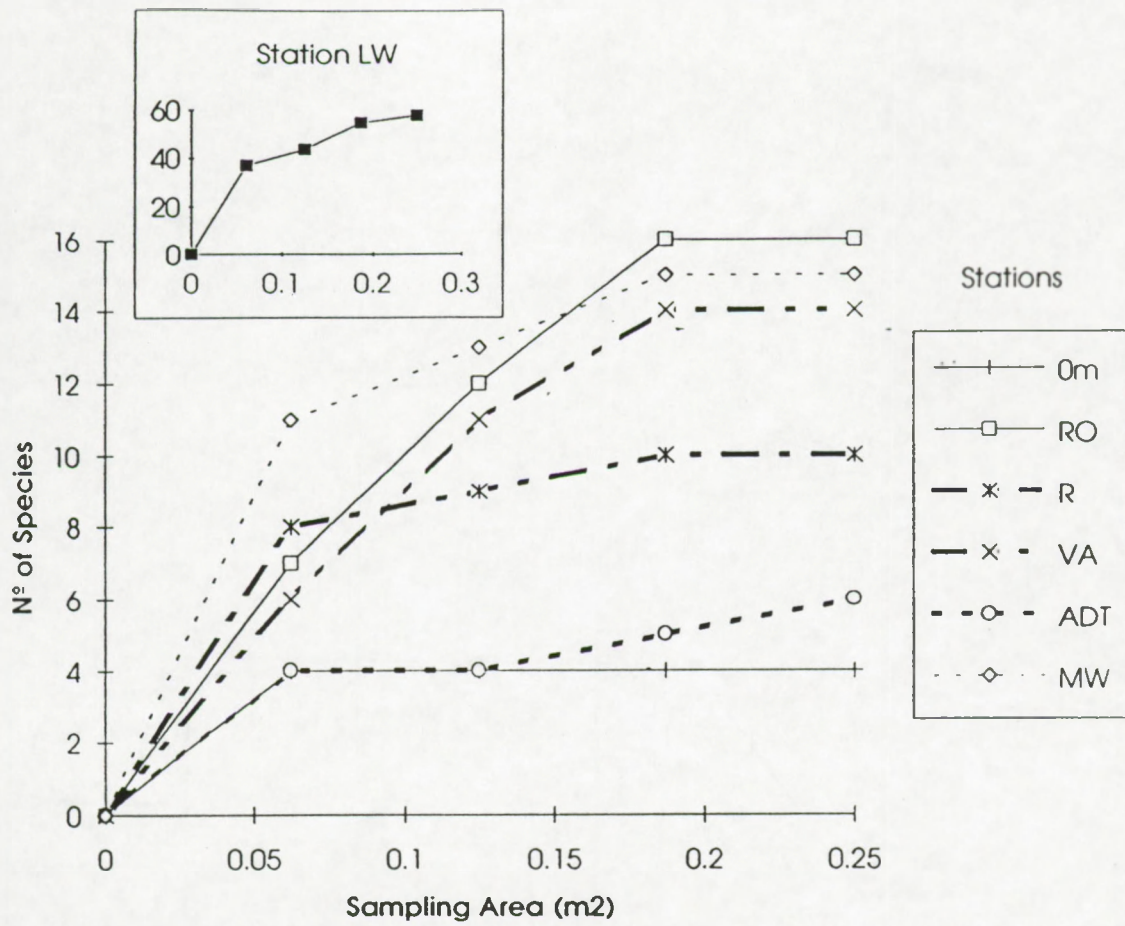


Fig. 3 a) - Species/Area curves in Saco mangrove (MIM/I).

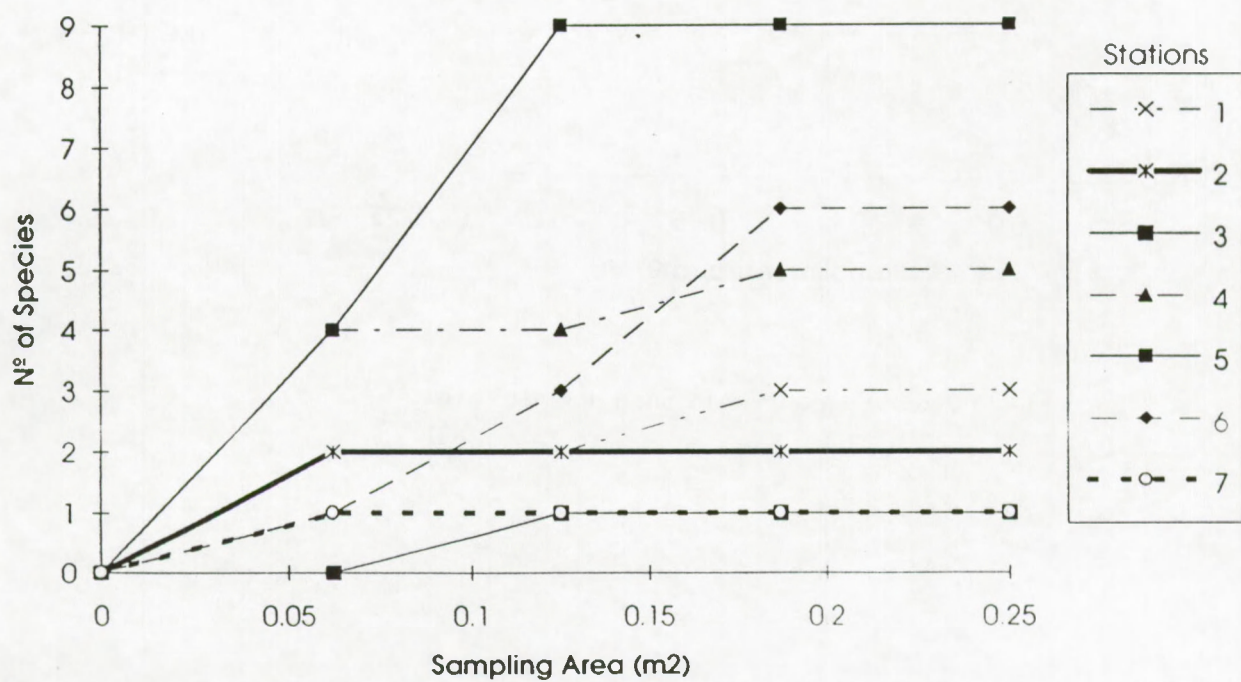


Fig. 3 b) - Species/Area curves in Ponta Rasà mangrove (MIM/II).

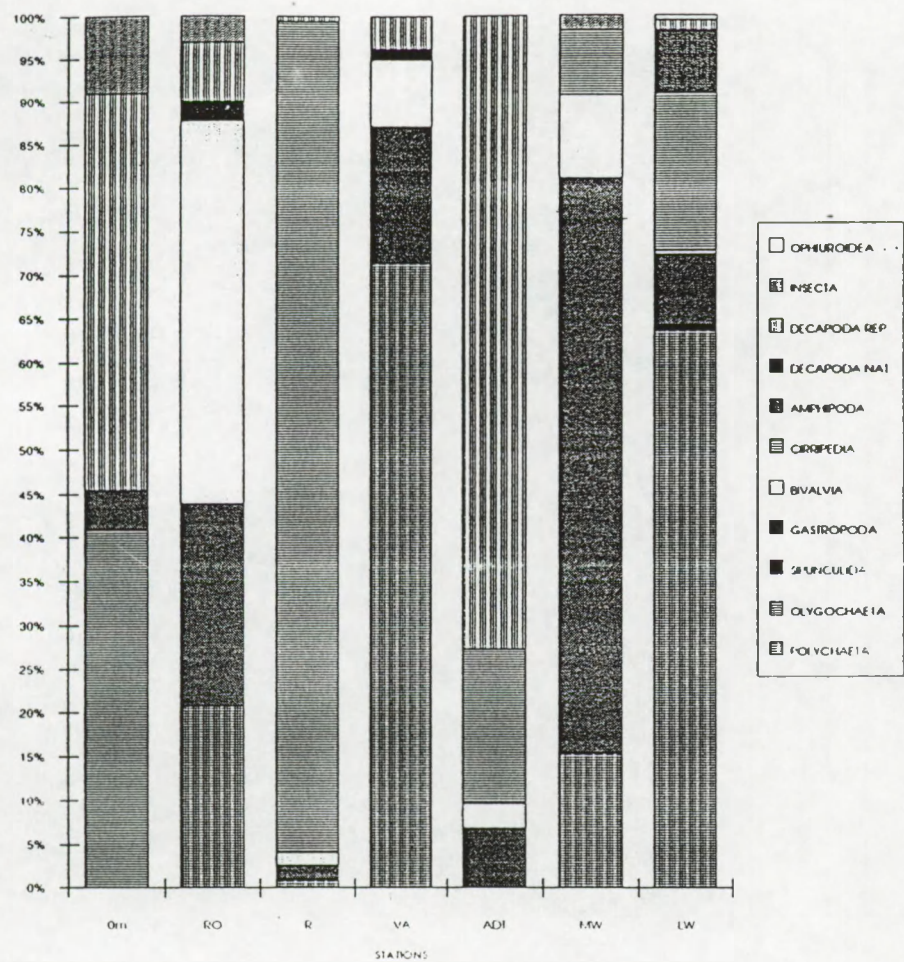


Fig.4 - Variation of relative frequencies of taxa in each station at Saco mangrove (MIM/I).

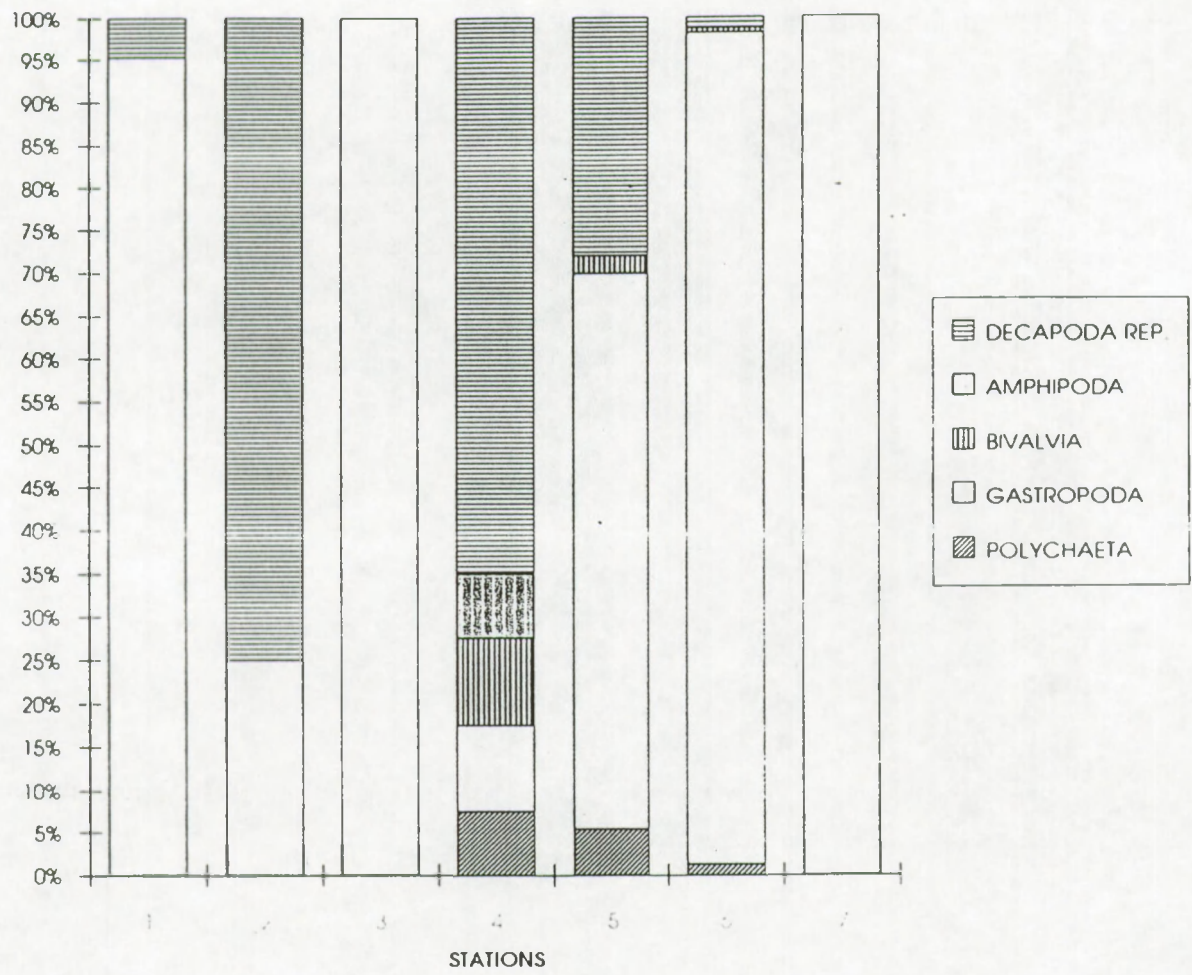


Fig. 5 - Variation of relative frequencies of taxa in each station at Ponta Rasa mangrove (MIM II).

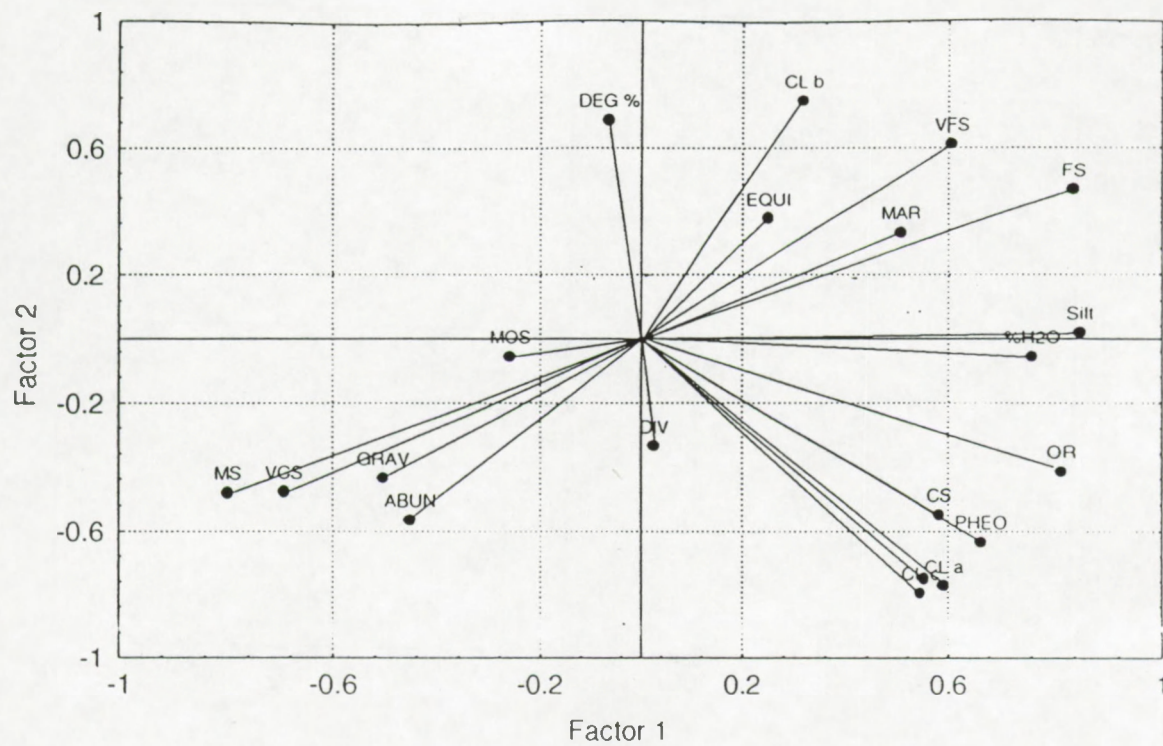


Fig 6 - Principal Components Analysis (PCA) on sediment and biological parameters expressed in Table I - Saco mangrove (MIM/I).

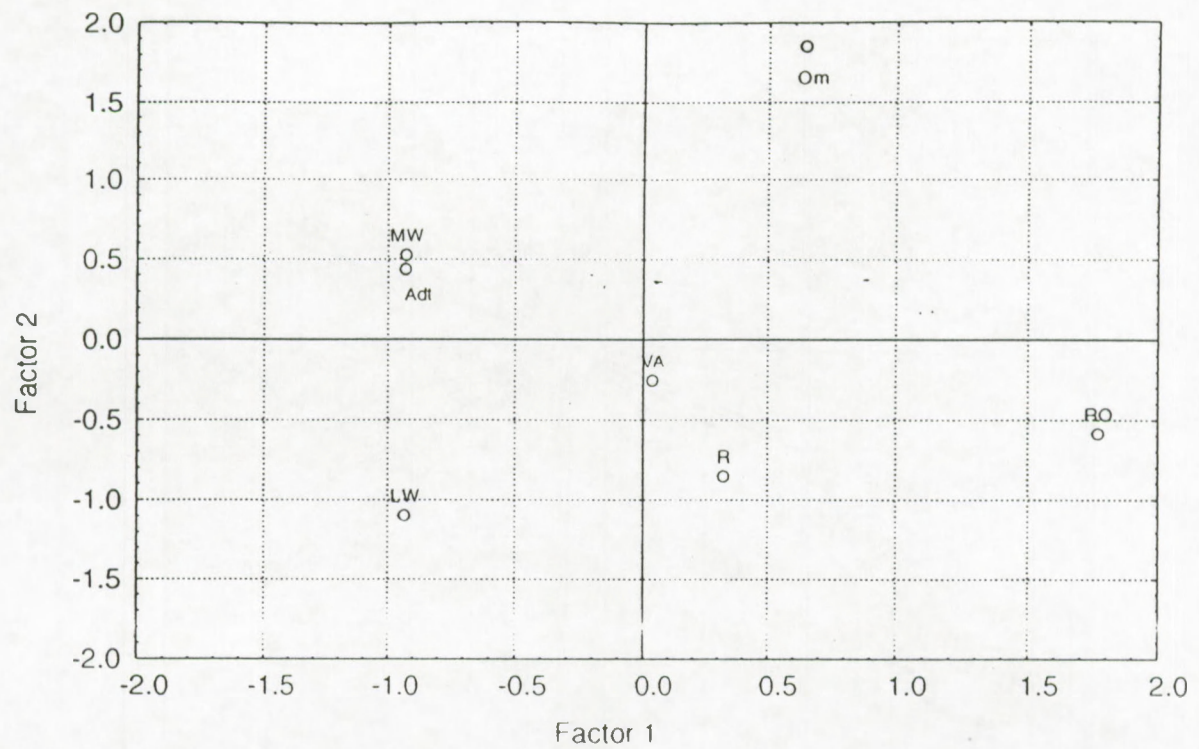


Fig. 7 - Principal Components Analysis (PCA) - representation of stations based upon factor1 and factor 2 - Saco mangrove (MIM/1).

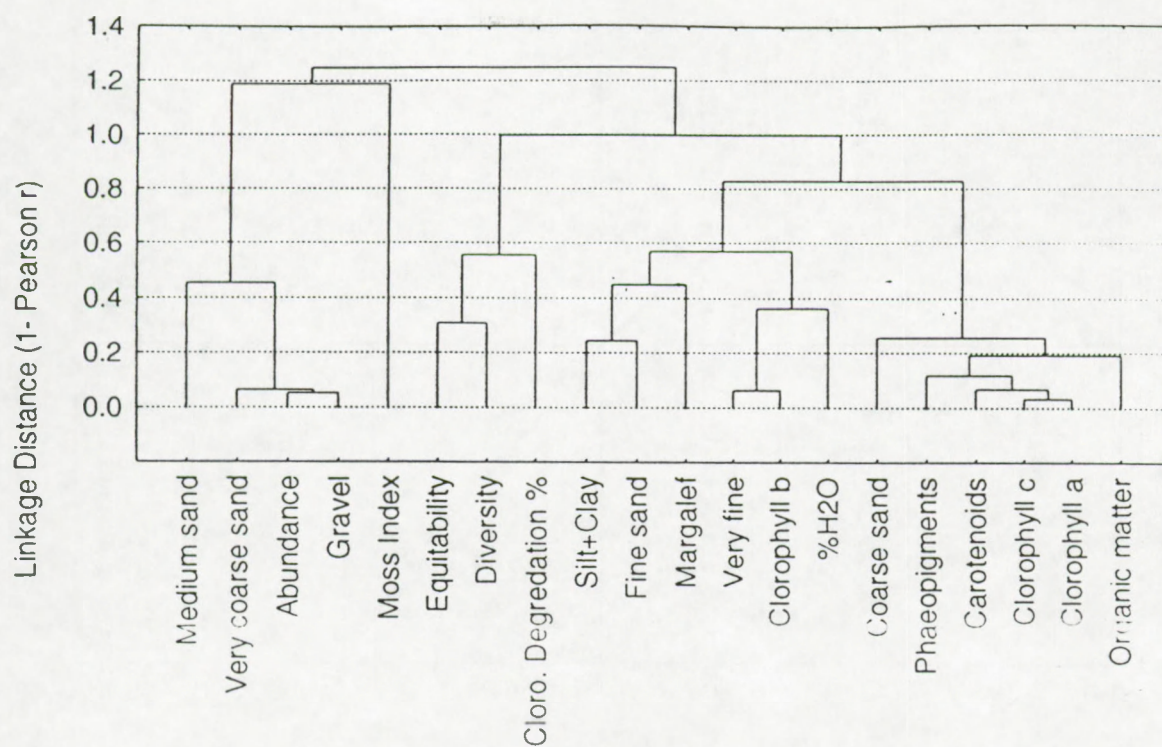


Fig 8 - Sediment parameters and biological indexes grouping (cluster analysis). Saco mangrove (MIM/I).

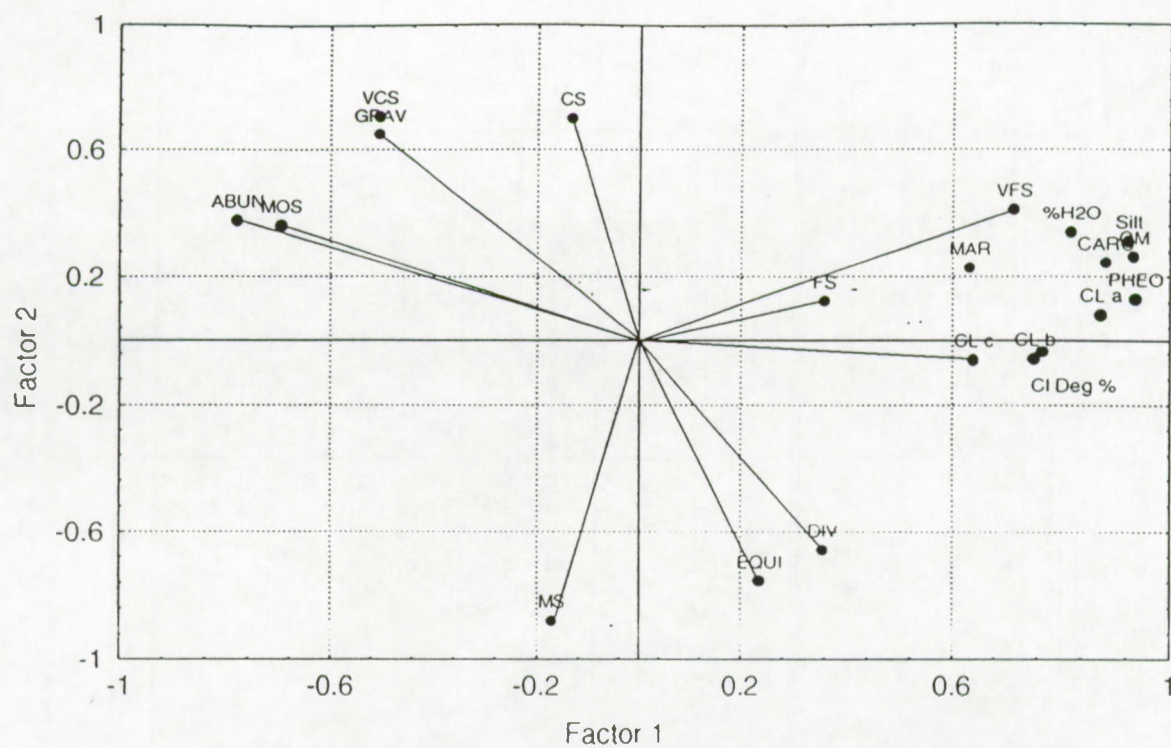


Fig 9 - Principal Components Analysis (PCA) - representation of stations based upon factor1 and factor 2 - Saco mangrove (MIM/I).

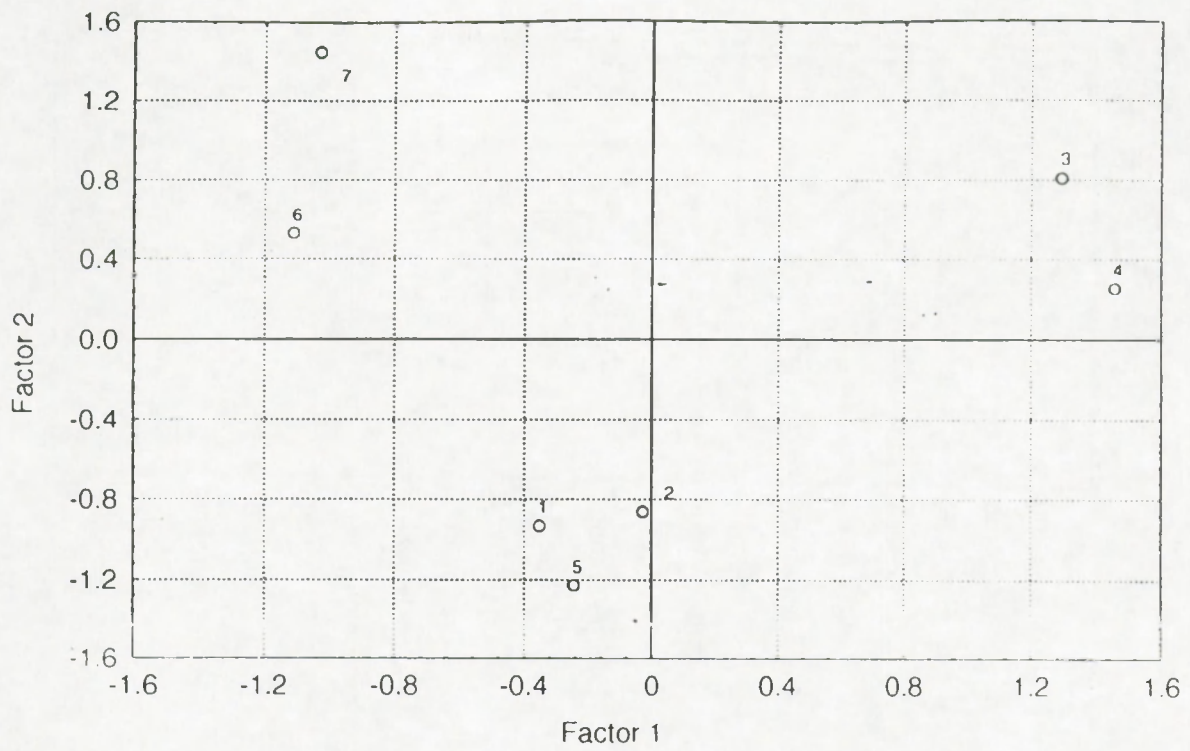


Fig. 10 - Principal Components Analysis (PCA) - representation of stations based upon factor1 and factor 2 - Ponta Rasa mangrove (MIM/II).

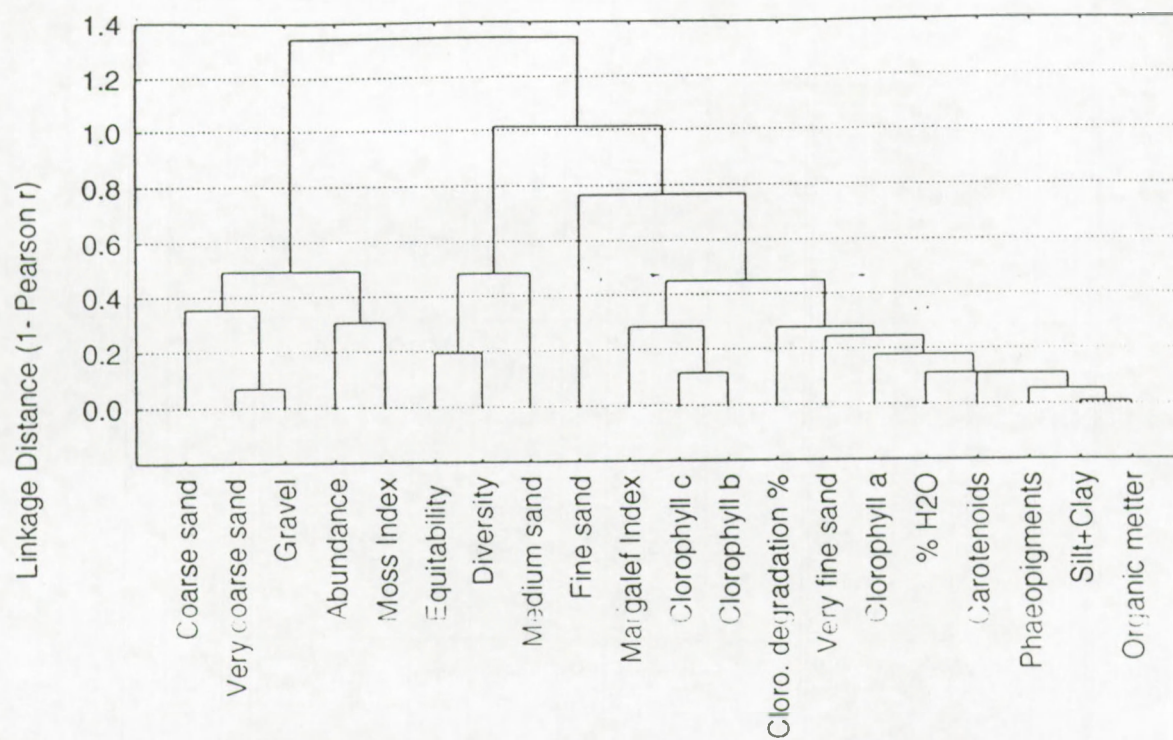


Fig.11 - Principal Components Analysis (PCA) - representation of stations based upon factor1 and factor 2 - Ponta Rasa mangrove (MIM/II).

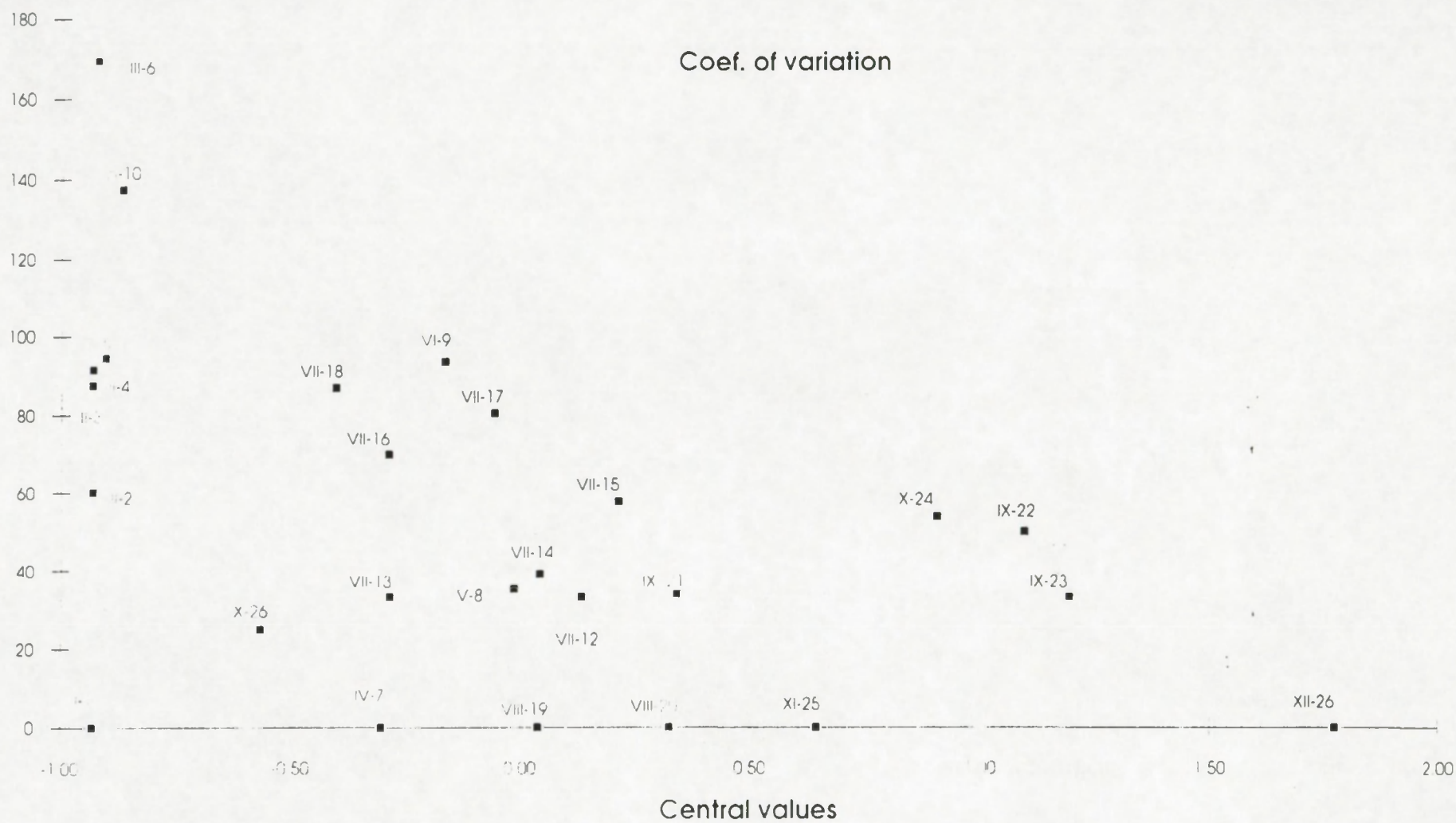


Fig.12 - Central values analysis based on taxa according to grain-size distribution in Saco mangrove (MIM/I).

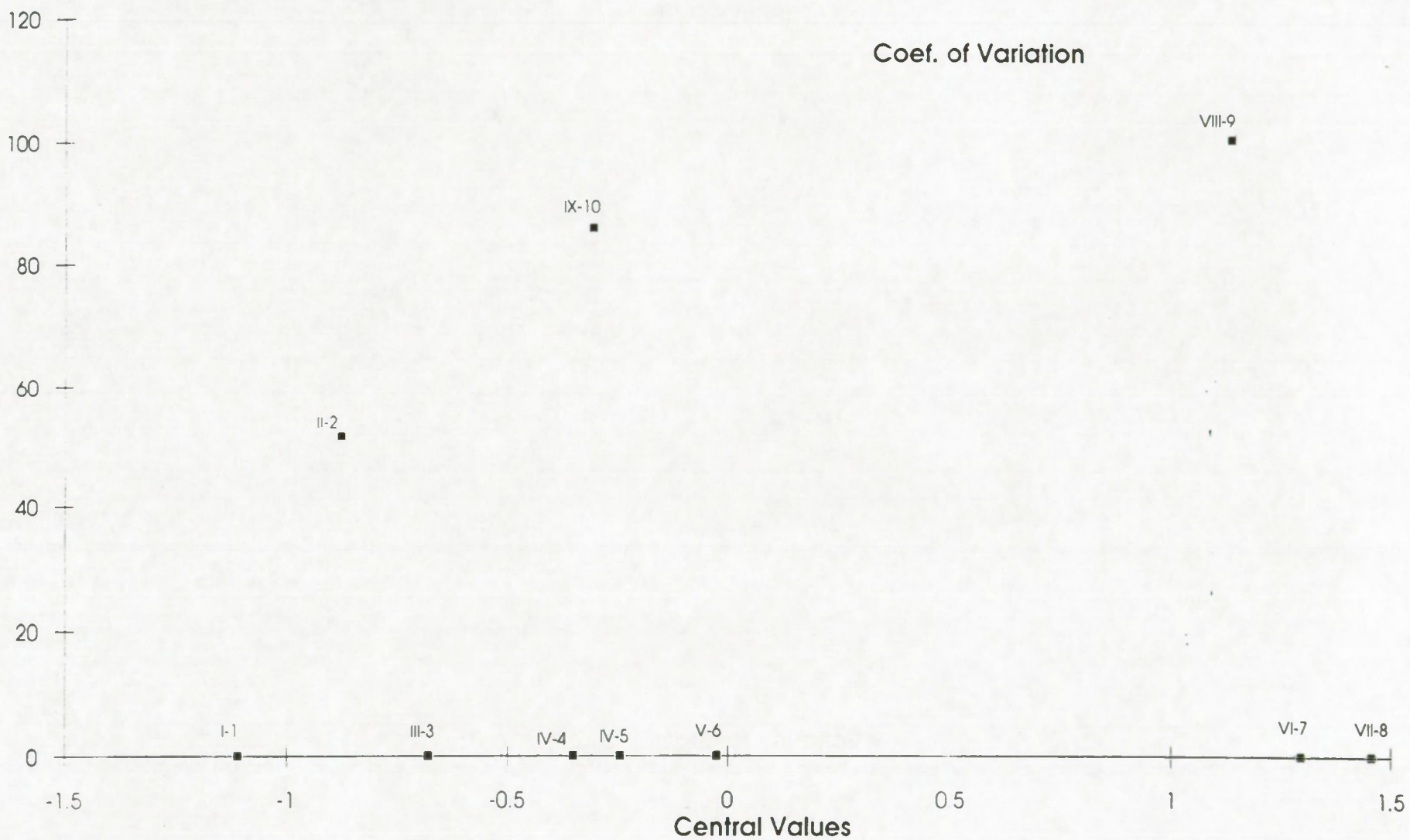


Fig.13 - Central values analysis based on taxa according to grain-size distribution in Ponta Rasa mangrove (MIM/II).

Parameters/Stations	I/Om	I/R	I/RO	I/VA	I/ADT	I/MW	I/LW
Temperature °C		27,8		27,9	23	24	24
Salinity %				35	35	40	40
Organic matter g/m ²	152	234	258,4	127,2	99	65,6	139,5
% H ₂ O	23,5	21,4	23,6	20	17,8	18	21,8
Clorophyll a (mg/m ²)	39,65	145,55	169,51	115,69	42,52	46,14	106,83
Clorophyll b (mg/m ²)	22,59	1,27	1,3	0	0	0	0,82
Clorophyll c (mg/m ²)	6,69	18,72	26,33	16,28	8,43	7,27	19,13
Phaeopigments (mg/m ²)	22,74	43,13	81,95	45,35	20,16	26,5	47,36
Carotenoids (mg/m ²)	39,99	178,55	158,06	102,59	32,13	38,23	104,05
Margalef Index	2,31	2,34	2,34	2,17	2,22	2,34	2,1
Moss Index	1,09	1,21	1,11	1,22	1,22	1,18	1,07
Chl a Degradation (%)	46,76	26,99	41,33	34,47	40,34	47,12	38,1
Gravel	0,04	0,47	0,31	0,38	0,39	3,24	11,96
Very coarse sands	0,03	0,43	0,08	0,27	0,4	0,74	1,42
Coarse sands	2,95	11,11	13,94	11,17	7,21	5,28	4,41
Medium sands	35,34	61,72	44,58	59,88	67,6	67,88	67,51
Fine sands	55,43	24,34	36,17	26,23	23,91	21,26	13,53
Very fine sands	5,03	1,45	2,29	1,33	0,31	0,83	0,8
Silt + C lay	1,18	0,48	2,63	0,74	0,18	0,77	0,37
Silt + Clay (mud)	1,18	0,48	2,63	0,74	0,18	0,77	0,37
Diversity Index	1,56	0,42	3	2,8	1,24	2,03	3,61
Eveness	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

Table 1. - Values of sediment parameters and biological indexes at Saco mangrove (MIM/I).

Parameters/Stations	II/1	II/2	II/3	II/4	II/5	II/6	II/7
Temperature °C	19,6	20,3	19,5	20	20,1	20,9	21,6
Salinity %			60	40	39	35	
Organic matter g/m2	236,6	329,4	919,8	928,8	95,4	101,4	136,8
% H2O	10,1	9,7	34,4	39,2	20,2	16	14,7
Clorophyll a (mg/m2)	42,79	40,14	72,71	58,97	33,12	7,46	33,36
Clorophyll b (mg/m2)	0	9,28	5,65	10,27	0,65	0	0
Clorophyll c (mg/m2)	0	19,57	14,45	15,89	10,32	3,27	6,53
Phaeopigments (mg/m2)	29,04	17,84	66,96	67,46	27,77	- 4,2	16,18
Carotenoids (mg/m2)	0	42,59	92,43	97,7	42,64	2,93	32,39
Margalef Index	0,79	2,41	2,82	3,59	2,79	1,6	2,43
Moss Index	0,89	1,02	0,98	0,87	1,02	1,24	1,1
Chl a Degradation (%)	54,55	37,5	66,67	76,85	62,5	46,43	41,18
Gravel	0,82	1,65	0,32	0,69	0,07	6,95	49,24
Very coarse sands	0,45	0,93	0,37	1,08	0,22	1,64	3,25
Coarse sands	3,16	3,7	3,18	5,92	1,86	5,8	5,89
Medium sands	50,26	63,4	29,91	35,51	83,63	44,48	23,3
Fine sands	41,31	25,89	41,69	35,07	12,72	39,07	15,64
Very fine sands	2,24	1,59	6,15	3,32	0,51	1,97	1,36
Silt + C lay	1,76	2,85	18,34		0,99	0,09	1,32
Silt + Clay (mud)	1,76	2,84	18,38	18,41	0,99	0,09	1,32
Diversity Index	1,12	0,81	0	1,78	1,41	0,22	0
Eveness	0,71	0,81	0	0,69	0,44	0,09	0
Abundance (ind./m2)	252	16	12	160	372	632	656

Table 2. - Values of sediment parameters and biological indexes at Ponta Rasa mangrove (MIM/II).

Extraction: Principal components

		% total	Cumul.	Cumul.
	Eigenval	Variance	Eigenval	%
1	9.269244	46.34622	9.269244	46.34622
2	4.071897	20.35949	13.34114	66.70571

Factor Loadings (Unrotated)
Extraction: Principal components
(Marked loadings are > .700000)

	Factor 1	Factor 2
MAOG	0.933264	0.261087
%H2O	0.820728	0.338189
CL_A	0.874564	0.079997
CL_B	0.755181	-0.05765
CL_C	0.640712	-0.06251
FEOP	0.93769	0.12873
CARO	0.88314	0.242592
IMAR	0.632511	0.226519
IMOS	-0.69566	0.359136
%_DEG	0.770128	-0.03616
FBAL	-0.50357	0.648098
AMG	-0.50452	0.706872
AG	-0.13337	0.70146
AM	-0.17024	-0.88257
AF	0.359914	0.120794
AMF	0.716328	0.410212
S_A	0.924185	0.310935
IDIV	0.357199	-0.6588
EQUI	0.23659	-0.75774
ABUN	-0.77939	0.374566
Expl.Var	9.269244	4.071897
Prp.Totl	0.463462	0.203595

Factor Scores
Rotation: Unrotated
Extraction: Principal components

	Factor 1	Factor 2
MIM/II/1	-0.35063	-0.93588
MIM/II/2	-0.02478	-0.86416
MIM/II/3	1.295916	0.808428
MIM/II/4	1.45753	0.252336
MIM/II/5	-0.24381	-1.23176
MIM/II/6	-1.10825	0.523617
MIM/II/7	-1.02598	1.447424

Extraction: Principal components

		% total	Cumul.	Cumul.
	Eigenval	Variance	Eigenval	%
1	6.838528	34.19264	6.838528	34.19264
2	5.649395	28.24697	12.48792	62.43961

Factor Loadings (Unrotated)
Extraction: Principal components
(Marked loadings are > .700000)

	Factor 1	Factor 2
MAOG	0.815905	-0.41664
%H2O	0.761284	-0.05568
CL_A	0.592129	-0.77379
CL_B	0.317817	0.749037
CL_C	0.545244	-0.7964
FEOP	0.664407	-0.6356
CARO	0.553507	-0.7513
IMAR	0.506063	0.329109
IMOS	-0.25924	-0.05625
%_DEG	-0.06506	0.687175
FBAL	-0.50453	-0.43742
AMG	-0.69214	0.48042
AG	0.582795	0.55107
AM	-0.79733	-0.4837
AF	0.83753	0.467082
AMF	0.607382	0.611098
S_A	0.849316	0.019685
IDIV	0.026205	-0.33636
EQUI	0.250298	0.374097
ABUN	-0.45274	-0.56714
Expl.Var	6.838528	5.649395
Prp.Totl	0.341926	0.28247

Factor Scores
Rotation: Unrotated
Extraction: Principal components

	Factor 1	Factor 2
Om	0.64796	1.850746
R	0.326073	-0.85777
RO	1.772604	-0.59081
VA	0.038852	0.25711
Adt	-0.92764	0.432059
MW	0.92739	0.523093
LW	-0.93046	-1.10017

Table 3. - Values of PCA analysis for Saco mangrove (MIM/I) and Ponta Rasa mangrove (MIM/II)

GROUP I Gravel, very coarse sands. Taxa presents in only (at the utmost in two) stations.	1 <i>Nereis falsa</i>	1 <i>Armandia sp</i>
	1 <i>Nereis operta</i>	1 <i>Loimia medusa</i>
	1 <i>Syllis cornuta</i>	1 <i>Polyophthalmus pictus</i>
	1 <i>Syllis ferrugina</i>	1 <i>Capitellidae nd</i>
	1 <i>Phyllodoce sp</i>	1 <i>Pulliella armata</i>
	1 <i>Phyllodoce capensis</i>	1 <i>Owenia fusiformis</i>
	1 <i>Glycera bengullana</i>	1 <i>Isolda pulchella</i>
	1 <i>Glycera longipinnis</i>	1 <i>Fabriciella mossambica</i>
	1 <i>Glycera natalensis</i>	1 <i>Sabella sp</i>
	1 <i>Glycinde kameruniana</i>	1 <i>Siphosoma sp</i>
	1 <i>Eunicidae nd</i>	1 <i>Sipunculoida nd</i>
	1 <i>Arabella iricolor</i>	1 <i>Diala conica</i>
	1 <i>Diopatra cuprea cuprea</i>	1 <i>Setia sp2</i>
	1 <i>Diopatra neapolitana</i>	1 <i>Tectonatica sp2</i>
	1 <i>Lumbrinereis latrilli</i>	1 <i>Modiolus philipinarum</i>
	1 <i>Aonides oxycephala</i>	1 <i>Ceradocus rubromaculatus</i>
	1 <i>Malacocerus indica</i>	1 <i>Maera inaequipes</i>
	1 <i>Spionidae nd</i>	1 <i>Amphipoda sp1</i>
	1 <i>Caulleriella acicula</i>	1 <i>Amphipoda sp2</i>
	1 <i>Cirratulus africanus</i>	1 <i>Amphipoda sp3</i>
	1 <i>Haploscoloplos cf. fragilis</i>	1 <i>Dotilla fenestrata</i>
	1 <i>Nainnereis laevigata</i>	1 <i>Ophicoma scolopendrina</i>
	1 <i>Scoloplos johnstanei</i>	1 <i>Ophicoma valenciae</i>
	1 <i>Scoloplos sp</i>	
GROUP II Gravel, very coarse sands in larger quantity. Taxa can exist in other stations in inferior proportions.	2 <i>Ophelina sp</i>	
	3 <i>Scoloplos madagascarensis</i>	
	4 <i>Parheteromastus tenuis</i>	
	5 <i>Gibbula obscura</i>	
GROUP III Gravel, very coarse sands in very larger quantity. Taxa can exist in other stations in very inferior quantities.	6 <i>Ceratonereis erythraeensis</i>	
GROUP IV Coars sands. Taxa exists in only two stations in equal number.	7 <i>Volema pyrum</i>	
	7 <i>Pagurus sp</i>	
GROUP V Medium sands, but also in coarse sand. Taxa appear in more than one station.	8 <i>Neridae nd</i>	
GROUP VI Medium sands in larger quantities. Ubiquitous taxa.	9 <i>Balanus amphitrite</i>	
	10 <i>Setia sp 1</i>	
GROUP VII Medium and fine sands. Taxa can exist in more than one station	11 <i>Phyllodoce castanea</i>	15 <i>Macrophthalmus grandidieri</i>
	12 <i>Glycera alba</i>	16 <i>Loripes clausus</i>
	13 <i>Tectonatica sp1</i>	17 <i>Prionospio sexoculata</i>
	14 <i>Dendronereis arborifera</i>	18 <i>Pseudophytina africana</i>
GROUP VIII Medium and fine sands. Taxa appear in only one station.	19 <i>Glycera convoluta</i>	20 <i>Glycera sp</i>
	19 <i>Lumbrinereis meteorana</i>	20 <i>Littorina scabra</i>
	19 <i>Polichaeta nd</i>	

Table 4. - Central values analysis - grouping of taxa at Saco mangrove (MIM/I) and Ponta Rasa mangrove (MIM/II) based upon sediment parameters.

GROUP IX Fine sands. Taxa exists in more than one station	21 <i>Dipteron</i> larval	23 <i>Natantia</i> nd
	22 <i>Xantidae</i> nd	
GROUP X Fine and very fine sands. Ubiquitous taxa.	24 <i>Uca annulipes</i>	
GROUP XI Very fine sands with some silts and clay	25 <i>Oligochaeta</i> nd	
	25 <i>Vitrinella</i> sp	
	26 <i>Perinereis cultrifera</i>	26 <i>Crassostrea cucullata</i>
GROUP XII Very fine sands with a larger quantity of silts and clay	26 <i>Perinereis nigropunctata</i>	26 <i>Alpheus crassimanus</i>
	26 <i>Capitella capitata</i>	26 <i>Eurycarcinus natalensis</i>
	26 <i>Cerithium caeruleum</i>	26 <i>Macrophthalmus</i> sp
	26 <i>Terebrallia palustris</i>	

MIM/II

GROUP I Medium and fine sands. Taxa present only in one station.	1 <i>Arabella iricolor</i>	1 <i>Planaxis sulcatus</i>
	1 <i>Glycera convoluta</i>	
GROUP II Ubiquitous taxa in stations with small quantity of silts and clay.	2 <i>Setia</i> sp1	
GROUP III Medium and fine sands. Taxa present in more than one station.	3 <i>Loripes clausus</i>	
GROUP IV Medium sands with great % of silts and clay.	4 <i>Setia</i> sp2	5 <i>Glycera natalensis</i>
	5 <i>Perinereis nigropunctata</i>	5 <i>Marphysa macintoshi</i>
	5 <i>Neridae</i> nd	5 <i>Modiolus phyllipinarum</i>
	5 <i>Glycera alba</i>	
GROUP V Fine and very fine sands	6 <i>Littorina scabra</i>	
GROUP VI Very fine sands, silts and clay, organic matter, water %, Cl a, fecopigments, carotenes, Margalef index, %of degradation	7 <i>Terebrallia pallustris</i>	
GROUP VII Great quantities of silts and clay. Taxa only in one station.	8 <i>Dendronereis zuzulandica</i>	8 <i>Alpheus crassimanus</i>
	8 <i>Melampus acinoides</i>	8 <i>Macrophthalmus</i> sp
	8 <i>Siliqua cf. radiata</i>	
GROUP VIII Great quantities of silts and clay. Ubiquitous taxa.	9 <i>Uca annulipes</i>	
GROUP IX Medium sands with inferior quantity of silts and clay and organic matter.	10 <i>Dotilla fenestrata</i>	

	OHI	R	RO	VA	ADI	MW	LW	Total
Phyllodoce capensis *								24
Phyllodoce castanea *					12		20	4
Phyllodoce sp.								112
Syllis cornuta								80
Syllis ferrugina *								4
Ceratonereis erythrocephala				4	4		16	1376
Dendronereis arborifera				36	12		40	24
Nereis falsa *								4
Nereis aperta *								48
Perinereis cultrifera *				4				
Perinereis nigripunctata *				12				
Nereidae nd				4	4			8
Glycera alba			8		16			
Glycera benguelana *								4
Glycera convaluta					8			
Glycera longipinnis *								4
Glycera natalensis *						16		
Glycera sp.			8					
Glycinde kameruniana *								4
Eunicidae nd								8
Arabella incolor *								4
Diopatra cuprea cuprea *								20
Diopatra neapolitana								8
Lumbrineres latreilli								4
Lumbrineres meteorana *					8			
Aonides oxycephala								148
Malacocerus indica *								40
Pionospio sexoculata *					148		16	
Spiroidae nd								8
Couleriella acicula *						*		4
Cirratulus africanus						4		4
Haploscoloplos cf. fragilis *								4
Nannereis laevigata						4		
Scoloplos johnstonei								12
Scoloplos madagascariensis						4		60
Scoloplos sp.								16
Armadora sp.								28
Ophelia sp. *						4		16
Polyophthalmus pictus								4
Capitella capitata *				48				
Capitellidae nd								16
Parheteromastus tenuis						36		804
Futiella armata								8
Owenia fusiformis								8
Isida pulchella *								4
Loimia medusa						12		
Fabriciella mossambica *								4
Saccella sp. *								4
Polichaeta nd					"			
Oligochaeta nd		36						
Siphosoma sp.								12
Sipunculida nd								16
Cerithium caeruleum *				80				
Dipla conica *								76
Gibbulin obscura					4			440
Littoraria scabra			4					
Setha sp1 *			20		36	64	76	138
Setha sp2 *								4
Tectonatica sp1 *					8	4		
Tectonatica sp2 *								4
Terebratilia palustris				40				
Vitrinella sp. *		4						
Valonia pyrum *			4					4
Crassostrea cucullata				208				
Loripes clivius			4		24	8	8	
Modiolus philippinarum								24
Pseudophytina africana *			24	20		16	100	
Balanus amphitrite			1648			138	84	844
Ceriodocus rubromaculatus *								4
Moeria inadempes								72
Amphipode sp1								226
Amphipode sp2								8
Alpheidae nd								4
Alpheus crassimanus				4				
Decapoda euphausiidae nd				6	4			
Dafnia fenestrata						608		
Eurycarinus nobilens				4				
Macrophthalmus grandisolei			4	4	12			4
Macrophthalmus sp.				4				
Polydora sp.			8					8
Thalassidroma sp.								4
Alpheidae nd		4		4				
Xanthidae nd				12				4
Insecta larvae		8		16			20	
Ophicordis scolopendrina								4
Ophicordis valenciense								4

ANNEX 1 - Original matrix of densities (ind./m²) in both transects. The species marked with *, are new records to Inhaca Island.

	1	2	3	4	5	6	7
<i>Dendronereis zuzulandica</i> *				12			
<i>Perinereis nigrpunctata</i> *					4		
Neridae nd					4		
<i>Glycera alba</i>					4		
<i>Glycera convoluta</i>						4	
<i>Glycera natalensis</i> *					4		
<i>Arabella iricolor</i> *						4	
<i>Marphysa macintoshi</i> *					4		
<i>Littoraria scabra</i>		4					
<i>Melampus acinoides</i> *				16			
<i>Planaxis sulcatus</i>						4	
<i>Setia</i> sp1 *	168				240	608	656
<i>Setia</i> sp2 *	72						
<i>Terebrallia palustris</i>			12				
<i>Loripes clausus</i>					4	4	
<i>Modiolus phillipinarum</i>					4		
<i>Siliqua</i> cf. <i>radiata</i> *				16			
<i>Alpheus crassimanus</i>				12			
<i>Dotilla fenestrata</i>					104	8	
<i>Macrophthalmus</i> sp				4			
<i>Uca annulipes</i>	12	12		100			

GROWTH AND PRODUCTION OF *MODIOLUS PHILLIPINARUM* IN THE INHACA ISLAND (MOZAMBIQUE)

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ABSTRACT

Growth and production as well as mortality rates (both total and fisheries mortality rates) were studied in a population of the Mytilidae *Modiolus phillipinarum*, in a large seagrass meadow at the SE coast of the Inhaca Island (Mozambique). Results showed that density increases with the percentage of cover by seagrass, reaching a value of 20 ind/m² in the *Thalassodendron/Cymodocea* association. Mortality rates (Z) reflect the influence of fisheries with maximum in the months of August and October where mussel fishery reached an estimated value of 15 TON. The production values estimated for the station placed at the *Thalassodendron/Cymodocea* association ($P = 16.38 \text{ gr/m}^2/\text{yr}$) are inferior to the values of the station placed at the *Thalassia sp/Allocladia sp.* association ($P = 40.69 \text{ gr/m}^2/\text{yr}$). Nevertheless, the former presents higher values of density and biomass thus reflecting the effect of fishery, once this is the only area exploited by the mussel catchers. Growth study revealed a maximum theoretical length of $L_{\infty} = 104.97 \text{ mm}$ and $K = 0.19$.

INTRODUCTION

In Mozambique bivalves are of crucial importance for local human populations, both for economical and nutritional reasons. In fact, molluscs, and particularly bivalves, are often one of the main sources of food for littoral human populations and also one of the main resources of artisanal invertebrate fisheries. Nevertheless, there are no statistics on mollusc fisheries and, when in the year of 1979 there was a need to establish a basic system of fisheries management, the solution found was to apply locally the knowledge on the dynamics of these littoral resources, in similar ecosystems of this geographical region of the world.

Inhaca Island, nearby Maputo, is one of the places where human population greatly depends on natural resources such as oysters, shrimps, crabs and mussels which constitute an important food resource and economical income. From these resources the mussel *Modiolus phillipinarum* is one of the bivalve species more heavily exploited by local population for human consumption, although little is known on its population dynamics and production.

Modiolus phillipinarum is a Mytilidae occurring in the indo-pacific region, usually found attached to the roots of seagrass or to shells and rocks and, according to Leobrera (1990) it may reach a length of 130mm. In Mozambique it was recorded on the seagrass meadows of Inhaca Island (Macnae & Kalk, 1969), at Bazaruto and at the north coast (Ribeiro, 1984). The aim of the present study was to contribute to the knowledge of the population dynamics and production of this species in the seagrass meadows of Inhaca Island in order to produce the basic scientific knowledge allowing a sustainable resource management.

The area studied was a large intertidal seagrass bed (Sangala bank - Fig. 1) on the SE coast of Inhaca Island reaching a surface of approximately 15 Km². Mortality rates, growth, biomass and production of the *M. phillipinarum* population was studied, and an estimate of fishery catch was attempted.

METHODS

Sampling

A preliminary survey was carried out in August 1993 in order to obtain a macroscopic biological cartography of Sangala bank, and also to establish the sampling area, based on the concept minimum area. Areas of 9m² (9*1m²) were sampled using a spade and hand catching at three distinct levels. These levels corresponded to different associations of seagrass species, from HMW to LW level - respectively *Allostodum/Thalassia* (level 1); *Thalassodendron/Cymodocea* (level 2) and *Allostodum/Thalassia* (level 3). Results of this preliminary survey suggested an appropriate sampling area of 3m² at each level, and the bivalves were sampled using a spade and hand catching within each area, once no other sampling method showed to be applicable. sampling was carried every month from August 1993 to July 1994. A sample of sediment was taken for grain size analysis in each of the levels considered.

The estimation of fishery effort was assessed by means of monthly inquiries and also weighting the catches of five randomly selected fishermen, at least three times a month. Total fishermen in activity in the Sangala bank were recorded every month. For the estimation of growth two specific samples were carried out in August 1993 and March 1994, corresponding to winter and summer periods, and using an area of approximately 50m².

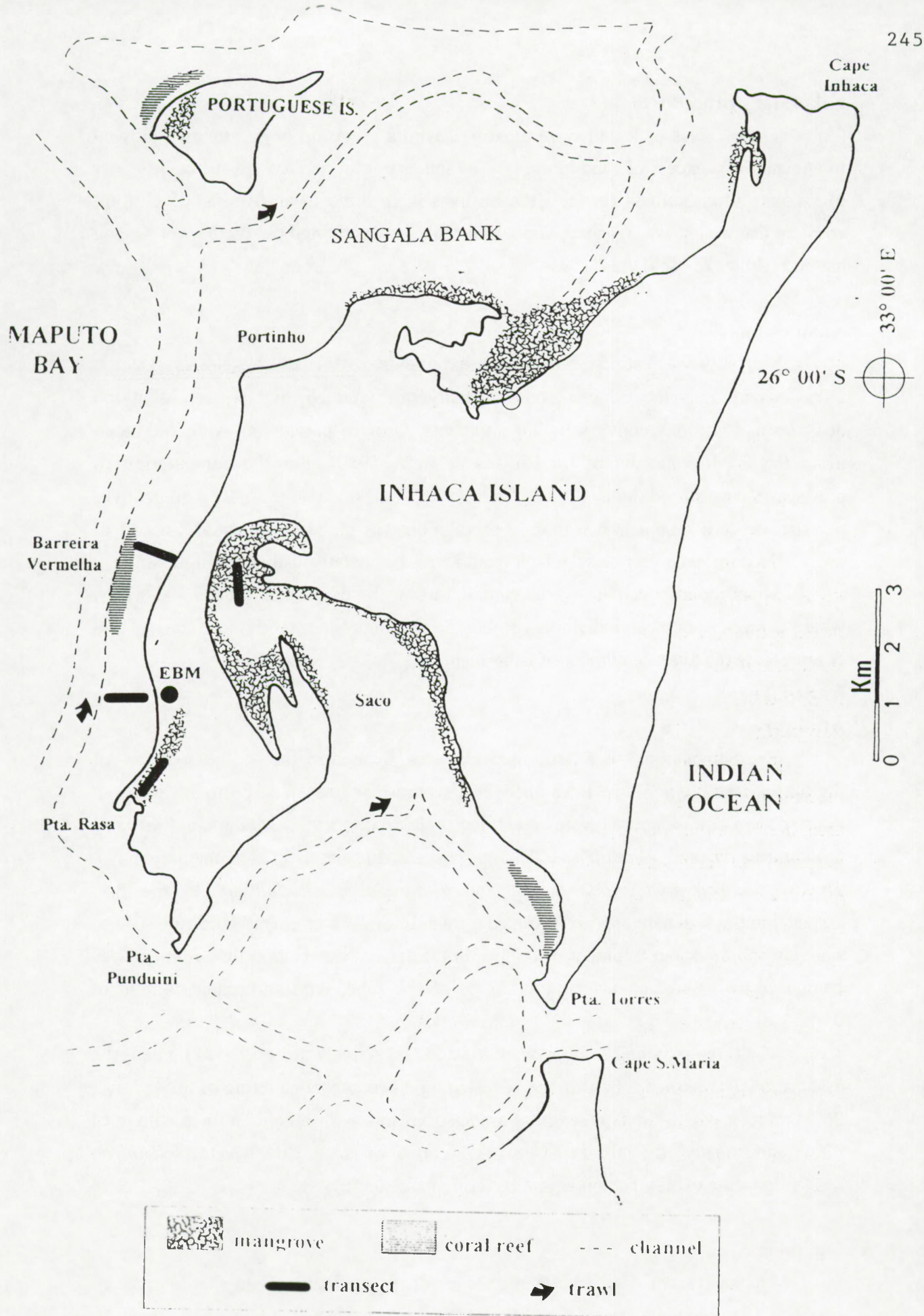


Fig. 1 - Localisation of the Sangala bank at the Inhaca Island in Mozambique.

Laboratory procedures

The bivalves collected were measured with a precision of 0.1mm and allowed to eliminate the excess of sand in the gut, by immersing in aerated sea water. In order to estimate total biomass (gr./m^2) the bivalves were dried in an oven at 65°C , until constant dry weight was reached. Grain size analysis was carried out by the wet sieving method (Buller & McManus, 1979).

Analysis tools

Mortality was estimated using the expression $Z = 1/\Delta t \log_e N_0/N_1$ (Caddy, 1979), where Z is the instantaneous mortality rate; and N_0 and N_1 represent the densities at two consecutive sampling moments. Growth parameters were estimated using the Ford Walford plot (*in* Rhoads & Lutz, 1980). For the computation of production it was used the method of Crisp (1982) but, once no more than 50 bivalves per station were sampled each month, production was globally estimated, instead of using values for each year class, which would have been statistically meaningless.

Mean monthly catches were estimated using the expression $\text{CPUE} = C \cdot D \cdot N$, where C represents mean individual catches; D accounts for total days of activity and N represents the average number of fishermen.

RESULTS

Study area

The Sangala bank is a large intertidal area, located at the southeast sector of the Inhaca Island where low tides uncover a seagrass bed reaching up to 2 Km wide. Four genera of seagrass were identified: *Thalassia sp.*; *Thalassodendron sp.*; *Cymodocea sp.* and *Allostema sp.* This species are associated in two major groups: *Thalassodendron sp./Cymodocea sp.* and *Thalassia sp/Allostema sp.* In the first association the sediment analysis revealed a fraction of 70% of coarse sand and 30% of silt+clay and an organic content of 0.95%, in the second association the sediment was composed by 80% of coarse sand and 20% of fine sand, with an organic content of 0.9%.

The three sampling stations were located respectively at Level 1(#1) where the association *Thalassia sp/Allostema sp.* revealed a percentage of covering of 30%; Level 2(#2) an area where the two seagrass associations mix with a covering percentage of 60% and finally the third level (#3) corresponds to the *Thalassodendron sp./Cymodocea sp.* association with a covering percentage of 80%.

Sampling Area

The analysis of Fig.2 shows the results of the preliminary sampling in order to establish the sampling area. In the first level prospected there were no mussels;

	Mean number of fisherman	Number of days of activity	Mean catch (Kg)	CPUE
AUG	101	16	9.5	15352.0
SEP	16	16	8.5	2170.9
OCT	63	16	14.4	14525.3
NOV	38	12	13.0	5928.0
DEC		9		0.0
JAN	0	9	0.0	0.0
FEB	7	11	10.3	793.1
MAR	13	14	8.0	1400.0
APR	12	12	3.8	540.0
MAY	23	11	8.8	2178.0
JUN	45	10	10.8	4878.0
JUL	0	13	0.0	0.0
Mean	28.8	12.4	7.9	2826.0

Table I - Evaluation of fishery effort on *Modiolus philipinarum* at the Inhaca Island.

Mortality Rates				
#2			#3	
	N			N
AUG.	3.2		AUG.	11.1
SEP.	4.8	-0.40	SEP.	27.5 -0.91
OCT.	1.9	0.93	OCT.	25.3 0.08
NOV.	11.7	-1.82	NOV.	23.2 0.09
DEC			DEC	12.2 0.64
JAN.	10.8		JAN.	13.4 -0.09
FEB.	9.5	0.13	FEB.	12.2 0.09
MAR	17.2	-0.59	MAR	12.9 -0.06
APR.	2.5	1.93	APR.	19.5 -0.41
MAY	9.2	-1.30	MAY	23.9 -0.20
JUN	8.2	0.12	JUN	34.9 -0.38
JUL.	13.2	-0.48	JUL.	23.8 0.38
		-0.08		-0.07
Annual	-0.13		Annual	-0.07

Table II - Estimation of instantaneous monthly mortality rates (Z) in #2 and #3 during sampling period.

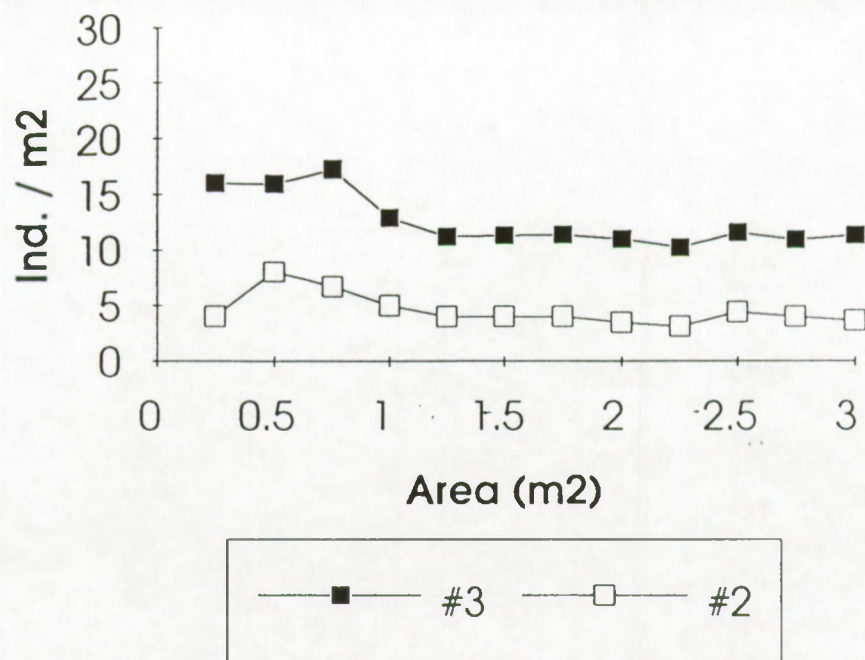


Fig. 2 - Abundance of individuals - n° ind./m² as a function of the sampling area.

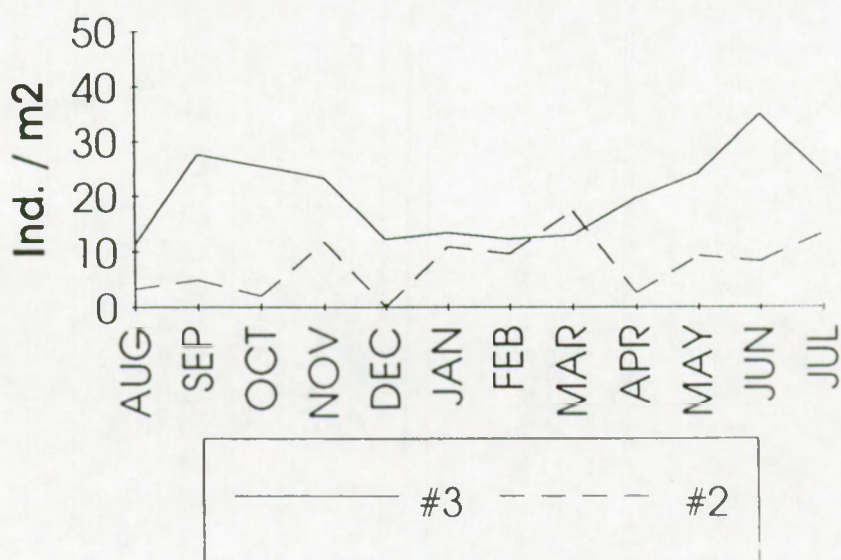


Fig. 3 - Variation of density (n° ind./m²) along the sampling period.

stations 2 and 3 presented an average density of 4 and 13/ind.m² respectively, with an average value of density stabilising near an area of 2m² for both cases. Results clearly indicate that density increases with the percentage of cover by seagrass and time of immersion.

Artisanal Fishery

Results expressed in table I show that the average number of fishermen has a strong variance during the year, reaching a maximum in August. This fishery is almost exclusively made by women and children. Mussels attached to the roots of seagrass, are collected by hand after felting the mussel with the feet. There is no selectivity in this fishery and other species, namely crustaceans and echinoderms are also caught. The period of more intensive exploitation seems to be between August and October. An individual average value of catch by day of 8 Kg. was found, and a fishery period of 12 days a month during low tides.

Density and Mortality

The analysis of Fig.3 and Table II shows that density is higher at station 3 with two major peaks in September and June. Station 2 presents an irregular pattern of density along the year an lower density. Mortality is higher in August at the beginning of winter but also matching of higher fishery with an estimated value for mussel fishery of 15352 Kg. Accordingly second highest rates of mortality were recorded in October/October when fishery reached also its second highest value (14525 Kg.). Recruitment occurred in March and July where 15% of population was constituted by individuals with a length inferior to 9 mm. The density of *M. phillipinarum* was always inferior to 1 ind./3m², and the sampling point was abandoned after three months of sampling.

Growth

Table III shows the results and statistics of the computation for growth parameters K and L_∞, respectively for the months of August, March and annual. Summer growth shows a maximum theoretical length of 104.63mm and a value of K= 0.16. In August the values of maximum theoretical length and of the constant K are lower, respectively L_∞= 103.5mm and K = 0.1. Annual growth shows the higher values for both parameters with L_∞= 104.97 mm and K = 0.19.

Production

The computation for production showed in Table IV reveals that although density is much lower at #2, its production reaches a value that is 2.5 times superior to

Regression Statistics

Multiple R	0.99
R Square	0.99
Adjusted R Square	0.98
Standard Error	2.86
Observations	6.00

Analysis of Variance

	<i>df</i>	<i>Sum of Squares</i>	<i>Mean Square</i>	<i>F</i>	<i>Significance F</i>
Regression	1.00	2532.10	2532.10	309.38	0.00
Residual	4.00	32.74	8.18		
Total	5.00	2564.83			

	<i>Coefficients</i>	<i>Standard Error</i>	<i>t Statistic</i>	<i>P-value</i>	<i>Lower 95%</i>	<i>Upper 95%</i>
Intercept	17.03	2.50	6.82	0.00	10.10	23.96
x1	0.91	0.05	17.59	0.00	0.76	1.05
L_{∞}	103.15					
K	0.10					

Regression Statistics

Multiple R	0.98
R Square	0.96
Adjusted R Square	0.95
Standard Error	4.71
Observations	6.00

Analysis of Variance

	<i>df</i>	<i>Sum of Squares</i>	<i>Mean Square</i>	<i>F</i>	<i>Significance F</i>
Regression	1.00	1950.93	1950.93	88.11	0.00
Residual	4.00	88.57	22.14		
Total	5.00	2039.50			

	<i>Coefficients</i>	<i>Standard Error</i>	<i>t Statistic</i>	<i>P-value</i>	<i>Lower 95%</i>	<i>Upper 95%</i>
Intercept	16.74	4.41	3.80	0.01	4.50	28.99
x1	0.85	0.09	9.39	0.00	0.60	1.10
L_{∞}	104.63					
K	0.16					

Regression Statistics

Multiple R	0.99
R Square	0.98
Adjusted R Square	0.97
Standard Error	3.51
Observations	7.00

Analysis of Variance

	<i>df</i>	<i>Sum of Squares</i>	<i>Mean Square</i>	<i>F</i>	<i>Significance F</i>
Regression	1.00	2731.11	2731.11	222.10	0.00
Residual	5.00	61.48	12.30		
Total	6.00	2792.59			

	<i>Coefficients</i>	<i>Standard Error</i>	<i>t Statistic</i>	<i>P-value</i>	<i>Lower 95%</i>	<i>Upper 95%</i>
Intercept	18.37	3.00	6.13	0.00	10.67	26.08
x1	0.83	0.06	14.90	0.00	0.68	0.97

L_{∞}	104.97
K	0.19

Table III - Estimation of growth parameters L_{∞} and K for, respectively for winter (August), summer (March) and annual.

#3

	\bar{W}_i	N	$N \bar{w}$	\bar{N}	\bar{W}	$-\Delta N$	$\Delta \bar{w}$	ΔP	ΔM	$\sum_0^t \Delta P$	$\sum_0^t \Delta M$	$\sum_0^t \Delta M + N \bar{w}$
AUG	2.40	11.10										
SEP	1.19	27.50	26.58	19.30	1.79	-16.40	-1.21	-33.25	22.89	-33.25	22.89	49.47
OCT	2.35	25.30	32.62	26.40	1.77	2.20	1.16	29.46	62.06	-3.78	84.95	117.56
NOV	3.09	23.23	59.47	24.27	2.72	2.07	0.73	17.06	74.86	46.52	136.91	196.38
DEC	1.60	12.20	71.66	17.72	2.34	11.03	-1.49	-18.15	28.29	-1.09	103.15	174.82
JAN	2.36	13.40	19.49	12.80	1.98	-1.20	0.76	10.16	30.15	-7.99	58.44	77.93
FEB	2.23	12.20	31.56	12.80	2.29	1.20	-0.12	-1.51	28.56	8.65	58.71	90.27
MAR	1.16	12.90	27.22	12.55	1.70	-0.70	-1.07	-13.80	14.58	-15.31	43.14	70.36
APR	2.25	19.50	14.98	16.20	1.71	-6.60	1.09	21.25	36.47	7.44	51.04	66.03
MAY	0.95	23.90	43.89	21.70	1.60	-4.40	-1.31	-31.19	20.53	-9.94	56.99	100.89
JUN	1.60	34.90	22.61	29.40	1.27	-11.00	0.65	22.84	47.05	-8.35	67.58	90.19
JUL	2.17	23.80	55.85	29.35	1.88	11.10	0.57	13.51	63.64	36.35	110.69	166.54
Total			33.83					16.38	429.07			

#2

	\bar{W}_i	N	$N \bar{w}$	\bar{N}	\bar{W}	$-\Delta N$	$\Delta \bar{w}$	ΔP	ΔM	$\sum_0^t \Delta P$	$\sum_0^t \Delta M$	$\sum_0^t \Delta M + N \bar{w}$
AUG	1.09	3.23										
SEP	1.15	4.80	3.50	4.02	1.12	-1.57	0.06	0.29	4.60	0.29	4.60	8.11
OCT	2.25	1.90	5.50	3.35	1.70	2.90	1.11	2.10	7.54	2.39	12.14	17.65
NOV	3.40	11.70	4.28	6.80	2.82	-9.80	1.14	13.38	23.09	15.48	30.63	34.91
DEC	0.00	0.00	39.72	5.85	1.70	11.70	-3.40	0.00	0.00	13.38	23.09	62.81
JAN	2.41	10.80	0.00	5.40	1.20	-10.80	2.41	25.99	13.00	25.99	13.00	13.00
FEB	2.20	9.50	25.99	10.15	2.30	1.30	-0.21	-1.96	22.33	24.03	35.33	61.32
MAR	1.12	17.20	20.90	13.35	1.66	-7.70	-1.08	-18.65	14.89	-20.62	37.22	58.13
APR	2.74	2.50	19.19	9.85	1.93	14.70	1.63	4.07	27.02	-14.58	41.91	61.10
MAY	2.21	9.20	6.86	5.85	2.48	-6.70	-0.54	-4.92	12.92	-0.85	39.94	46.79
JUN	1.75	8.20	20.31	8.70	1.98	1.00	-0.46	-3.78	15.20	-8.70	28.12	48.43
JUL	3.58	13.20	14.33	10.70	2.66	-5.00	1.83	24.18	38.30	20.40	53.49	67.82
Total			13.38186					40.69	178.88			

Table IV - Computation for production of *Modiolus philippinarum* between August 1993 and July 1994, according to the method of Crisp.

#3, respectively #2 $P = 40.69 \text{ gr/m}^2/\text{yr}$ and #3 $P = 16.38 \text{ gr/m}^2/\text{yr}$. On the other hand, the values of mortality shows the high mortality rates of August and October, computing strong negative values for production in these months. The values for mortality in #3 $\Delta M = 429.07 \text{ gr/m}^2/\text{yr}$ are 2.4 times greater than in #2 where $\Delta M = 178.88 \text{ gr/m}^2/\text{yr}$, thus in a way justifying the higher production values of #2. In fact, although biomass is higher in #3 (33.83 g/m^2) than in #2 (13.38 g/m^2), productivity is clearly higher in the later station.

DISCUSSION

The density of *Modiolus philippinarum* is clearly dependent of a substrate where to settle, and consequently its density at the Sangala Bank of the Inhaca Island increases with percentage of covering by seagrass. Also, time of immersion seems to be determinant for the values of density which reached its higher values in the *Thalassodendro/Cymodocea* association nearby low water level. Mortality values reflected the effects of mussel exploitation reaching near 15 TON in August and October, when accordingly mortality rates were higher. This result may reflect the greater need for mussels as food resource for local populations during winter.

Production values are also highly influenced by fishery, as can be easily shown by the lower values of the #3 (*Thalassodendro/Cymodocea* association) although is higher density and biomass; nevertheless this area is the only under exploitation in what concerns mussels. Productivity of this bank is also shown by the mean monthly value of catches (CPUE = 2.8 TON) if an average value of 12 days/month for mussel fishery is considered, as revealed by the inquiries.

The study of growth showed a maximum theoretical length of $L_{\infty} = 104.97 \text{ mm}$, inferior to the one considered by Leobrera (1990) $L_{\infty} = 13 \text{ mm}$. Recruitment was recorded in two periods (March and July) which may suggest two reproductive periods during summer.

Results of the present study although may be biased by the fact that age classes were not followed separately, nevertheless show the importance of the mussel *Modiolus philippinarum* as a natural resource for human population in Inhaca island, as well as the high productivity within the seagrass meadows ecosystem.

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BIOLOGICAL AND ECOLOGICAL ASPECTS OF THE POPULATIONS OF THE CRAB *DOTILLA FENESTRATA* (HILGENDORF, 1869) (BRACHYURA, OCYPODIDAE) IN THE TIDAL FLATS OF INHACA ISLAND

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INTRODUCTION

The sand-bubbler crab *Dotilla fenestrata* is a small species belonging to the family Ocypodidae, one of the major brachyuran tropical groups, occupying a variety of coastal biotopes, as tidal flats, sandy shores and mangroves. *D. fenestrata* inhabits intertidal sandy or muddy sand flats, with preference for well drained areas (Hartnoll, 1973). This species distributes from South Africa to Kenya, including Madagascar and the Comores islands (Barnard, 1950). In northern Kenya the species is substituted by *D. sulcata*.

Dotilla fenestrata plays a major role on the ecology of sandy shores, presenting locally patches of high density. These crabs are responsible for a rapid turnover of the sediment (burrowing) and contribute significantly for the consumption of the available organic matter in the superficial layer of the sediment (feeding). All species within the genus *Dotilla*, except *D. blanfordi*, produce semi permanent burrows, which depth is related to distance from water at low tide (Junk, 1983). At lowest levels the crabs do not make burrows, just sink into the sediment.

Granulometry is one of the major factors determining the distribution of the genus *Dotilla* (McIntyre, 1968; Hails & Yaziz, 1982; Hartnoll, 1973). The distribution of *Dotilla* burrows is not affected by tidal amplitude fluctuations as seen in the genus *Ocypode* (Jones, 1972), however other factors may affect it, as rain and strong wind (Junk, 1983; Hartnoll, 1973). McIntyre (1968) suggests seasonal changes for the species *D. myctiroides*.

These crabs feed on the superficial layer of sediment, depending on the incoming tides for a replenishment of its feeding resources (Junk, 1983). As in other ocypodids (e.g. Harada & Kawanale, 1955) the burrowing area is the feeding area also, and the animals keep close to their respective burrows.

The main objective of this study was to quantify the abundance and distribution of *Dotilla fenestrata* in the sandy tidal flats of the west coast of Inhaca island.

MATERIAL AND METHODS

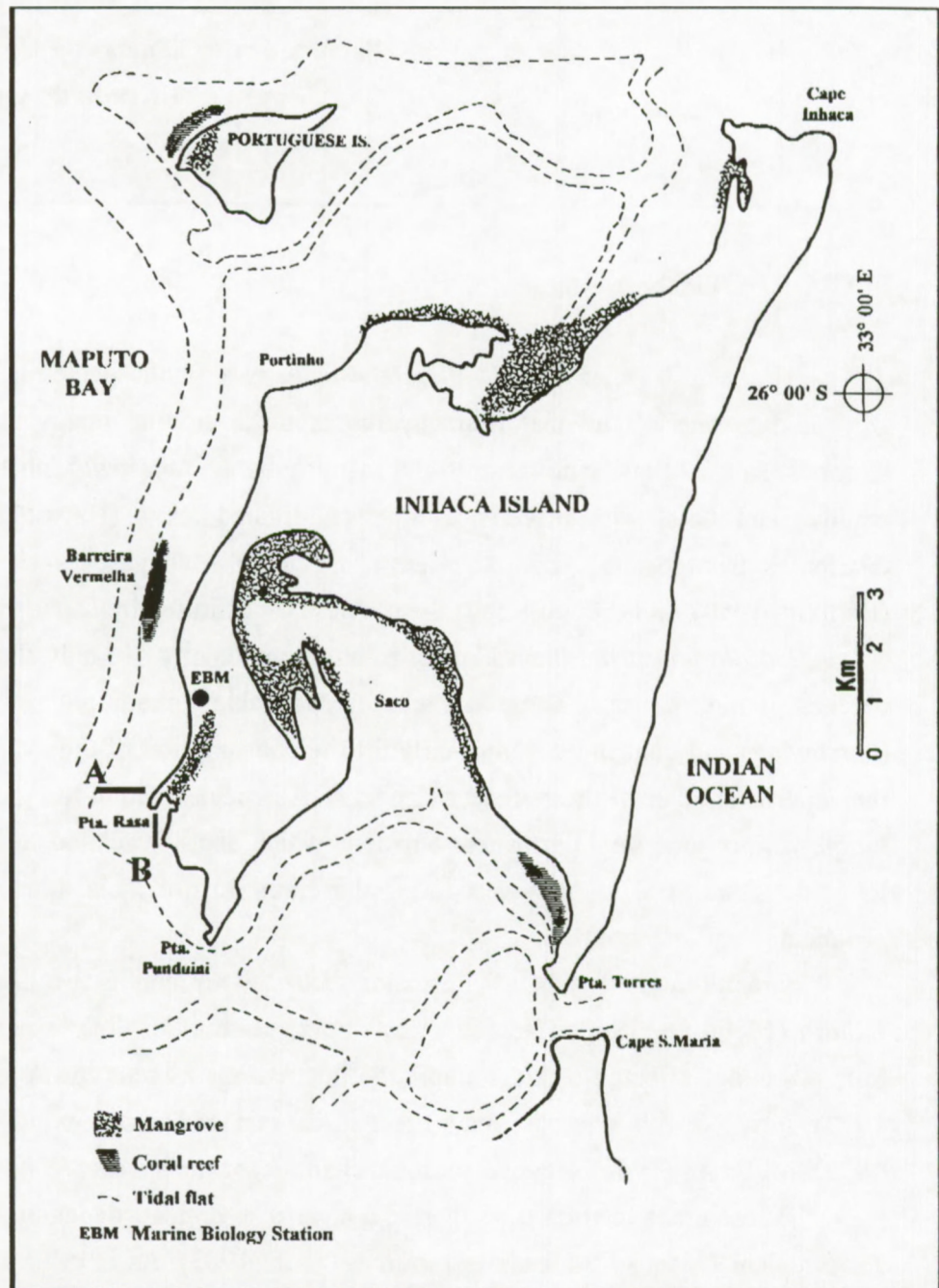


Fig. 1 - Map of Inhaca island, showing the position of transects A and B.

Semilunar sampling was done in 2 transects on the west coast of Inhaca island, at 3 different levels (Fig. 1). The two extreme levels correspond to the vertical limits of *Dotilla* population. Levels were measured with vertical rulers and water level. In each level were taken 3 replicates of 0.0665 m², down to 20 cm, and crabs were sorted in a 1.5mm net, sexed, measured and dry weighted. Sampling was repeated during 8 consecutive spring tide periods, from February to March 1994. Fertility was studied by counting female eggs in relation to carapace width. Crab dimension was analysed in relation to burrow diameter and weight of sediment feeding pallets.

RESULTS

Abundance and distribution

Figure 2 shows the mean abundance on both transects Over the consecutive sampling periods. The transects showed differences in abundance, and within each transect abundance can be very unstable on consecutive samples. This can be due to the mobility of the substratum, which displaces the whole population. Except for the last sample of transect B, in which no crabs could be found, minimum and maximum mean densities were 238 and 872.9 ind./m².

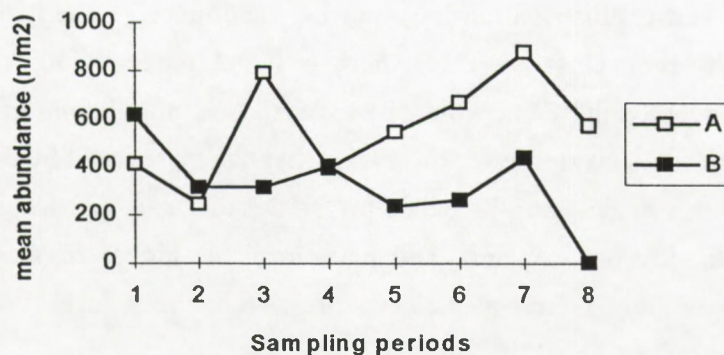


Fig. 2 - Mean abundance on both transects over the consecutive sampling periods.

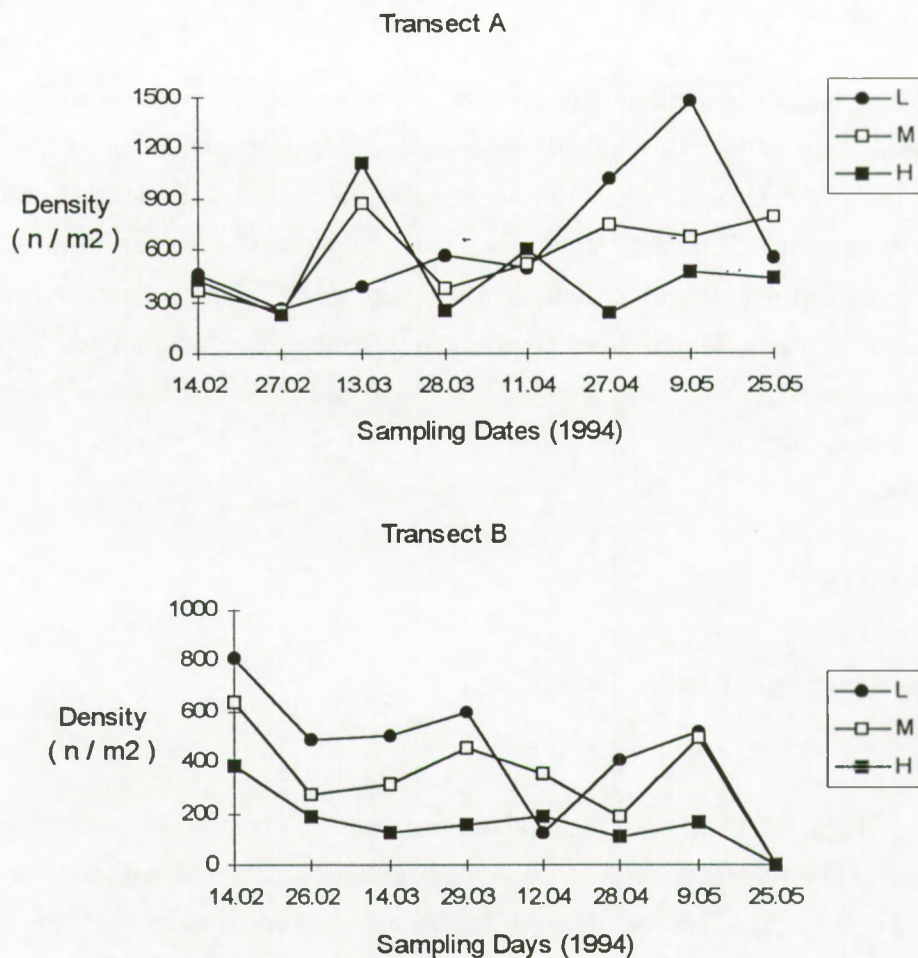


Fig. 3 - Mean densities on both transects, at the 3 levels.

Figure 3 presents the mean densities on both transects, at the different levels. On transect A, vertical distribution is somewhat random, with the highest densities shifting from low to high level. On transect B there is a net tendency for decreasing abundance with increasing level height. This would be expected, as population tends to concentrate in areas with high interstitial water level, or at least that can be reached by their burrows.

Males, females, and juveniles prefer the low and mid level, which suggests that they have less dissection problems, and have available higher organic matter contents of these layers (Figs. 4 and 5). Juveniles clearly prefer the lowest level, which probably indicates that this area has stronger recruitment than the others.

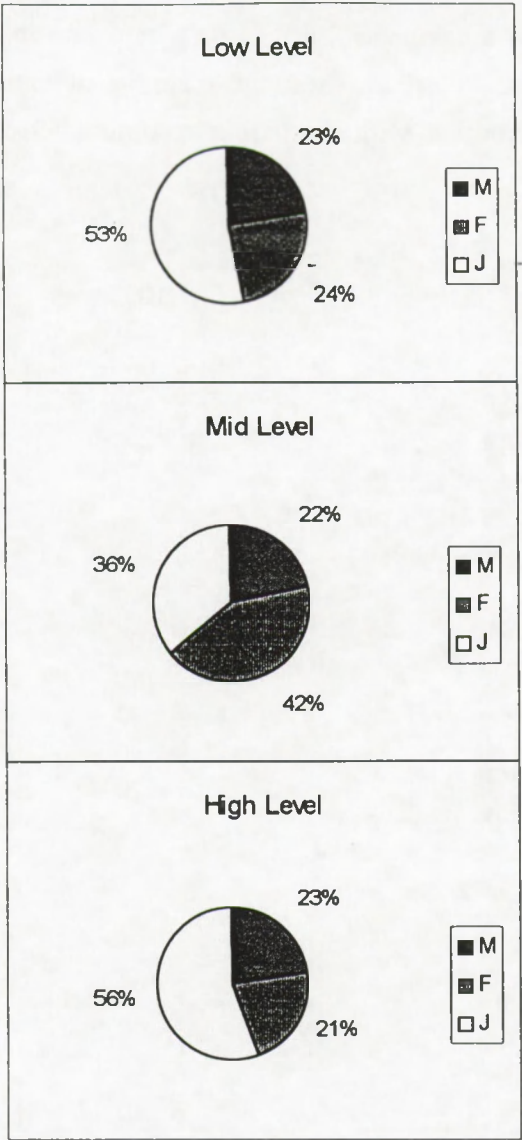


Fig. 4 - Distribution of relative abundance of males, females and juveniles, at each level.

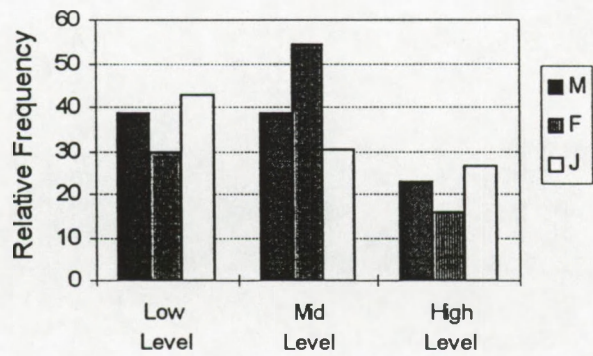


Fig. 5 - Relative abundance of males, females and juveniles at 3 levels.

Most crabs show a carapace width of 4, 5 or 6 mm, being rare specimens with more than 8 mm (Figs. 6 and 7). Males form the majority of bigger classes. Juveniles have an interesting temporal fluctuation, with alternating maximum between the 2 and 3 mm classes.

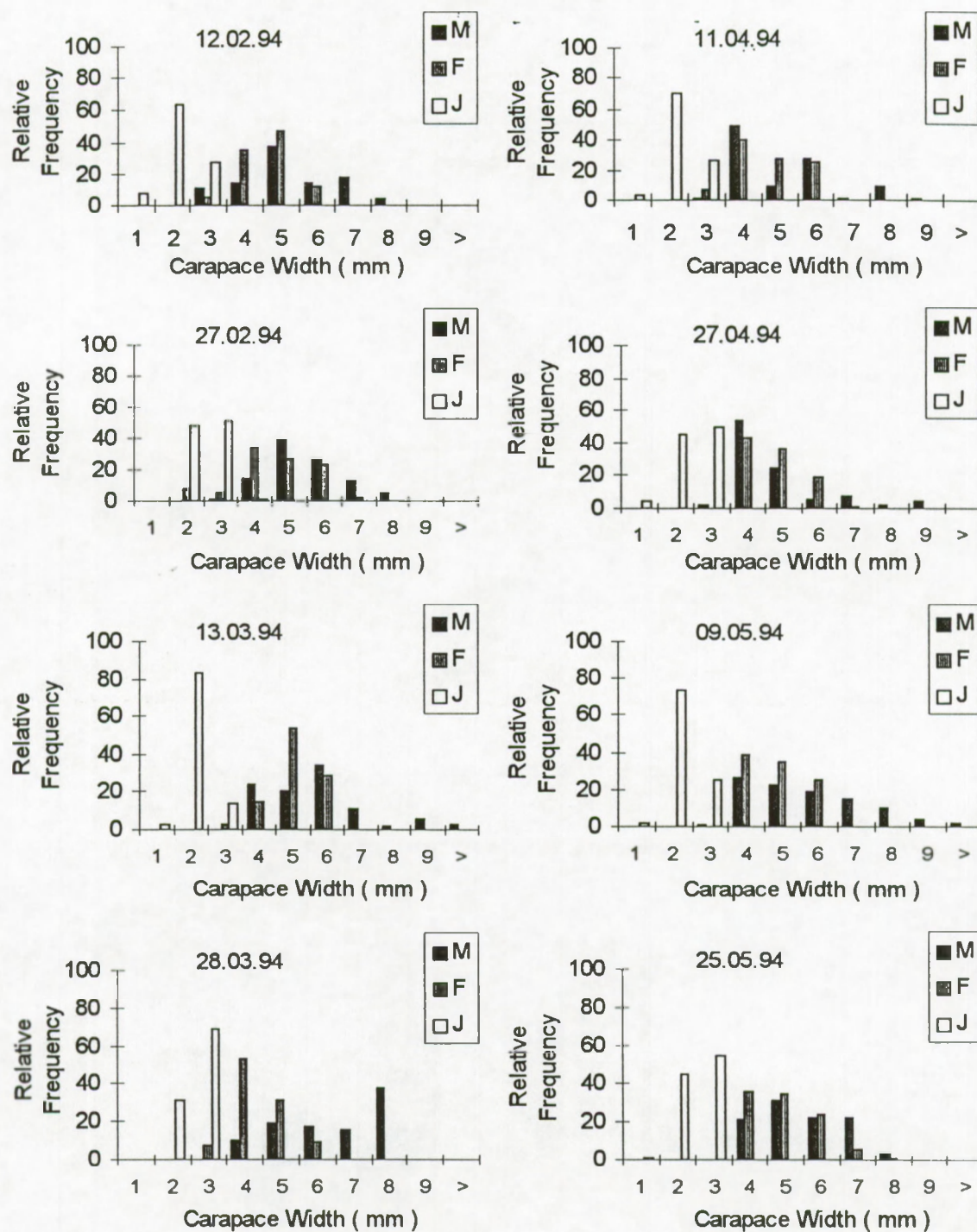


Fig. 6 - Size frequency classes at transect A.

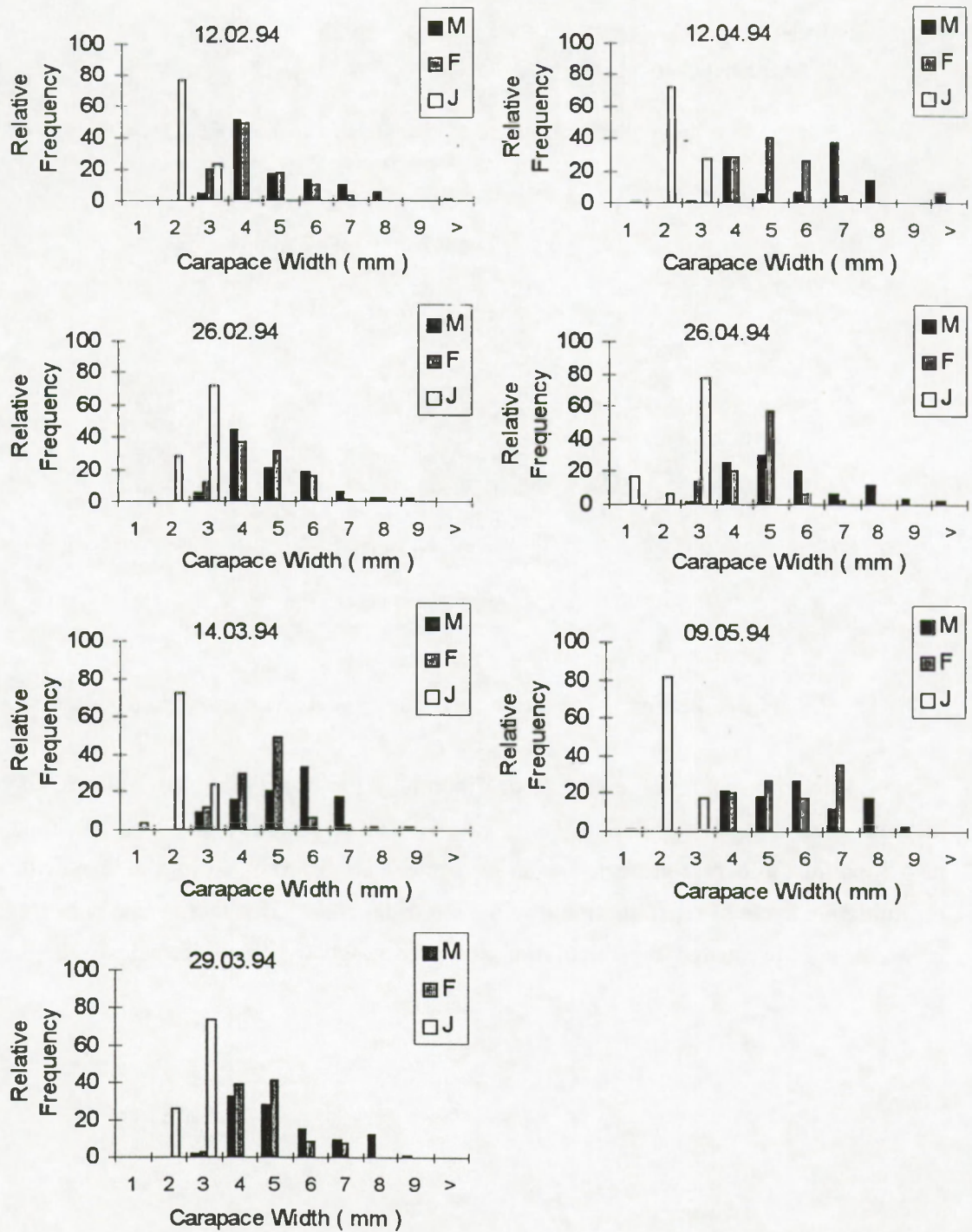


Fig. 7 - Size frequency classes at transect B.

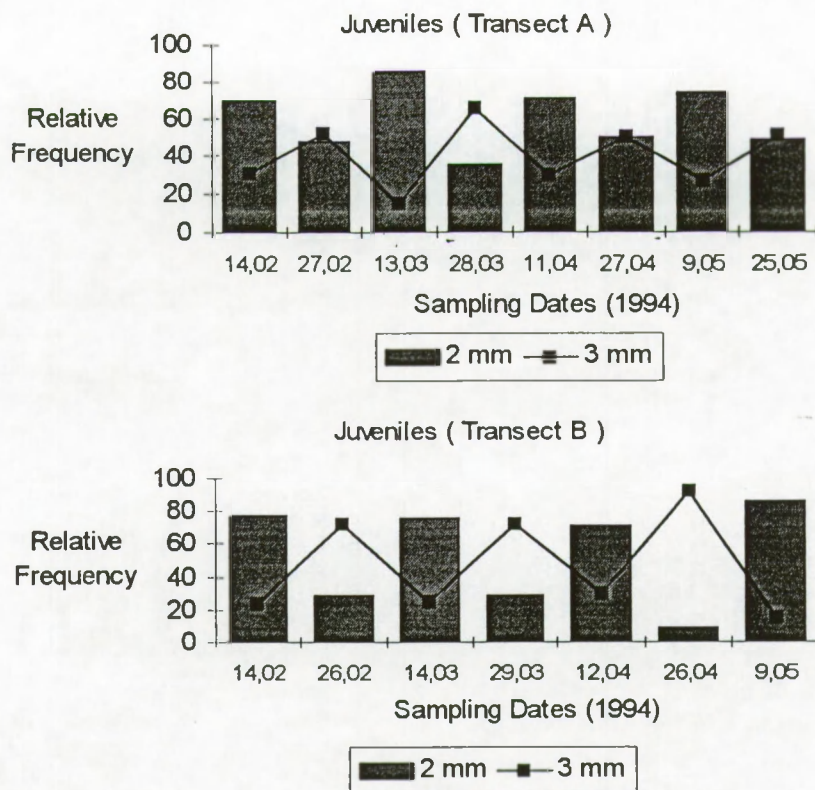


Fig. 8 - Relative abundance of size frequency classes corresponding to juveniles.

Both transects suggest a lunar (monthly) periodicity in the relative abundance of juvenile size frequency classes (Fig. 8). This fact strongly suggests a lunar cycle of megalopal/juvenile recruitment, which is somewhat different from the classical semi-lunar reproductive cycle of reproduction of most intertidal crabs. This fact is also supported by Fig. 9, in which it is presented the fluctuations of percentage ovigerous females over the sampling period.

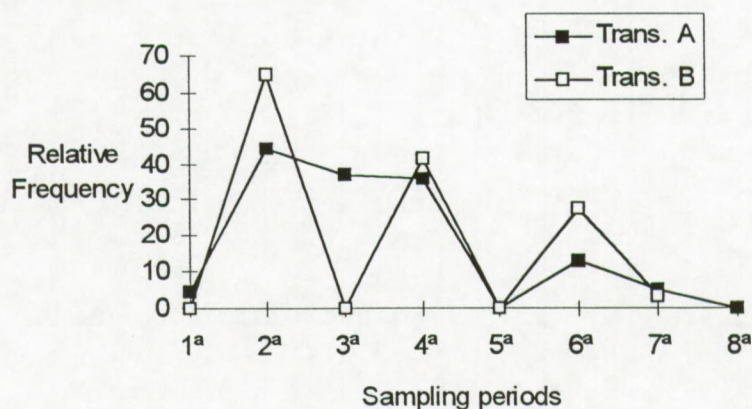


Fig. 9 - Relative abundance of ovigerous females on both transects.

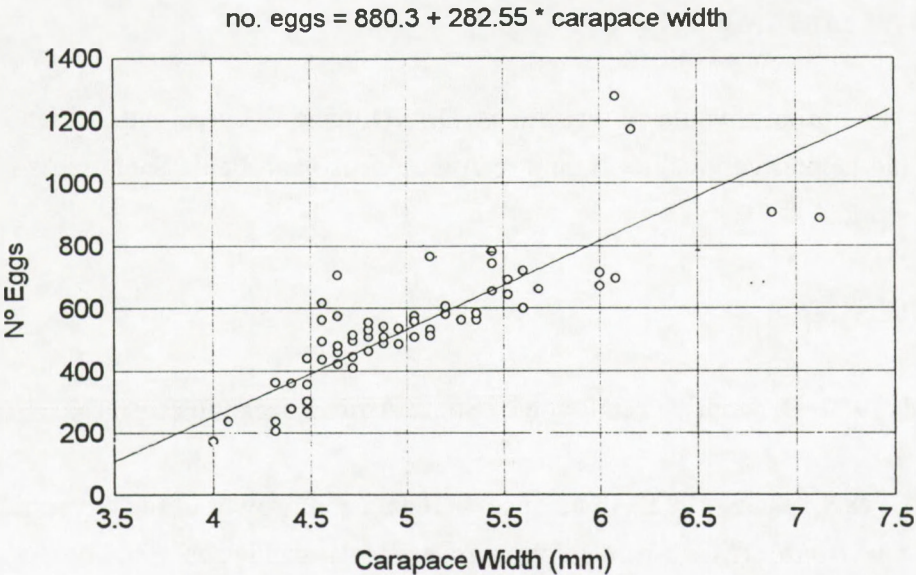


Fig. 10 - Relation of carapace width and egg number for the ovigerous females.

Fig. 10 presents the relation between ovigerous female carapace width and egg number. The correlation is high ($r=0.85$, $p<0.0000$).

In Fig. 11 it is presented the relation between crab dimension and burrow diameter. The correlation is very high, which indicates that burrow diameter may in some cases be used for a rapid assessment of the size structure of the populations, thus avoiding the problems of escaping and damaging.

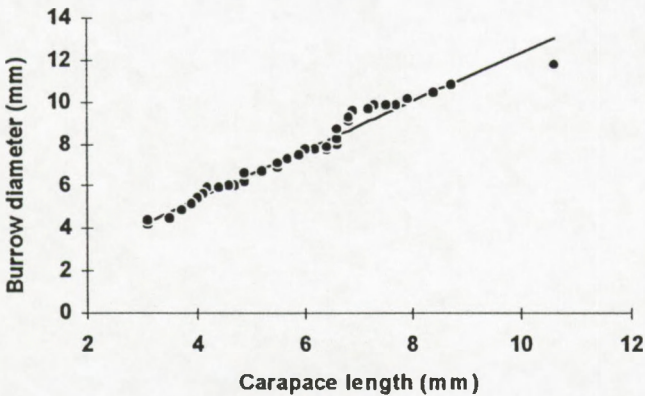


Fig. 11 - Relation between carapace width and burrow diameter.

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NEWLY-HATCHED STAGES OF DECAPOD CRUSTACEANS FROM INHACA ISLAND, MOZAMBIQUE

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INTRODUCTION

The global aim of this work was to obtain reliable descriptions of the larval stages of decapod crustaceans from the east coast of Africa, in order to make a base for identification of larvae from plankton samples. This is a essential base for developing life cycles and recruitment studies in coastal biotopes.

A total of 36 species of decapod crustaceans were obtained ovigerous during the project, and the larvae hatched successfully in the laboratory, allowing descriptive work. Basic work of dissection and microscope description is now finished, but the extreme time consuming process of making the final art is still in process, as larval cultures went on until October 1995. In this final report we present the complete list of species obtained by the programme, and a basic description for larval stages of brachyuran crabs, the dominant crustaceans on mangroves and tidal flats. Complete analysis of the obtained material, concerning standard descriptions, will be published in a refereed journal in due time.

MATERIAL AND METHODS

Ovigerous females of decapod crustaceans were collected using a variety of sampling methods, in a diversity of Inhaca island coastal habitats, as mangroves, seagrass meadows, coral reefs, polychaet reefs and tidal flats. Females were taken to the laboratory of Inhaca Marine Biology Station (Estação de Biologia Marítima) of the University Eduardo Mondlane, and placed in plastic jars according to female size. Water was gently aerated, changed each day, and females were kept unfed during the experiment. Each evening and morning jars were checked for active swimming larvae. When present, larvae were immediately preserved in buffered 4% formaldehyde. Females were kept in 70% ethanol, and stored in the collections of Inhaca Marine Biology Station. Sampling was carried out between June 1993 and October 1995.

Larvae were described at Guia Marine Laboratory of the University of Lisbon, being dissected and measured under a Wild M5 stereoscopic microscope, and drawn using a Olympus BHT2 optical microscope with drawing tube. Measures taken were (CL) carapace length from between the eyes to the posterior margin, (CW) carapace width, between tips of lateral spines when present, and for brachyurans also (TT) the distance between tips of rostral and dorsal spines. Setal counts refer proximal to distal sequence.

STANDARD DESCRIPTION

The following description is the model to be used for all species when final art is done. It is provided here as example.

Pilumnus vespertilio

(Figure 1)

Two hatchings were obtained, from several females captured under dead coral on the tidal flats near the Marine Biology Station at Inhaca island.

Carapace: All carapace spines present, dorsal shorter than carapace length and curved backwards, rostral very short, not reaching tip of antennule. One pair of setules near the base of dorsal spine, postero-lateral margins with 10-12 denticles.

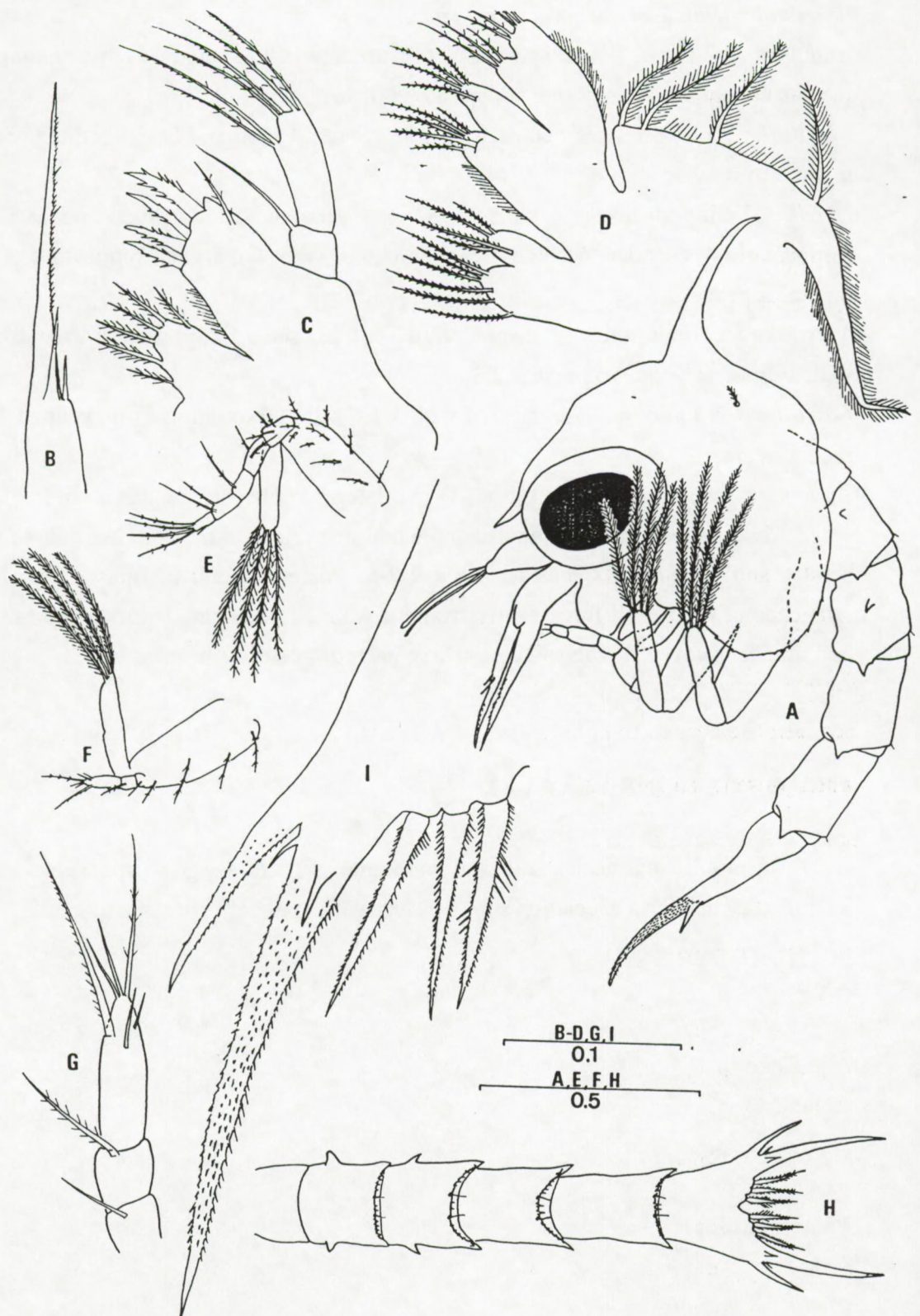


Figure 1 - Newly-hatched stage of *Pilumnus vespertilio* Fabricius. (A) Lateral view, (B) tip of exopod of antenna, (C) maxillule, (D) maxilla, (E) 1st maxilliped, (F) 2nd maxilliped, (G) endopod of 2nd maxilliped, enlarged, (H) abdomen, dorsal view, (I) telson, enlarged. Scales in millimetres.

Antennule: With 2 aesthetascs and 2 setae.

Antenna: As long as dorsal spine. Spinous process of the same length of exopod, this with 2 median subequal spines. Small endopod bud present.

Maxillule: Endopod 2-segmented with 1,2+4 setae. Coxal and basial endites with respectively 6 and 5 processes.

Maxilla: Endopod unsegmented with 8 setae, arranged 3,2,3. Coxal and basial endites with respectively 4+6 and 4+5 setae. Scaphognathite with 4 marginal plumose setae plus a stout posterior process.

Maxilliped 1: Endopod 5-segmented with 3,2,1,2,5 setae. Exopod with 4 natatory setae. Basis with 10 medial setae, arranged 2,2,3,3.

Maxilliped 2: Endopod 3-segmented with 1,1,6 setae. Exopod as in maxilliped 1. Basis with 4 medial setae.

Abdomen: Five somites plus telson. Dorso-lateral knobs on somites 2 and 3, on the second anteriorly directed, and on the third acute and posteriorly directed. One pair of postero-dorsal setules and 4 pairs of spines on somites 2-5. Postero-lateral margins of somites 2-5 acute. Branches of the telson furca nearly straight, with 2 lateral and 1 dorsal spines. Longest spine and branches covered with spinules. Three pairs of posterior processes.

LIST OF OBTAINED LARVAE

A number of species collected were impossible to assign to species level, which due to its difficulty implies a specialists suport. That work is under process.

Alpheidae

Alpheidae sp.1

Alpheidae sp.2

Alpheidae sp.3

Palaemonidae

Anchistus inermis

Hyppolitidae

Hyppolitidae sp.1

Coenobitidae*Coenobita cavipes***Diogenidae***Dardanus deformis**Clibanarius virescens**Calcinus latens***Porcellanidae***Porcellana dehaanii**Pachycheles natalensis***Majidae**

(Figure 2)

*Cyphocarcinus capreolus**Menaethius monocerus**Menaethiops fascicularis***Grapsidae**

(Figure 3)

*Grapsus fourmanoiri**Pachygrapsus minutus**Sesarma guttatum***Portunidae**

(Figure 4)

*Thalamita crenata**Thalamita admete***Pilumnidae**

(Figure 1)

Pilumnus vespertilio

Xanthidae

(Figure 4)

Eurycarcinus natalensis

Leptodius exaratus

Eriphia smithii

Trapezia cymodoce

Xanthidae sp. 1

Xanthidae sp. 2

Ocypodidae

(Figure 5)

Uca vocans

Uca gaimardi

Uca urvillei

Uca annulipes

Macrophthalmus boscii

Macrophthalmus grandidieri

Macrophthalmus depressus

Dotilla fenestrata

Pinnotheridae

(Figure 3)

Arcotheres palaensis

Leucosiidae

(Figure 4)

Philyra platychira

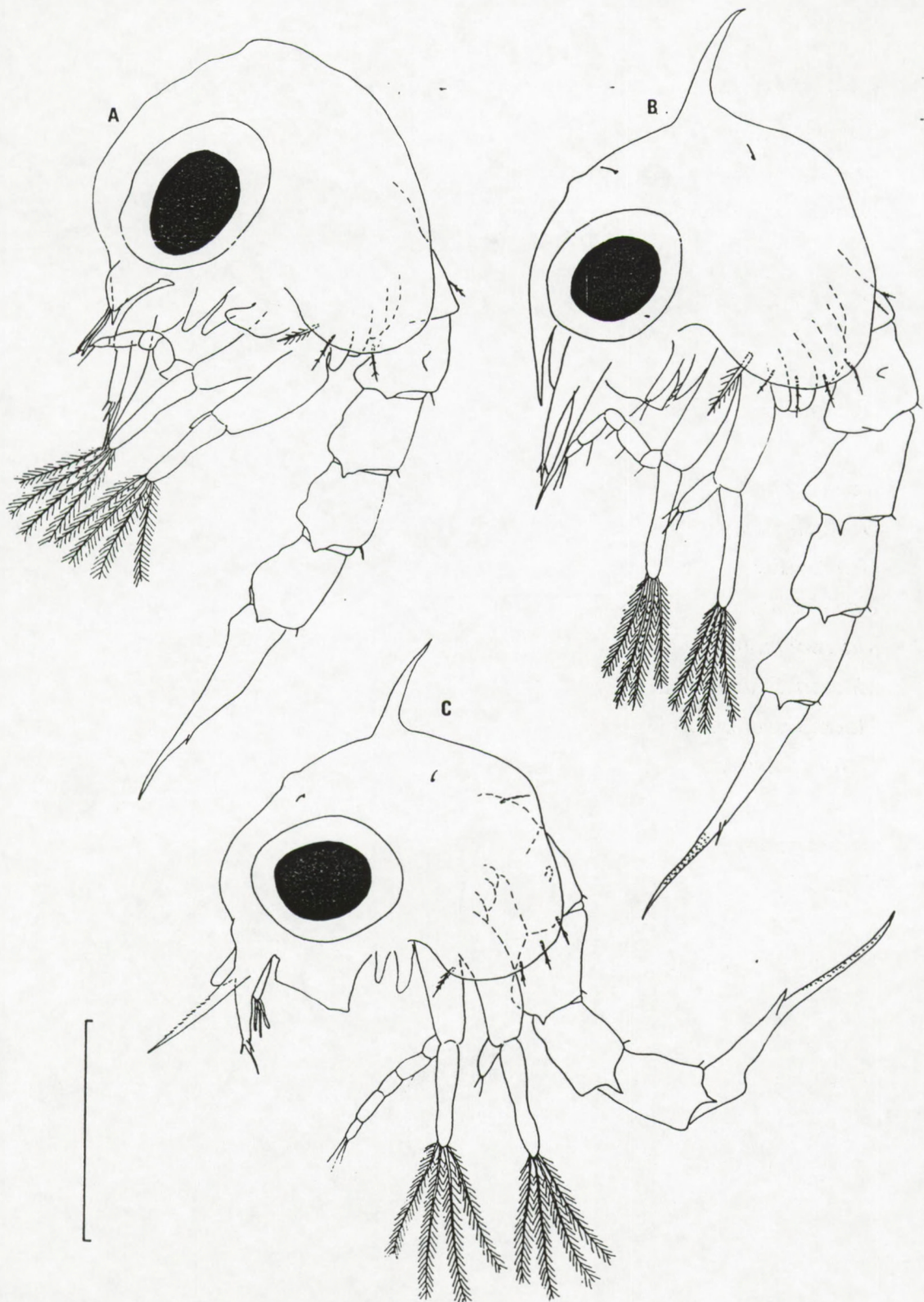


Figure 2 - Newly hatched stages from the family Majidae. (A) *Menaethius monocerus*, (B) *Cyphocarcinus capreolus*, (C) *Menaethiops fascicularis*. Scale in millimetres.

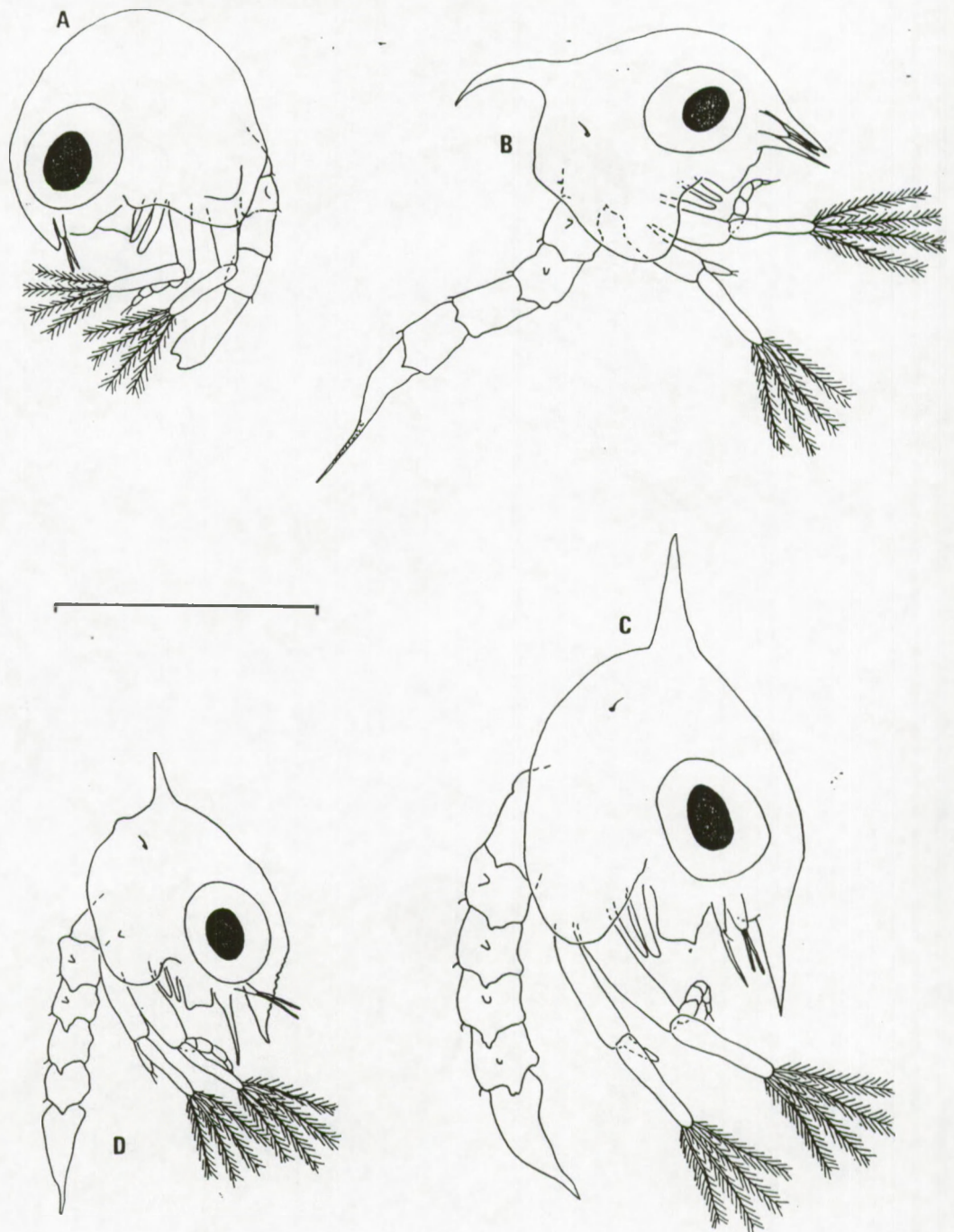


Figure 3 - Newly hatched stages from the families Leucosiidae and Grapsidae. (A) *Phylira platychira*, (B) *Sesarma gultatum*, (C) *Grapsus fourmanoiri*, (D) *Pachygrapsus minutus*. Scale in millimetres.

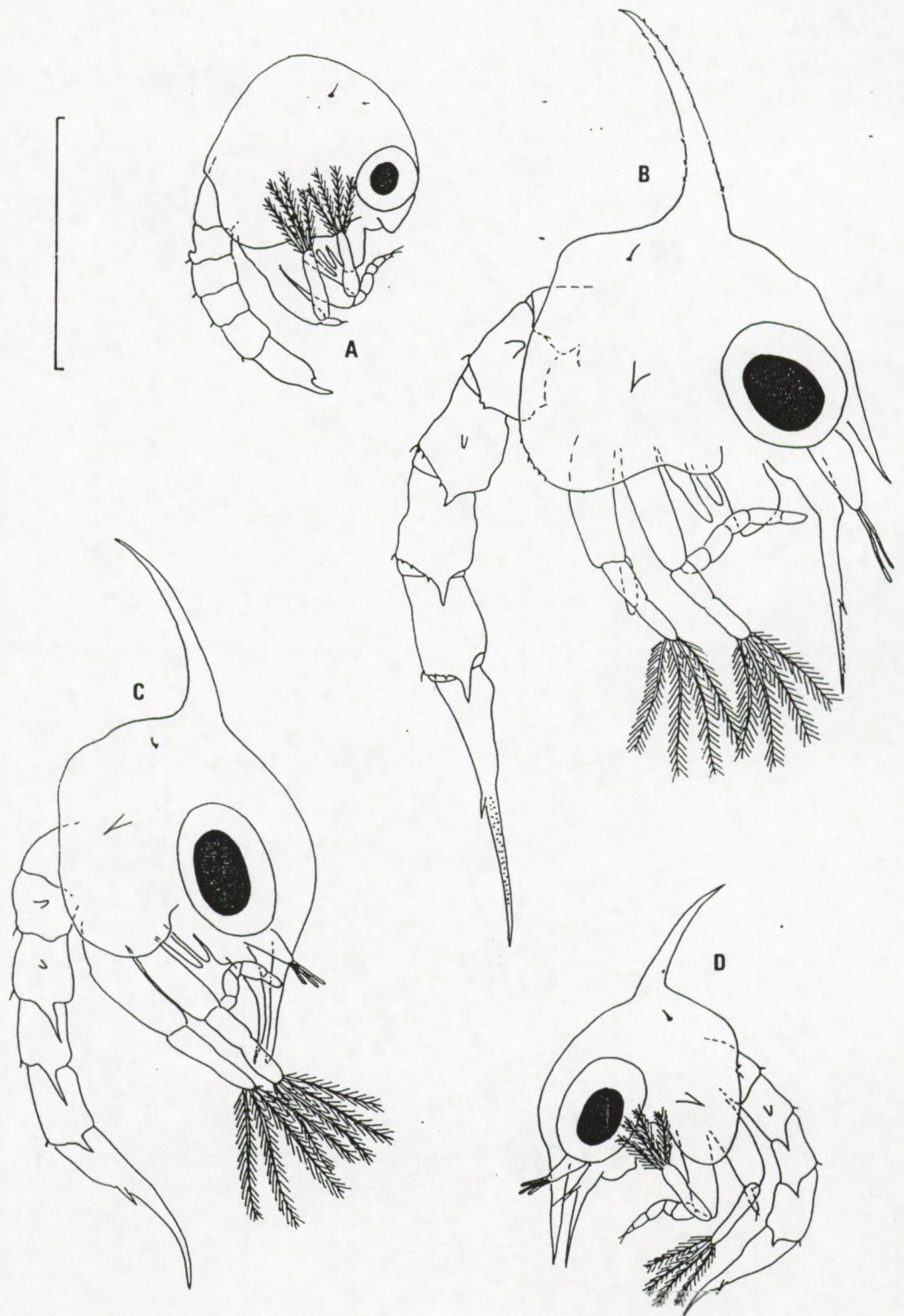


Figure 4 - Newly hatched stages from the families Pinnotheridae, Xanthidae and Portunidae. (A) *Arcotheres palaensis*, (B) *Eurycarcinus natalensis*, (C) *Thalamita crenata*, (D) *Thalamita admete*. Scale in millimetres.

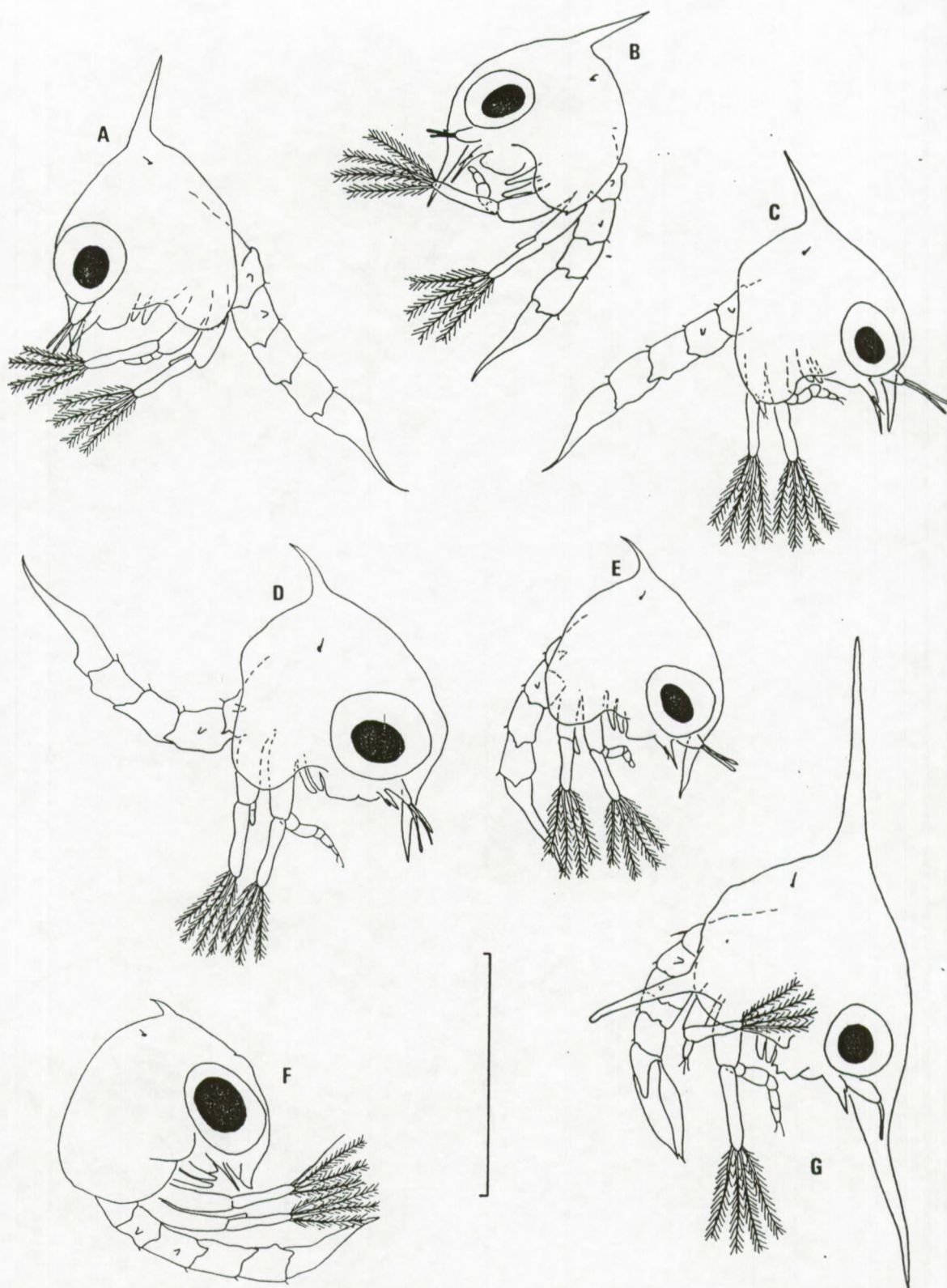


Figure 5 - Newly hatched stages from the family Ocypodidae. (A) *Macrophthamus grandidieri*, (B) *M. boscii*, (C) *M. depressus*, (D) *Uca annulipes*, (E) *U. urvillei*, (F) *U. gaimardi*, (G) *Dotilla fenestrata*. Scale in millimetres.

ACNOWLEDGEMENTS

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ANNUAL CYCLE OF PLANKTONIC COMMUNITIES AT INHACA ISLAND, MOÇAMBIQUE

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INTRODUCTION

The main objective of this work was to describe the annual cycle of planktonic communities at the east coast of Inhaca island, namely phytoplankton abundance and distribution, and its relation to nutrients and physical parameters, and zooplankton abundance, distribution and seasonal fluctuations. Particular attention was made on distribution and abundance of larval stages of crustaceans and molluscs.

MATERIAL AND METHODS

Research area

The study area was the west coast of Inhaca island. Three collecting stations were defined (Fig. 1): Portinho, Estação de Biologia Marítima and Saco.

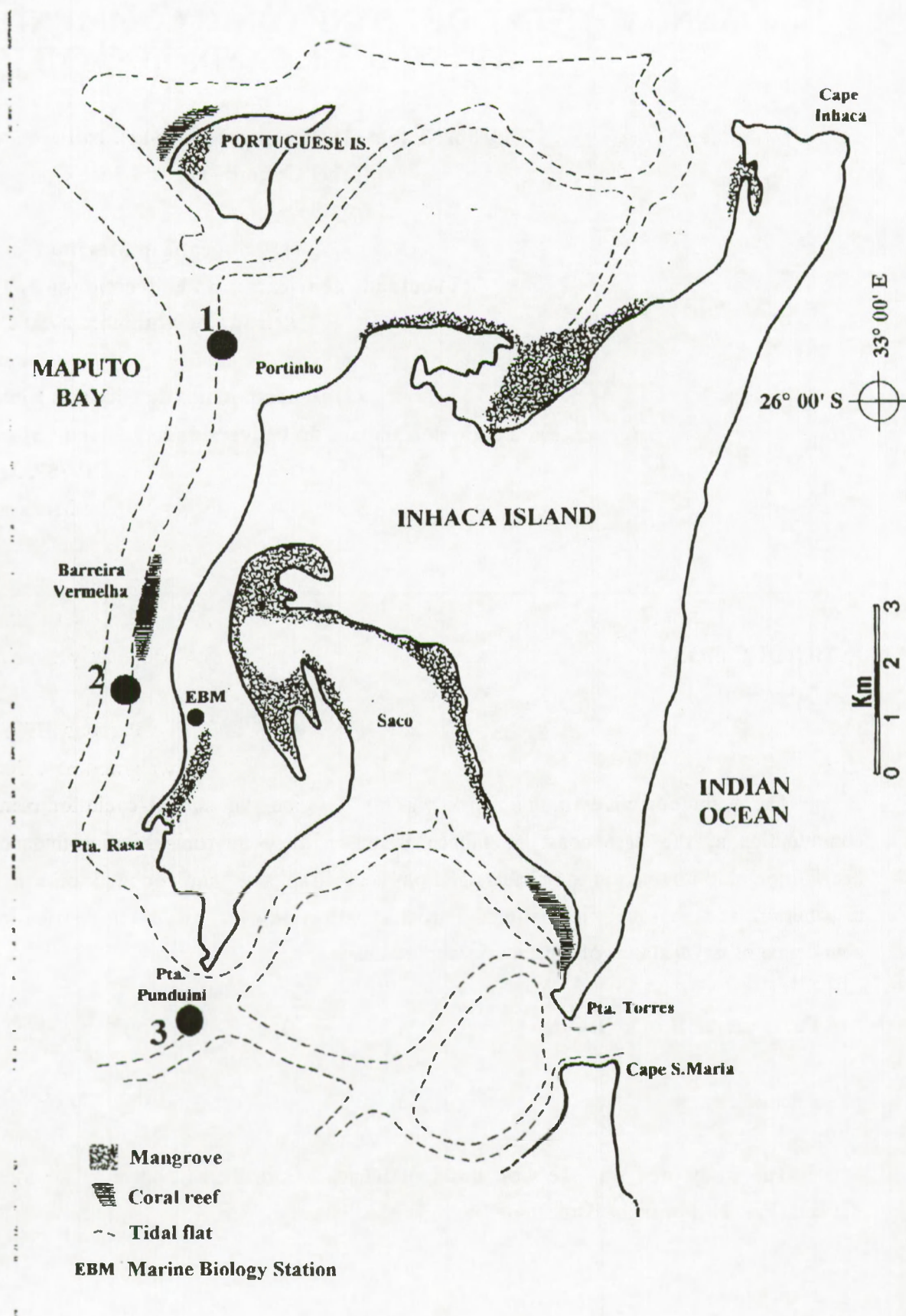


Figure 1 - Map of Inhaca island showing position of plankton collecting stations.

Sampling strategy

Regular sampling was made monthly, during 13 months. The timing for sampling was during the neap water period, at high tide, in order to minimize the dislocation of the water mass and maintain similar physical conditions throughout the collecting stations. Sampling is made from north to south, following the tidal front.

Nutrients and phytoplankton

In view of the low depth at the collecting stations, significative stratification of the water column is not significant. Sampling was made subsuperficially, at approximately 1 meter deep. The following parameters were sampled: temperature (0.1°C), salinity (‰), light penetration (sechii disc), nutrients (phosphorus, nitrogen - nitrite, nitrate, ammonia, silicium), total seston, and chlorophyll *a*.

For qualitative purposes a vertical haul was made, using a plankton net of 25 µm of pore aperture, and sample was preserved in buffered 4% formaldehyde. A quantitative sample of 250 ml was taken, for cell quantification under inverted optical microscope, preserved in lugol. Water for nutrient analysis was collected with 6 and 12 litre VanDorn bottles. Nutrient samples were immediately frozen, and water for total seston and phytopigments was filtered in 1.2 µm filters, with a vacuum pump. After filtration, filters were immediately frozen until analysis.

Nutrient analysis will follow general procedures by Strickland e Parsons (1979). For total seston, filters will be dried at 100 C during 24 hours, being weighted at 0.0001 gr. Pigments are extracted with methanol, and quantified with spectrophotometer. The identification and counting of phytoplanktonic organisms used inverted optical microscope.

Zooplankton

For zooplankton 2 trawls were made: one horizontal subsuperficial trawl with a net of 125 µm of pore aperture for 3 minutes, and a similar trawl with a net of 330 µm of pore aperture for 5 minutes. The nets were equiped with Hidrobios flowmeters, and samples were preserved in buffered 4% formaldehyde.

Sedimentation volume was determined with a conical jar. Sample fraction used a Folsom plankton splitter. Identification of most abundant organisms and counting of major zooplanktonic groups was made using an Olympus stereo microscope.

RESULTS

Physical conditions

Temperature fluctuated between 18.6 °C in July and 37.0 °C in January at collecting station 1 (Fig. 2). The maximum value clearly reflects local conditions at a particular sampling moment, due to the low depth of water column and strong insulation. The global cycle of temperatures at collecting sites followed a clear maximum during Summer and a minimum in Winter, reflecting the sub-tropical conditions of Maputo Bay. Salinity showed an irregular pattern (Fig. 2), fluctuating between 30 and 42 ‰. Salinity fluctuations reflect a complex set of factors, namely the hydrological circulation in the bay, in which discharge 3 rivers, and evaporation due to insulation and dilution due to rainy periods, over a short water column (at sampling sites between 0.75 and 5 meters deep). The maximum temperature occurred simultaneously with the maximum salinity.

Due to the low depth of the collecting stations, light penetration with sechii disc followed very closely the total water column depth, thus not representing really the light attenuation conditions of the water mass.

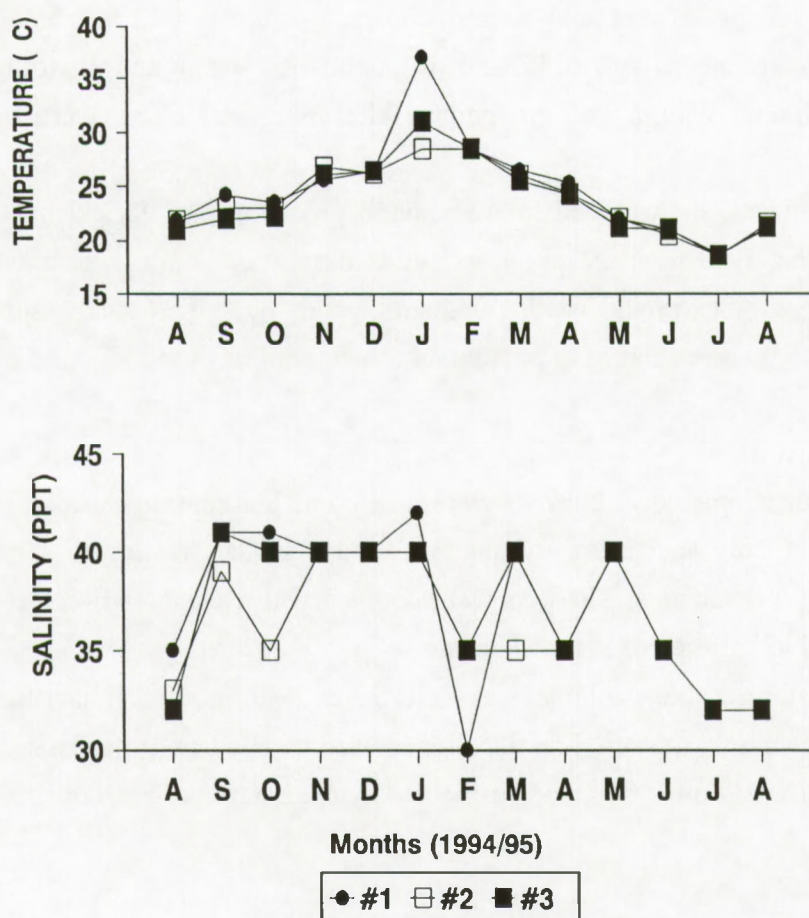


Figure 2 - Temperature and salinity fluctuation at collecting stations.

Nutrients and phytoplankton

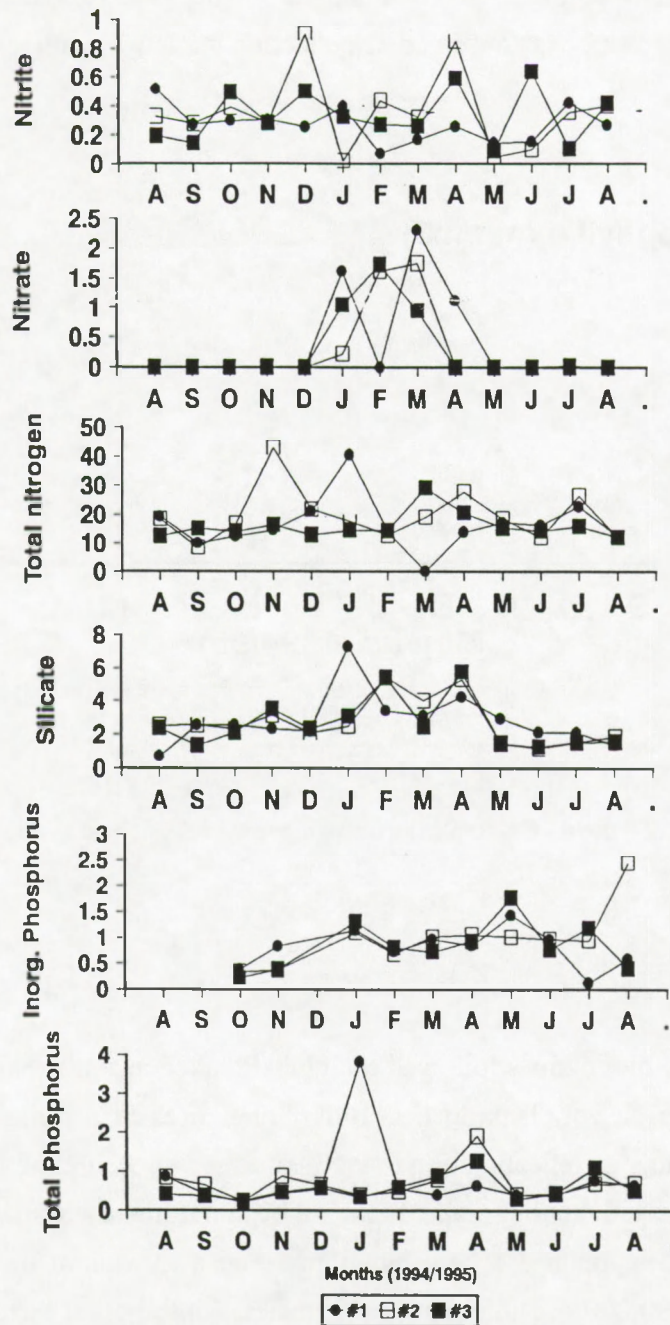


Figure 3 - Nutrient fluctuations at the collecting stations ($\mu\text{mol/l}$).

Figure 3 shows the concentration of nutrients in the sampled layer of the water column. The nutrients that show a net tendency are the nitrates, silicates and to some extent total phosphorus, all showing an increase during the warmest months, probably coupled with the maximum values of precipitation in the hydrographic bassins of the rivers which discharge to Maputo Bay.

Due to the accumulation of nutrients during the Summer period, maximum values of Chlorophyll *a* were reached in March (Fig. 4), with a decrease towards the cooler months, and with a minor peak in September, where temperature begins to rise. During the peak of chlorophyll the highest value was observed at collecting station 3, with a decrease towards the entrance of the bay.

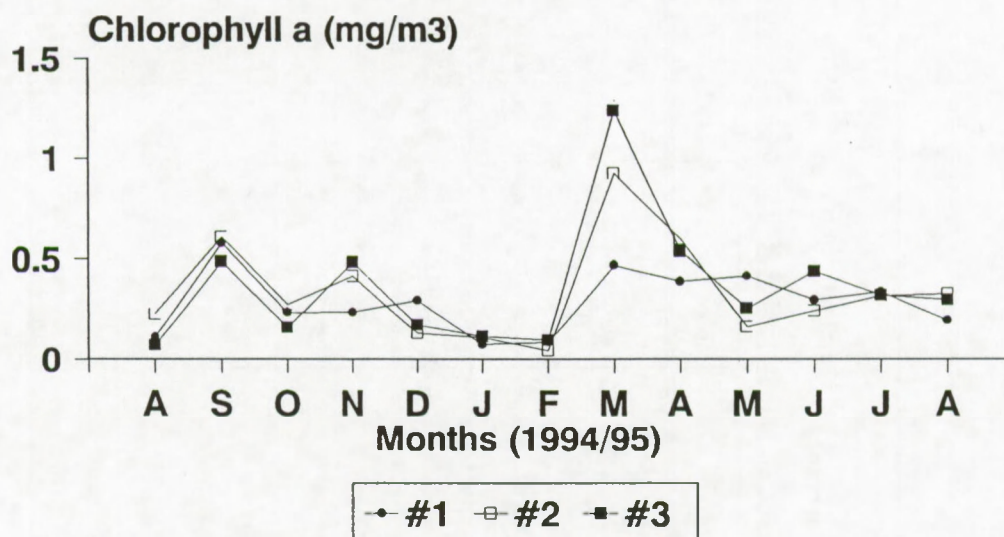


Figure 4 - Chlorophyll *a* fluctuations over the annual cycle.

Zooplankton

Sedimentation biovolumes followed the global tendencies of the total organism number per cubic meter, in each zooplankton net. Biovolumes present a more biased estimation of zooplankton abundance, as reflecting non living matter and specially the presence of large jelly organisms as medusae and ctenophorans. In the 125 μm net highest abundance and biovolumes were reached during September, where biovolume had a maximum of nearly 20 ml/m^3 and abundance reached 400,000 organisms per cubic meter. On the other hand, in the samples from the 330 μm net, peak was reached just in November, where biovolume showed a maximum of approximately 17 ml/m^3 and abundance around 5,000 organisms per cubic meter. This last peak was reached at collecting station 3, at the entrance of Saco mangrove, and reflects a high abundance of brachyuran larval stages in the water mass. On the other hand, the peak of the 125 μm net reflects abundance of larval stages of molluscs.

The organisms collected by the 125 μm net are mainly herbivorous species, which could be expected to match the peaks of phytoplankton. It seems that the chlorophyll peak of early warm season from September to November, has a better response in the trophic chains

than the highest values during March, where abundance of zooplankton was not very high. However, and for the 330 μm net, the high values of density of November were observed only at one collecting station, and as mainly formed by larval brachyurans, not necessarily due to planktonic stimuli but to cues for larval releasing factors.

Globally, results suggest that a favorable period occurs from September to November, where temperature raises and phytoplankton grows, and a second period of planktonic abundance occurs by March, where phytoplankton grows due to nutrient accumulation. However, it is not possible to say if this is the common tendency in the area, as theses results represent only one annual cycle. It was a draft period in the area, and most likely the planktonic environment in the Maputo bay will reflect the particular hydrological conditions in each moment.

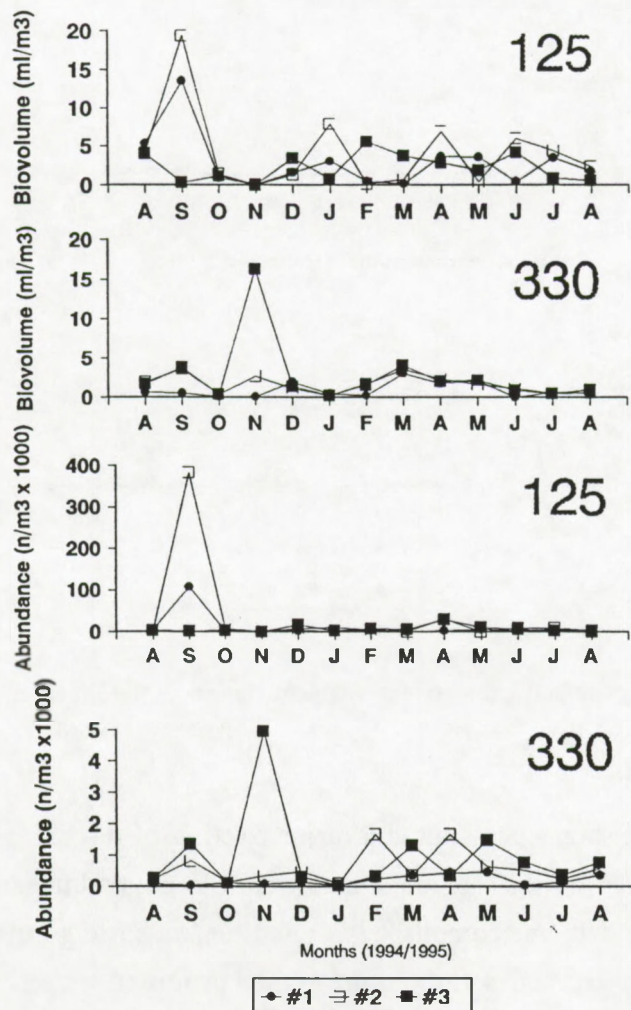


Figure 5 - Zooplankton biovolumes and densities over the annual cycle, for both nets used (125 and 330 μm of pore aperture).

Analysing the abundance fluctuations of the larval stages of molluscs, it is interesting to observe that bivalves have their maximum in April following the chlorophyll peak. These organisms were more abundant at stations 2 and 3, which are placed close to the major oyster banks around Inhaca island. Unfortunately, larval stages of this group are very difficult to identify, and further research is needed before ascribing these larvae to adults. Gastropod larvae, the most abundant organisms of the zooplankton, reached highest densities in September with nearly 350,000 individuals per cubic meter. It is practically impossible to identify these forms, due to the state of knowledge and given their diversity in the area.

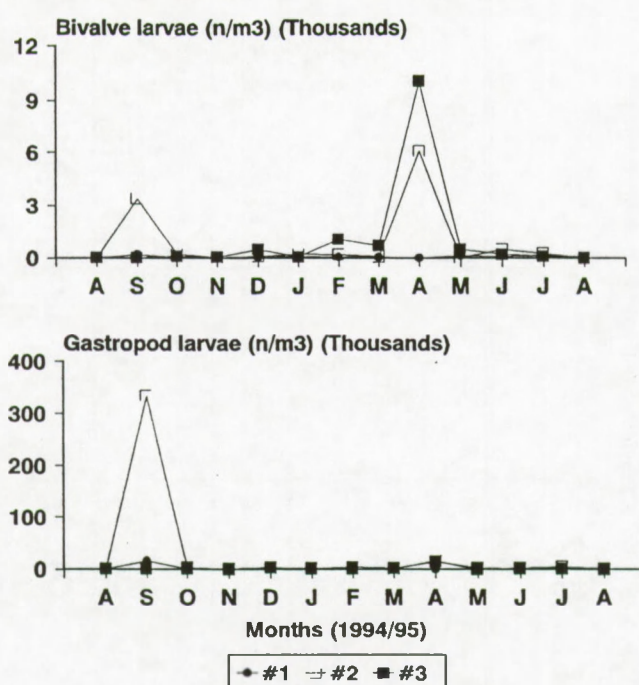


Figure 6 - Bivalve and gastropod larvae fluctuations over the annual cycle (125 μ m net).

Decapod larval stages constituted a major fraction of the organisms collected with the 330 μ m net. Brachyuran newly hatched stages were the most abundant forms. The complete analysis of these forms will be accomplished in due time, as sorting out from plankton samples has just terminated, and larval descriptions are in final progress.

Larvae of the Brachyura showed their maximum of abundance in September and November, at station 3 placed at the entrance of Saco mangrove. This suggests that this period constitute the peak of reproductive output for mangrove crabs. Other decapod larvae, mainly shrimps and pagurids, were more abundant by May, also at station 3.

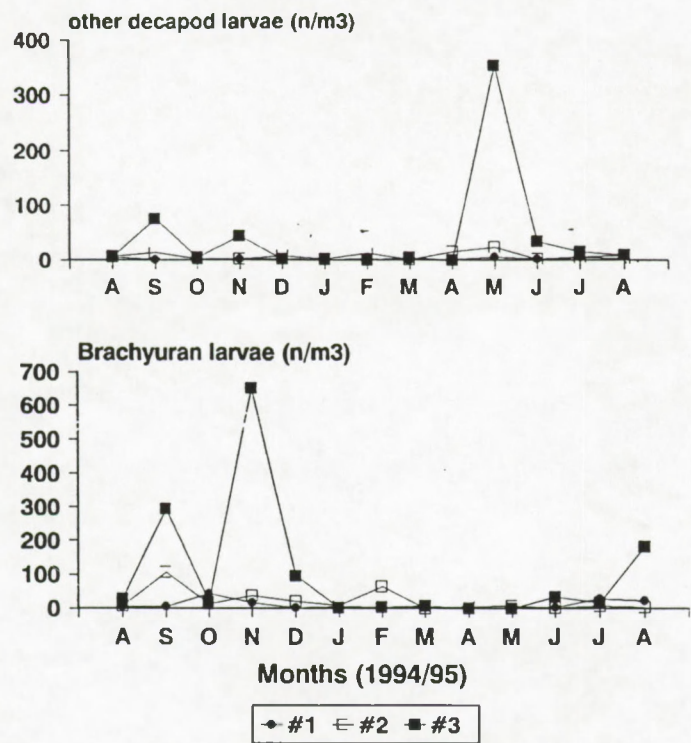


Figure 7 - Brachyuran and other decapod larvae fluctuations over the annual cycle (330 μ m net).

The results of the annual cycle of planktonic communities at Inhaca island support the subtropical conditions of Maputo bay, with a marked seasonality of sampled parameters. During the Summer months nutrients accumulated in the bay, inducing a maximum of chlorophyll *a* by March. A second period of phytoplankton growth seems to occur by September, when temperature begins to raise in the bay. Zooplankton abundance is higher during this period, although reflecting peaks of larval release by molluscs and crustaceans.

FISHES OF THE SEAGRASS BEDS OF THE INHACA ISLAND (MOZAMBIQUE) - COMMUNITY STRUCTURE AND DYNAMIC

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Two sampling areas were chosen in order to study the structure and dynamic of the fish fauna associated with seagrass beds of *Thalassodendro ciliatum* / *Cymodocea serrulata* at Inhaca island (Mozambique). The stations were all located in areas of high densities of seagrass and submitted to exploitation by local population. The thirty six samples show that three species (*Paramonocanthus barnardi*, *Siganus sutor* and *Pelates quadrilineatus*) are resident species at the two samplings areas. The fish fauna associated with seagrass are essentially composed by young fishes

Material and methods

Material was collected through twelve samplings operations carried out in June 1993 to July 1994 in two stations located in areas of *Thalassodendro ciliatum* / *Cymodocea serrulata* association (fig 1). Sampling was performed during day time by means of a beam trawl net (rectangular mouth of 50x150 cm and 1 cm mesh aperture) towed during 10 minutes at a velocity of 1.5 knots. At station I sampling was carried out also during the night. The material was obtained at high tide at the first quarter of the moon phases in a total of thirth six samples.

The collected individuals were identified to the species level. Individuals of *Apogon nigripinnis*, *Leptoscarus vaigiensis* and *Siganus sutor* were measured to the nearest milimeter (total length), and weighted (total weight). The weight of stomach contents were also determined. The stomach content was preserved in 10 % formalin for posterior analysis.

Results

The thirty six samples supplied 5922 individuals representing 66 species from 30 families (Table I, II, and III)

In these samples the Families Labridae (with 7 species), Lethrinidae (with 6 species), Scorpaenidae (with 5 species) and Syngnathidae (with 4 species) were the best represented in number of species.

Station I (Estação de Biologia Marinha)

Diurnal samples

The twelve day samples show that seven species could be considered as resident (frequency of capture ≥ 75 %) (species in bold at the tables), nine species as transitive (frequency of capture > 25 % - 75 % $<$) and the other twenty six species as occasional (frequency of capture ≤ 25 %) (Table I).

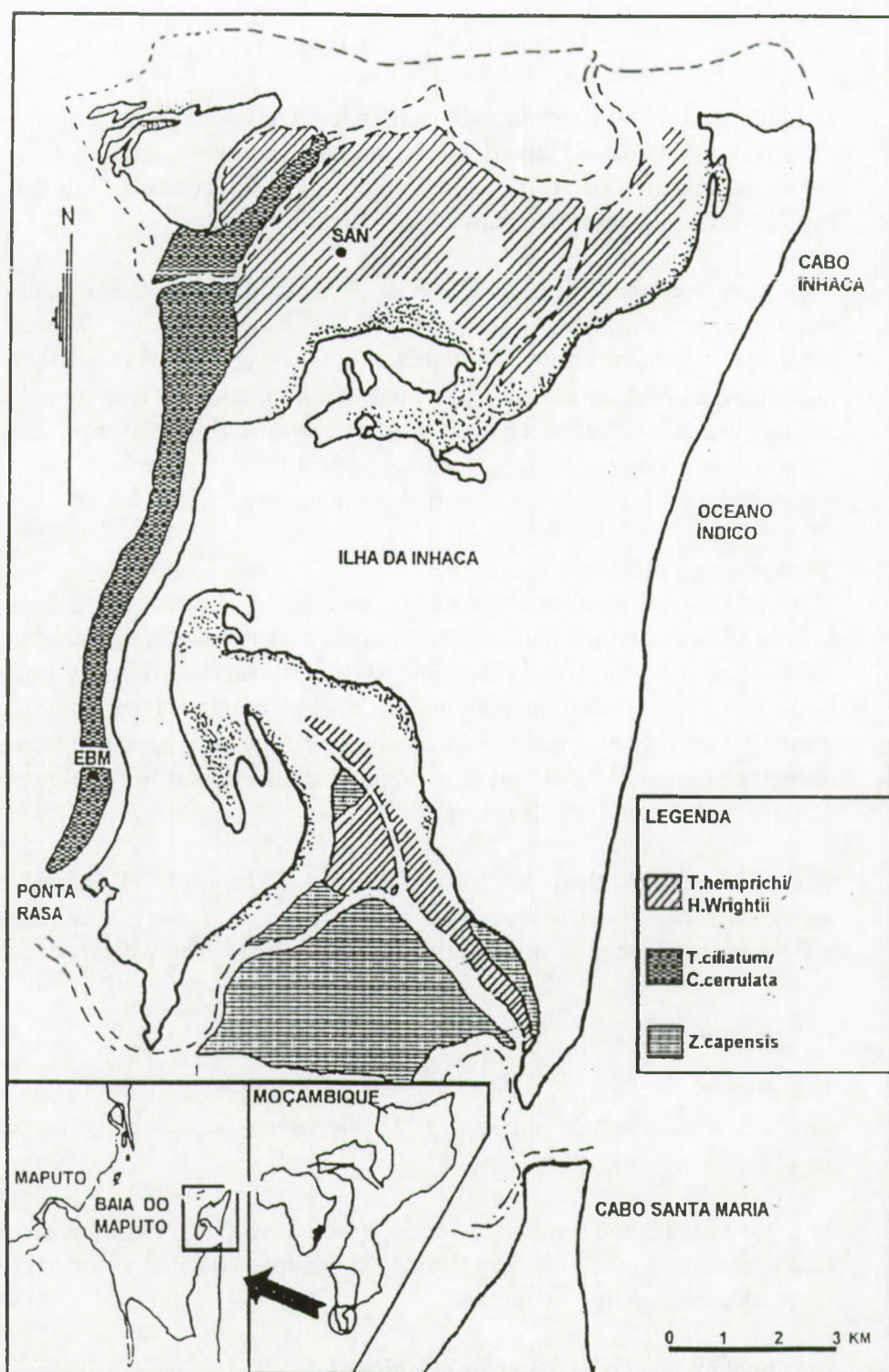


Fig 1 - Sampling areas.:

EBM - Estação de Biologia Marinha - Station I

SAN - Banco da Sangala - Station II

Table I

Station I (First quarter of moon)	BM	BM	BM	BM	BM	BM	BM	BM	BM	BM	BM	BM	% F
Diurnal samples	D	D	D	D	D	D	D	D	D	D	D	D	
Month	7	8	9	10	11	12	1	2	3	4	6	7	
	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	
<i>Apogon nitidus</i>				1									8.33
<i>Apogon cooki</i>			3	1	1		41		4	2		1	58.33
<i>Apogon nigripinnis</i>	1	13	19	24	13	2	21	6	30	20	1	1	100.00
<i>Archamia mozambiquensis</i>		1											8.33
<i>Petroscirtes breviceps</i>		1		2		3		3		1	1	1	58.33
<i>Aeoliscus punctulatus</i>	1		5	4	9		11		10	2	3		66.67
<i>Chaetodon auriga</i>				1						1			16.67
<i>Lophodiodon calori</i>			3	4	6		1					2	41.67
<i>Cheilio inermes</i>		1	2	3					1	1			41.67
<i>Novaculichthys macrolepidopus</i>	7				4	2	2			1	2		50.00
<i>Novaculichthys taeniourus</i>					1								8.33
<i>Pteragogus flagellifer</i>	2	1											16.67
<i>Stethojulis interrupta</i>	1	1	2		12	4	6		4	4	1		75.00
<i>Paracheilinus sp</i>				4	11								16.67
<i>Cirrhitilabrus exquesitus</i>				1									8.33
<i>Lethrinus lentjen</i>				2		2	3						25.00
<i>Lethrinus nebulosus</i>	1												8.33
<i>Lutjanus ehrembergi</i>											1		8.33
<i>Lutjanus fulviflamma</i>			2				1		4				25.00
<i>Paramonocanthus barnardi</i>	9	40	86	46	62	5	36		11	16	8	17	91.67
<i>Parupneus rubescens</i>					5			1	1		2	1	41.67
<i>Parupneus indicus</i>												2	8.33
<i>Upeneus tragula</i>						1							8.33
<i>Lactoria cornuta</i>					1								8.33
<i>Sorsogona prionata</i>	1	1							1				25.00
<i>Plotosus lineatus</i>								654					8.33
<i>Chrysiptera annulata</i>	2	1	5	3	6	1	6		8	18	2		83.33
<i>Pseudochromis natalensis</i>		1											8.33
<i>Calotomus spinidens</i>	3			1		1							25.00
<i>Leptoscarus vaigiensis</i>	1	1	2	2	5	3	3		2	2	1	2	91.67
<i>Scarus scaber</i>				1									8.33
<i>Dendrochirus brachypterus</i>						1							8.33
<i>Parascorpaena mossambica</i>	1		1							5	1	1	41.67
<i>Scorpaenodes guamensis</i>				1									8.33
<i>Sebastapistes strongia</i>						1							8.33
<i>Epinephelus rivulatus</i>				1									8.33
<i>Epinephelus septemfasciatus</i>				1									8.33
<i>Siganus sutor</i>	5	15	16	3	13	1	3	27	23	9	10	63	100.00
<i>Hippocampus camelopardalis</i>					1		1						16.67
<i>Syngnathoides biaculeatus</i>	3	1	1	1			2	2	2			1	66.67
<i>Saurida gracilis</i>	1												8.33
<i>Palates quadrilineatus</i>	23	5	2	6	9		2	72	8	7	2	43	91.67
<i>Arothron hispidus</i>													0.00
<i>Canthigaster solandri</i>										1		1	16.67
N° TOTAL OF INDIVIDUALS	62	83	149	113	159	27	139	765	109	90	35	136	1867
N° SPECIES	16	14	14	22	16	13	15	7	14	15	13	13	

The diurnal catch at station I (table I) was characterized by the presence of four species (excluding *Plotosus lineatus* because this species only appear in February and with a large number of individuals - 654, that explained the high total weight in this catch): *Paramonocanthus barnardi* (336 individuals - 27,7 % in numbers), *Apogon nigripinnis* (151 individuals - 12,5 % in numbers), *Siganus sutor* (188 individuals - 15,5 % in numbers) and *Pelates quadrilineatus* (179 individuals - 14,7 % in numbers).

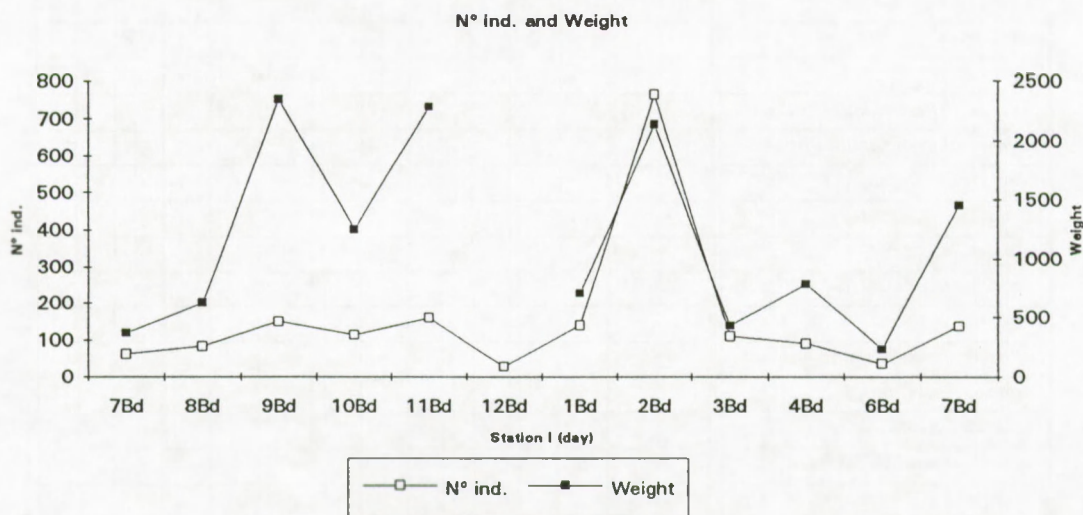


Fig 2 - Evolution of the number of individual (N°) and weight (g) along the 12 months at Station I (day samples)

At the Station I (day samples) the high values in February in the number of individuals and weight is due to the presence of 645 young *Plotosus lineatus* who represented 85 % of the total catch of that month and also responsible for the small values of the Shannon index, Equitability and Margalef's index (Fig. 3)

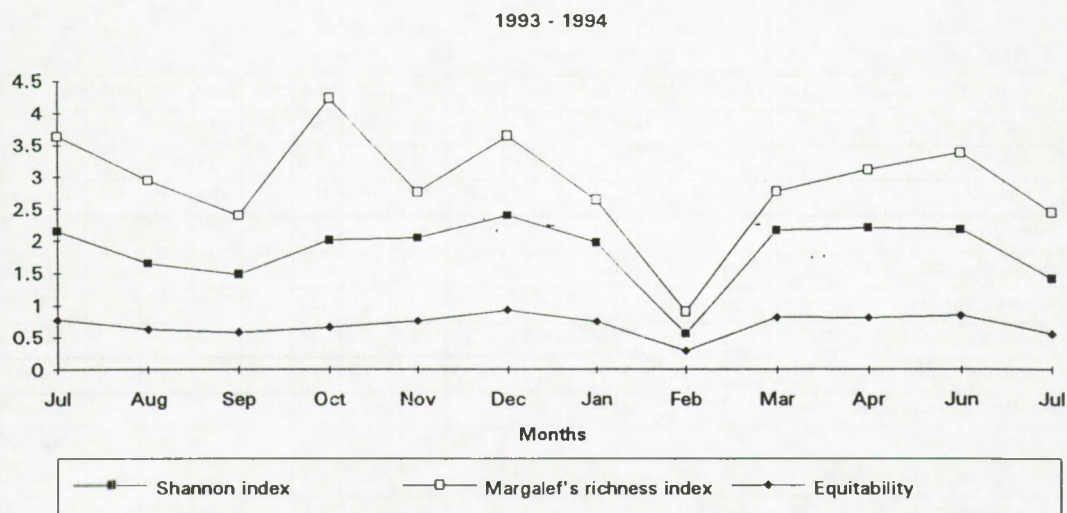


Fig. 3 - Month variation of the different index at Station I (day samples)

Station I (Estação de Biologia Marinha) Night samples

The twelve night samples show also seven resident species (some are different from the residents species of the day samples), eleven are transitive and twenty-six are occasional) (Table II).

The trawls made at night in Station I contributed with almost the double of individuals then the ones observed during the day at the same station (3220 -1867 respectively).

Thirteen species were caught only at night (*Ptarmus jubatus*, *Cynoglossus durbanensis*, *Cynoglossus lachneri*, *Pletorhinchus flavomaculatus*, *Lethrinus hypselopterus*, *Lethrinus rubrioperculatus*, *Lethrinus ramak*, *Stephanolepis auratus*, *Parupneus cinnabarinus*, *Plotosus nkunga*, *Crenidens crenidens*, *Trachyrhamphus bicoartatus* and *Arathron immaculatus*). (Table II).

In the night samples (Table II) the most important species in number were *Siganus sutor* (946 individuals - 29,4 %), *Pelates quadrilineatus* (692 individuals - 21,5 %), *Paramonocanthus barnardi* (374 individuals - 11,6 %) and *Apogon nigripinnis* (318 individuals - 9,9 %).

Only four species have the statute of resident at these two samples conditions (day and night) (*Apogon nigripinnis*, *Paramonocanthus barnardi*, *Siganus sutor* and *Pelates quadrilineatus*).

Table II

Station I (First quarter of moon)	BM	BM	BM	BM	BM	BM	BM	BM	BM	BM	BM	BM	% F
Night samples	N	N	N	N	N	N	N	N	N	N	N	N	
Month	7	8	9	10	11	12	1	2	3	4	6	7	
	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	
<i>Ptarmus jubatus</i>				2	-	1			-3		1		33.33
<i>Apogon nitidus</i>					1								8.33
<i>Apogon cooki</i>	16	4	4		8	1	36	21	31	4	61		83.33
<i>Apogon nigripinnis</i>	16	13	32	12	25	33	28	34	45	17	55	8	100.00
<i>Petrosirtes breviceps</i>	2	1		2	1	1	1		4			3	66.67
<i>Aeoliscus punctulatus</i>	4	12	5		3	2	2	3	10		30		75.00
<i>Chaetodon auriga</i>			1		1		1				2		33.33
<i>Cynoglossus durbanensis</i>				5									8.33
<i>Cynoglossus lachneri</i>	1												8.33
<i>Lophodiodon calori</i>					16		1	2			10		33.33
<i>Pterorhynchus flavomaculatus</i>	1		5		2						2		33.33
<i>Novaculichthys macrolepidopus</i>					8								8.33
<i>Pteragogus flagellifer</i>	1												8.33
<i>Stethojulis interrupta</i>					1								8.33
<i>Lethrinus hypselopterus</i>		3											8.33
<i>Lethrinus lentjen</i>	6	1			7								25.00
<i>Lethrinus rubrioperculatus</i>		1		1									16.67
<i>Lethrinus ramak</i>		1											8.33
<i>Lutjanus ehremergi</i>											4		8.33
<i>Lutjanus fulviflamma</i>	1		1			1		2	8				41.67
<i>Paramonocanthus barnardi</i>	22	3	105	6	47	18	20	3	80	5	62	3	100.00
<i>Stephanolepis auratus</i>											3		8.33
<i>Parupneus rubescens</i>						3	2	1			8		33.33
<i>Parupneus cinnabarinus</i>	1												8.33
<i>Parupneus indicus</i>					1		1				3		25.00
<i>Lactoria cornuta</i>						1	1						16.67
<i>Sorsogona prionata</i>	2			7		5							25.00
<i>Plotosus lineatus</i>	1		7		1			36	286		1		50.00
<i>Plotosus nkunga</i>	1												8.33
<i>Chrysiptera annulata</i>	4		2		4	1	1	5	18		7		66.67
<i>Calotomus spinidens</i>				1	1	6	1	1	1				50.00
<i>Leptoscarus vaigiensis</i>	5		14		3	1			5		9		50.00
<i>Parascorpaena mossambica</i>	2				3	1					1		33.33
<i>Epinephelus rivulatus</i>					1								8.33
<i>Siganus sutor</i>	8	86	19	275	12	158		58	166	9	150	5	91.67
<i>Crenidens crenidens</i>									1				8.33
<i>Hippocampus camelopardalis</i>			2										8.33
<i>Syngnathoides biaculeatus</i>	3	1	11		2	2	2	1	3		4		75.00
<i>Trachyrhamphus bicoartatus</i>							1						8.33
<i>Saurida gracilis</i>								6			2		16.67
<i>Peletes quadrilineatus</i>	38	27	42	48	27	32	15	65	235	65	88	10	100.00
<i>Arothron immaculatus</i>						1							8.33
<i>Canthigaster solandri</i>									1				8.33
N° TOTAL OF INDIVIDUALS	135	153	250	359	175	268	113	238	897	100	503	29	3220
N° SPECIES	20	12	14	10	22	18	15	14	16	5	20	5	

In December *Siganus sutor* with big individuals is the species responsible for 65 % of the total weight. And the pick observed at Marsh was caused by the presence of young *Plotosus lineatus* ,*Pelates quadrilineatus* and *Siganus sutor* (Fig. 4)

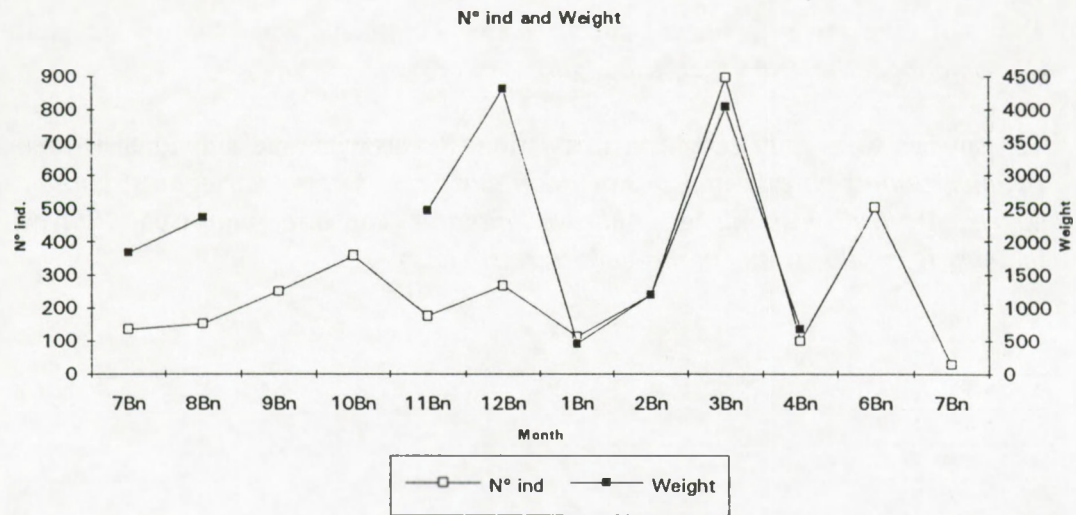


Fig 4 - Evolution of the number of individual (N°) and weight (g) along the 12 months at Station I (nigh samples)

The richness index of Margalef and the Shannon index have small values in April 95 because only 5 species were caught (Fig. 5)

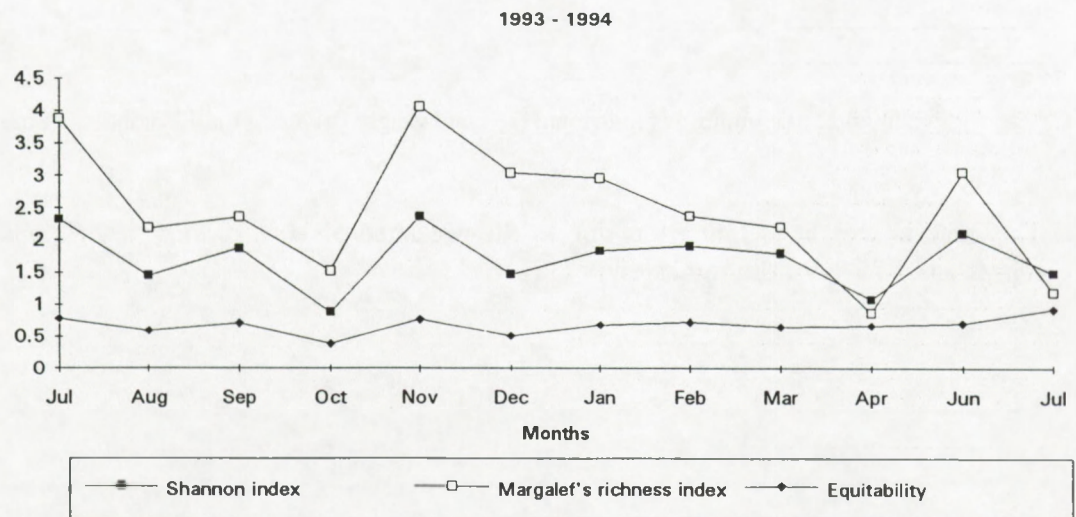


Fig. 5 - Month variation of the different index at Station I (night samples)

Station II (Banco da Sangala)

In Station II (table III) four species were dominant in numbers: *Pelates quadrilineatus* (124 individuals - 14,8 %), *Paramonocanthus barnardi* (124 individuals - 14,8 %), *Siganus sutor* (98 individuals - 11,7 %) and *Chrysiptera annulata* (77 individuals - 9,2 %).

Two of the five resident species are common with those of station I (*Paramonocanthus barnardi*, and *Siganus sutor*)

Ten species were only caught at this station. Seven with one individual (*Antennarius striatus*, *Bothus paratherinus*, *Chaetodon auriga*, *Lethrinus variegatus*, *Hippocampus histrix*, *Arothron hispidus* and *Ablabys binotatus*) and three with two (*Platycephalus indicus*, *Dascyllus trimaculatus* and *Pterois milas*).

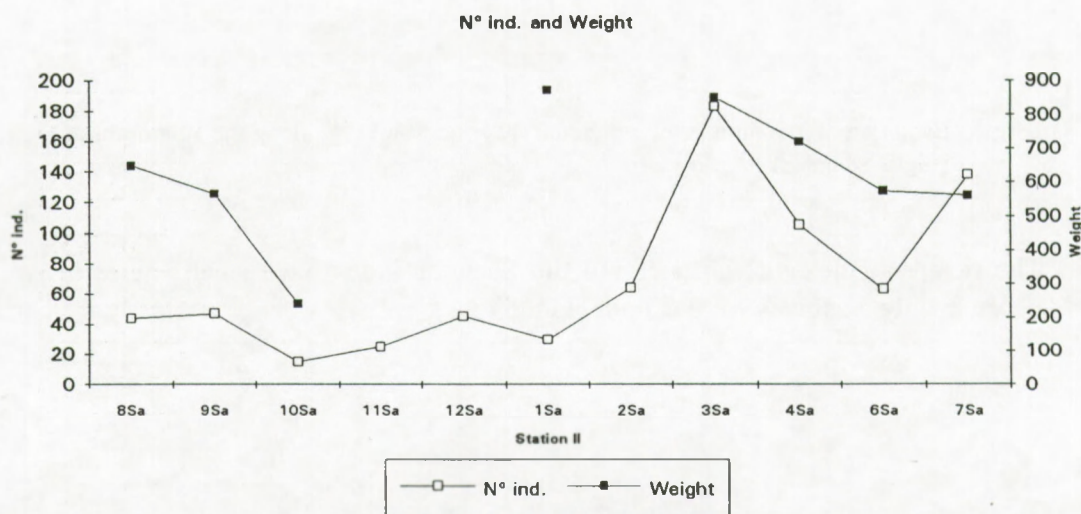


Fig 6 - Evolution of the number of individual (N°) and weight (g) along the 12 months at Station II

The peak in weight in January is due to the presence of 10 *Lutjanus fulviflamma* that represented 75 % of the total weight (Fig. 6).

Table III

Station II (first quarter of monn)	San	San	San	San	San	San	San	San	San	San	San	San	%F
Diurnal samples	D	D	D	D	D	D	D	D	D	D	D	D	
Month	7	8	9	10	11	12	1	2	3	4	6	7	
	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	N°	
<i>Antennarius striatus</i>	1												8.33
<i>Apogon cooki</i>										3			8.33
<i>Apogon nigripinnis</i>									7	9	1		25.00
<i>Petroscirtes breviceps</i>								1	6	2	3	3	41.67
<i>Bothus paratherinus</i>						1							8.33
<i>Aeoliscus punctulatus</i>	2		7		3	11					2		41.67
<i>Chaetodon auriga</i>	2	3	4								1		33.33
<i>Chaetodon vagabundus</i>			1										8.33
<i>Cynoglossus durbanensis</i>		1											8.33
<i>Cynoglossus lachneri</i>	1												8.33
<i>Lophodiodon calori</i>	1					3	2		3				33.33
<i>Cheilio inermes</i>		1	1					1			1	30	41.67
<i>Novaculichthys macrolepidopus</i>		4	1		3	1		1		2	4	1	66.67
<i>Pteragogus flagellifer</i>		3											8.33
<i>Stethojulis interrupta</i>	13	4					2	2		3	5	21	58.33
<i>Lethrinus lentjen</i>	7												8.33
<i>Lethrinus nebulosus</i>				1									8.33
<i>Lethrinus variegatus</i>	4												8.33
<i>Lutjanus ehrembergi</i>										4	2		16.67
<i>Lutjanus fulviflamma</i>	5						10		3				25.00
<i>Paramonocanthus barnardi</i>	13	7	10	3	9	18	9	11	8	3	20	13	100.00
<i>Stephanolepis auratus</i>			1										8.33
<i>Parupneus rubescens</i>												1	8.33
<i>Lactoria cornuta</i>						1		1				1	25.00
<i>Platycephalus indicus</i>	1							1					16.67
<i>Sorsogona prionata</i>						1							8.33
<i>Plotosus lineatus</i>	2	1									3		25.00
<i>Chrysiptera annulata</i>	1	1		1	1			7	42	17	3	4	75.00
<i>Dascyllus trimaculatus</i>		2		1									16.67
<i>Calotomus spinidens</i>	1	1	3				1	2					41.67
<i>Leptoscarus vaigiensis</i>	5	3	1	1		1	1		2	2	2	4	83.33
<i>Parascorpaena mossambica</i>			2			3							16.67
<i>Pterois miles</i>			1					1					16.67
<i>Siganus sutor</i>	8	10	12	3	5	1	1	10	6	4	9	29	100.00
<i>Hippocampus camelopardalis</i>		1					1						16.67
<i>Hippocampus histrix</i>	1												8.33
<i>Syngnathoides biaculeatus</i>	7	1	1	4	4	4	3	1			5	4	83.33
<i>Saurida gracilis</i>	1		1									3	25.00
<i>Pelates quadrilineatus</i>		1	1					25	106	55	1	22	58.33
<i>Arothron hispidus</i>				1									8.33
<i>Canthigaster solandri</i>										1	1	1	25.00
<i>Ablabys binotatus</i>												1	8.33
N° TOTAL OF INDIVIDUALS	76	44	47	15	25	45	30	64	183	105	63	138	835
N° SPECIES	19	16	15	8	6	11	9	13	9	12	16	15	

The month of March is the one who presented the small values for the different indexes (Fig. 7)

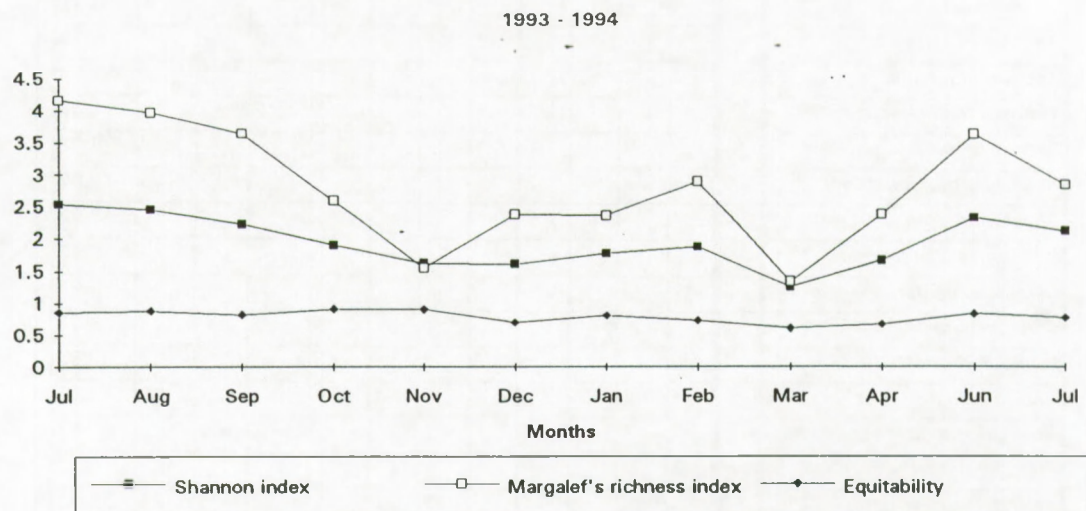


Fig. 7 - Month variation of the different index at Station II

Table IV resume the status of the 66 species at the different sample conditions.

Table IV

STation (first quarter of moon)	EBM/D	EBM/N	SAN
<i>Antennarius striatus</i>			O
<i>Ptarmus jubatus</i>		T	
<i>Apogon nitidus</i>	O	O	
<i>Apogon cooki</i>	T	R	O
<i>Apogon nigripinnis</i>	R	R	O
<i>Archamia mozambiquensis</i>	O		
<i>Petroscirtes breviceps</i>	T	T	T
<i>Lophodion colori</i>	T	O	O
<i>Bothus paratherinus</i>			O
<i>Aeoliscus punctulatus</i>	T	R	T
<i>Chaetodon auriga</i>	O	T	T
<i>Chaetodon vagabundus</i>			O
<i>Cynoglossus durbanensis</i>		O	O
<i>Cynoglossus lachneri</i>		O	O
<i>Lophodiodon calori</i>	O	O	O
<i>Pletorhinchus flavomaculatus</i>		T	
<i>Cheilio inermes</i>	T		T
<i>Novaculichthys macrolepidopus</i>	T	O	T
<i>Novaculichthys taeniourus</i>	O		
<i>Pteragogus flagellifer</i>	O	O	O
<i>Stethojulis interrupta</i>	R	O	T

<i>Paracheilinus</i> sp	O		
<i>Cirrhilabrus exquesitus</i>	O		
<i>Lethrinus hypselopterus</i>		O	
<i>Lethrinus lentjen</i>	O	O	O
<i>Lethrinus nebulosus</i>	O		O
<i>Lethrinus rubrioperculatus</i>		O	
<i>Lethrinus variegatus</i>			O
<i>Lethrinus ramak</i>	-	O	-
<i>Lutjanus ehrembergi</i>	O	O	O
<i>Lutjanus fulviflamma</i>	O	T	O
<i>Paramonocanthus barnardi</i>	R	R	R
<i>Stephanolepis auratus</i>		O	O
<i>Parupneus rubescens</i>	T	T	O
<i>Parupneus cinnabarinus</i>		O	
<i>Parupneus indicus</i>	O	O	
<i>Upeneus tragula</i>	O		
<i>Lactoria cornuta</i>	O	O	O
<i>Platycephalus indicus</i>			O
<i>Sorsogona prionata</i>	O	O	O
<i>Plotosus lineatus</i>	O	T	O
<i>Plotosus nkunga</i>		O	
<i>Chrysiptera annulata</i>	R	T	R
<i>Dascyllus trimaculatus</i>			O
<i>Pseudochromis natalensis</i>	O		
<i>Calotomus spinidens</i>	O	T	T
<i>Leptoscarus vaigiensis</i>	R	T	R
<i>Scarus scaber</i>	O		
<i>Dendrochirus brachypterus</i>	O		
<i>Parascorpaena mossambica</i>	T	T	O
<i>Scorpaenodes guamensis</i>	O		
<i>Pterois miles</i>			O
<i>Sebastapistes strongia</i>	O		
<i>Epinephelus rivulatus</i>	O	O	
<i>Epinephelus septemfasciatus</i>	O		
<i>Siganus sutor</i>	R	R	R
<i>Crenidens crenidens</i>		O	
<i>Hippocampus camelopardalis</i>	O	O	O
<i>Hippocampus histrix</i>			O
<i>Syngnathoides biaculeatus</i>	T	R	R
<i>Trachyrhamphus bicoartatus</i>		O	
<i>Saurida gracilis</i>	O	O	O
<i>Pelates quadrilineatus</i>	R	R	T
<i>Arothron immaculatus</i>		O	
<i>Arothron hispidus</i>			O
<i>Canthigaster solandri</i>	O	O	O
<i>Ablabys binotatus</i>			O
N° SPECIES	44	44	43

The distribution of the most abundant species is different in Station I and II and also between diurnal and night samples (fig 8).

Apogon nigripinnis is always present at station I (Estação de Biologia Marinha) but only in March, April and June at station II (Banco da Sangala) with few individuals (fig 8a)

Paramonocanthus barnardi is not very abundant at station II but in some samples it is more abundant than the diurnal samples of the station I (fig 8b).

Plotosus lineatus shows a very interesting distribution with a high number of juveniles in February / March at Station I. (fig 8c).

Apogon cooki is one of the most important species at night at station I (fig. 8d).

Siganus sutor presented a distribution very irregular varying from low to high density at successive months (fig 8e).

Pelates quadrilineatus seems to be more abundant in February/March/April at the two stations (fig 8f).

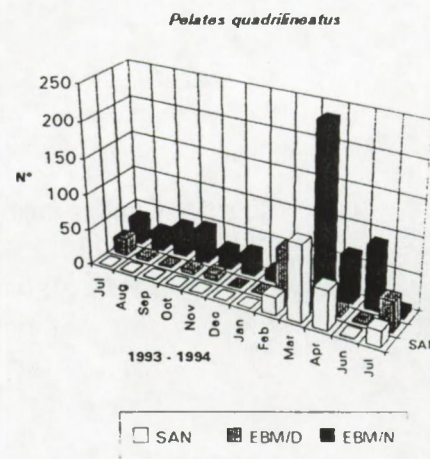
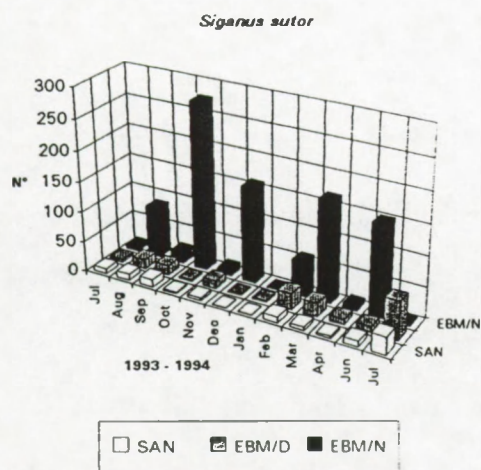
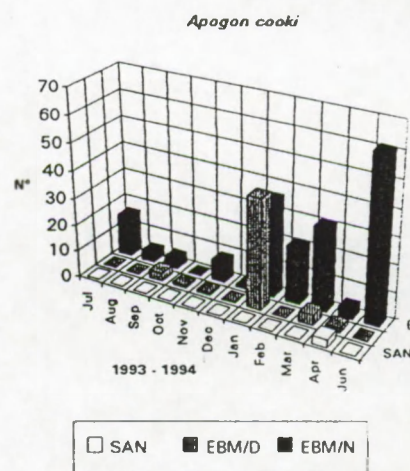
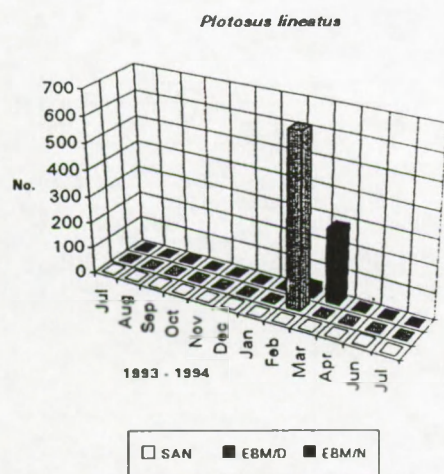
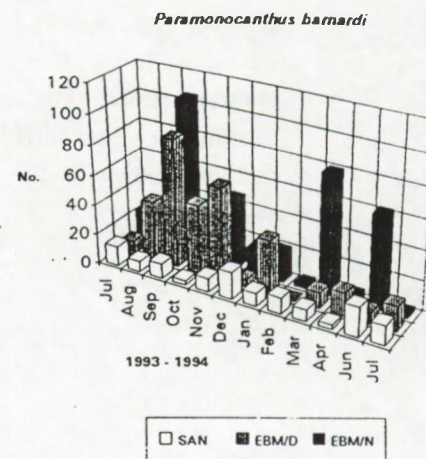
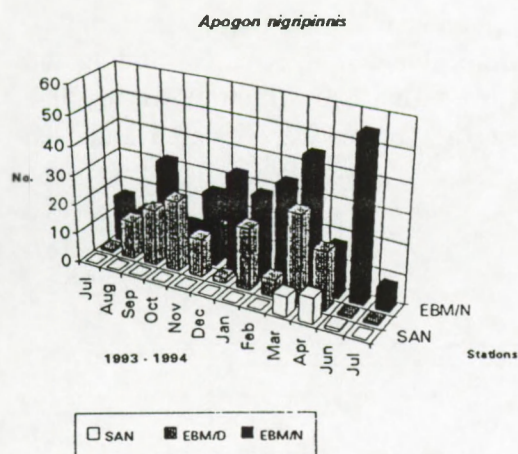


Fig 8 - Distribution of the most abundant species at Station I (Estação de Biologia Marinha) and Station II (Banco da Sangala)

SAN - Banco da Sangala

EBM/D - Estação de Biologia Marinha - diurnal samples

EBM/N - Estação de Biologia Marinha - night samples

Cluster analysis and analysis of factorial correspondence of the thirty six samples, based in the number of individuals of the 44 more abundant species (excluding the species represented by only one individual, showed that the structure of the fish community was different at the two areas where the station were located and also during the day and the night (Fig. 9).

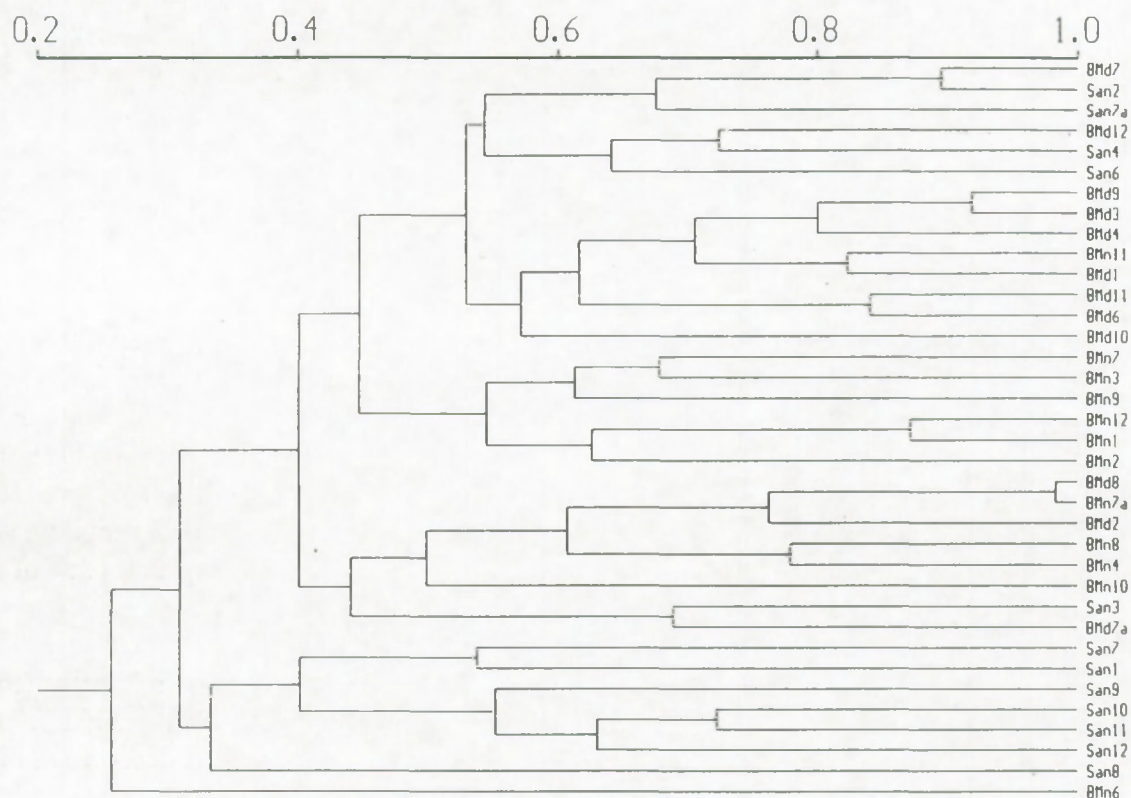


Fig 9 - Cluster analysis of the different fish samples collected at Inhaca island since July 1993 until July 1994.

BMd - Station I (Estação de Biologia Marinha) day samples

BMn - Station I (Estação de Biologia Marinha) night samples

San - Station II (Banco da Sangala)

The numbers indicate the month of the sample (7a - represents July 1994)

FISHES OF THE SEAGRASS BEDS OF THE INHACA ISLAND (MOZAMBIQUE) - COLD SEASON

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Three sampling areas were chosen in order to study the fish fauna associated with seagrass beds of *Thalassodendro ciliatum* / *Cymodocea serrulata* and *Thalassia hemprichii* / *Halodule wrightii*.

The stations were all located in areas of high densities of seagrass and subjected to exploitation by local population.

Material and methods

Material was collected during June- August, 1993 in three stations located in areas of different seagrass beds associations (Fig. 1). Station I and II were located in areas of *Thalassodendro ciliatum* / *Cymodocea serrulata* association while Station III in an area of *Thalassia hemprichii* / *Halodule wrightii*. Sampling was performed during day time by means of a beam trawl net (rectangular mouth of 50x150 cm and 1 cm mesh aperture) towed during 10 minutes at a velocity of 1.5 knots. At station I sampling was also carried out during the night. The material was obtained at high tide on each of the moon phases in a total of sixteen trawls.

The collected individuals were identified and measured to the nearest millimeter (total length), and weighted to the nearest miligram (total weight). The weight of the gonads as well as of the liver and of the stomach contents were also determined. The stomachal content was preserved for posterior analysis.

Results

The sixteen samples supplied 1290 individuals representing 65 species from 33 families (Table I, II, III and IV). Families Labridae (with 5 species), Scorpaenidae (with 4 species) and Syngnathidae (with 4 species) were the best represented in number of species.

The three stations had 14 species in common. Seventeen species were exclusive of the Saco station (station III), while seven species appear solely at the Banco da Sangala station (station II) and only one was exclusive of the Estação de Biologia Marinha station (station I)

The trawls made at night in station I contributed with the double of individuals then the ones observed during the day at the same station. Eleven species were caught only at night.

The diurnal catch at station I (table I) was characterized by the presence of two species: *Paramonocanthus barnardi* (51 individuals - 22,1 % in numbers

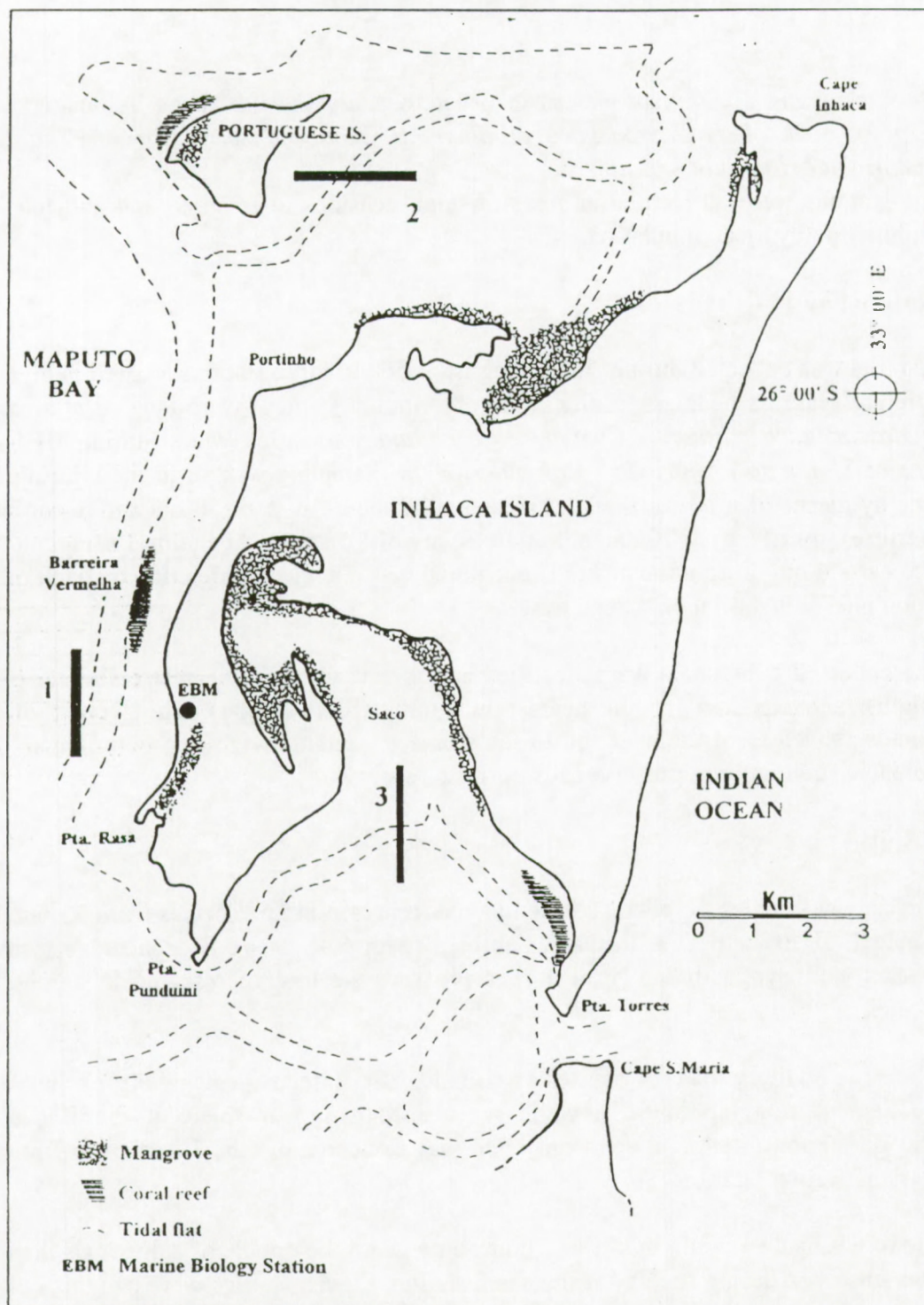


Fig 1 - Sampling areas:

- 1- Estação de Biologia Marinha - Station I
- 2 - Banco da Sangala - Station II
- 3 - Saco da Inhaca - Station III

corresponding to 360,41 g - 17 % of the biomass) and *Apogon nigripinnis* (32 individuals - 13,8 % in numbers corresponding to 422,81 g - 19,9 % of the biomass). *Aeoliscus punctulatus* is an important species in term of numbers (16,4 %) but represents only 4,5 % of the biomass. On the other end *Leptoscarus vaigiensis* is an important in term of biomass (26 %) but irrelevant in numeri terms (3,9 %).

	Estação de Biologia Marinha (Day)								Ind/sp	Biom/sp
	11.7.93 C		20.7.92 O		27.7.93		2.8.93 O			
	N	B	N	B	N	B	N	B		
<i>Ptamus jubatus</i>	0	0	0	0	0	0	1	3,18	1	3,18
<i>Apogon cooki</i>	0	0	1	5,87	0	0	2	15,6	3	21,47
<i>Apogon nigripinnis</i>	0	0	15	170,36	1	15,89	16	236,56	32	422,81
<i>Petroscirtes breviceps</i>	0	0	0	0	1	3,24	1	7,46	2	10,7
<i>Aeoliscus punctulatus</i>	5	12,21	14	46,22	7	22,87	12	12,71	38	94,01
<i>Novaculichthys macrolepidopus</i>	0	0	0	0	2	13,33	1	12,83	3	26,16
<i>Pteragogus flagellifer</i>	0	0	5	35,46	0	0	1	12,82	6	48,28
<i>Stethojulis interrupta</i>	1	5,3	0	0	1	1,88	2	8,18	4	15,36
<i>Lethrinus lentjan</i>	2	24,42	0	0	0	0	0	0	2	24,42
<i>Lethrinus nebulosus</i>	0	0	1	8,56	1	14,22	1	9,65	3	32,43
<i>Cantherrhines fronticinctus</i>	0	0	1	33,21	0	0	0	0	1	33,21
<i>Paramonocanthus barnardi</i>	7	54,78	21	155,88	9	52,8	14	96,95	51	360,41
<i>Parupeneus indicus</i>	0	0	0	0	0	0	1	14,38	1	14,38
<i>Sorsogona prionata</i>	1	27,98	0	0	1	12,51	0	0	2	40,49
<i>Chrysiptera annulata</i>	1	3,71	5	21,55	2	9,73	0	0	8	34,99
<i>Stegastes fasciolatus</i>	0	0	0	0	0	0	2	28,08	2	28,08
<i>Calotomus spinidens</i>	0	0	1	32,22	3	51,84	1	38,51	5	122,57
<i>Leptoscarus vaigiensis</i>	0	0	2	62,55	1	1,04	6	489,41	9	553
<i>Parascorpaena mossambica</i>	0	0	2	43,21	1	23,25	1	24,69	4	91,15
<i>Siganus sutor</i>	0	0	2	11,89	5	21,79	2	18,07	9	51,75
<i>Hippocampus camelopardalis</i>	0	0	2	7,02	0	0	0	0	2	7,02
<i>Syngnathoides biaculeatus</i>	4	25,67	1	7,31	3	10,89	2	12,97	10	56,84
<i>Saurida gracilis</i>	0	0	0	0	1	28,26	0	0	1	28,26
<i>Pelates quadrilineatus</i>	1	6,07	6	48,4	23	83,97	1	4,57	31	143,01
<i>Canthigaster solandri</i>	0	0	0	0	0	0	1	2,66	1	2,66
TOTAL	22	160,1	79	689,71	62	367,51	68	1049,3	231	2123,63

Table I - List of species obtained during the day at station I. N - number of individuals, B - biomass (g).

In the night samples (Table II) the most important species were *Siganus sutor* (17,8 % in numbers corresponding to 18,6 % in biomass), *Pelates quadrilineatus* (21 % in numbers corresponding to 11,4 % in biomass), *Paramonocanthus barnardi* (16,1 % in numbers corresponding to 8 % in biomass) and *Apogon nigripinnis* (10,1 % in numbers corresponding to 9,5 % in biomass). Biomass of *Leptoscarus vaigiensis* represented 23,5 %, being an important species in terms of biomass.

Five species were captured in this station only at night: *Parupneus cinnabarinus*, *Plotosus nkunga*, *Scorpaenodes littoralis*, *Epinephelus andersoni* and a juvenil of *Sphyrna sp.* (only one individual of each species were captured).

	Estação de Biologia Marinha (night)								Ind/sp	Biom/sp
	10.07.93 C		18.07.93 O		26.07.93		3.08.93 O			
	N°	B	N°	B	N°	B	N°	B		
<i>Ptamus jubatus</i>	5	14,41	0	0	0	0	0	0	5	14,41
<i>Apogon cooki</i>	7	48,02	4	38,68	16	136,3	2	19,85	29	242,88
<i>Apogon nigripinnis</i>	30	350,1	8	88,72	16	169,3	3	43,6	57	651,72
<i>Petroscirtes breviceps</i>	2	71,82	0	0	2	7,12	0	0	4	78,94
<i>Aeoliscus punctulatus</i>	0	0	5	13,96	4	14,04	0	0	9	28
<i>Cynoglossus lachneri</i>	11	140,8	1	15,45	1	18,08	0	0	13	174,3
<i>Pterorhinchus flavomaculatus</i>	2	71,56	0	0	1	22,35	0	0	3	93,91
<i>Pteragogus flagellifer</i>	1	21,75	10	145	1	1,14	0	0	12	167,89
<i>Lethrinus lentjan</i>	6	39,89	7	70,8	6	64,1	1	6,9	20	181,69
<i>Lethrinus variegatus</i>	0	0	3	11,09	0	0	0	0	3	11,09
<i>Lutjanus fulvivittatus</i>	3	46,82	3	75,25	1	16,84	0	0	7	138,91
<i>Paramonocanthus barnardi</i>	26	119,7	38	293	22	136,7	0	0	86	549,36
<i>Parupneus cinnabarinus</i>	0	0	0	0	1	6,27	0	0	1	6,27
<i>Parupneus indicus</i>	0	0	2	114,4	0	0	0	0	2	114,35
<i>Upeneus tragula</i>	0	0	1	12,79	0	0	0	0	1	12,79
<i>Lactoria diaphana</i>	1	7,52	0	0	0	0	0	0	1	7,52
<i>Sorsogona prionata</i>	6	52,4	2	43,65	2	34,36	1	7,11	11	137,52
<i>Plotosus lineatus</i>	2	22,74	4	50,42	1	19,81	0	0	7	92,97
<i>Plotosus nkunga</i>	0	0	0	0	1	22,82	0	0	1	22,82
<i>Chrysiptera annulata</i>	2	7,5	1	4,7	4	19,81	0	0	7	32,01
<i>Calotomus spinidens</i>	8	19,33	1	28,77	0	0	1	39,88	10	87,98
<i>Leptoscarus vaigiensis</i>	3	217,6	10	700,6	5	695,8	0	0	18	1614,08
<i>Scarus tricolor</i>	1	13,05	0	0	0	0	0	0	1	13,05
<i>Parascorpaena mossambica</i>	2	30,46	1	35,17	2	47,56	0	0	5	113,19
<i>Scorpaenodes littoralis</i>	1	2,72	0	0	0	0	0	0	1	2,72
<i>Epinephelus andersoni</i>	0	0	1	170	0	0	0	0	1	170
<i>Siganus sutor</i>	55	417,8	14	403,5	8	139,5	18	315,9	95	1276,7
<i>Sphyræna sp.</i>	1	0,24	0	0	0	0	0	0	1	0,24
<i>Hippocampus camelopardalis</i>	1	0,84	0	0	0	0	0	0	1	0,84
<i>Syngnathoides biaculeatus</i>	2	5,97	2	15,43	3	19,68	1	7,38	8	48,46
<i>Pelates quadrilineatus</i>	21	97,01	43	327,1	38	285,2	10	75,53	112	784,76
<i>Canthigaster solandri</i>	0	0	1	4,67	0	0	0	0	1	4,67
TOTAL	199	1820	162	2663	135	1877	37	516,1	533	6876,04

Table II - List of species obtained during the night at Station I. N - number of individuals, B - biomass (g).

In Station II (table III) two species were dominant in numbers and biomass: *Paramonocanthus barnardi* and *Siganus sutor*. At this station it was verified that *Leptoscarus vaigiensis* was dominant in biomass (14,5 %). Only five species were captured at this station: *Antennarius pictus*, *Hippocampus histrix*, *Hippocampus kuda*, *Arothron imaculatus* (with one individual each) and *Lophodiondon calori* (with two individuals).

	Banco da Sangala								Ind/sp	Biom/sp
	12.7.93 G		18.7.93 O		28.7.93		31.7.93 O			
	Nº	B	Nº	B	Nº	B	Nº	B		
<i>Antennarius pictus</i>	0	0	0	0	1	122	0	0	1	122
<i>Apogon nigrispinnis</i>	0	0	2	23,7	0	0	0	0	2	23,7
<i>Aeoliscus punctulatus</i>	0	0	2	5,94	2	6	5	17,71	9	29,65
<i>Chaetodon auriga</i>	0	0	0	0	2	6	2	9,46	4	15,46
<i>Cynoglossus lachneri</i>	0	0	0	0	1	17,73	0	0	1	17,73
<i>Lophodiodon calori</i>	0	0	0	0	1	13,48	1	35,94	2	49,42
<i>Pterorhynchus flavomaculatus</i>	0	0	1	11,89	0	0	0	0	1	11,89
<i>Chellio inermes</i>	0	0	1	150	0	0	0	0	1	150
<i>Novaculichthys macrolepidopus</i>	0	0	12	213,33	0	0	0	0	12	213,33
<i>Pteragogus flagellifer</i>	0	0	9	23,98	0	0	1	25,55	10	49,53
<i>Stethojulis interrupta</i>	1	3,06	0	0	13	45,89	0	0	14	48,95
<i>Lethrinus hypselopterus</i>	0	0	1	14,25	7	83,61	0	0	8	97,86
<i>Lethrinus rubrioperculatus</i>	0	0	0	0	4	13,93	0	0	4	13,93
<i>Lutjanus fulviflamma</i>	0	0	0	0	5	98	0	0	5	98
<i>Paramonocanthus barnardi</i>	3	10,19	39	323,18	13	97,47	25	255,42	80	686,26
<i>Lactoria comuta</i>	0	0	0	0	0	0	1	25,99	1	25,99
<i>Papilloculiceps longiceps</i>	0	0	1	126	0	0	0	0	1	126
<i>Platycephalus indicus</i>	0	0	0	0	1	245	0	0	1	245
<i>Sorsogona prionata</i>	0	0	1	18,72	0	0	2	70,93	3	89,65
<i>Plotosus lineatus</i>	0	0	0	0	2	161,24	0	0	2	161,24
<i>Chrysiptera annulata</i>	1	10,19	1	3,69	1	3,71	1	1,89	4	19,48
<i>Calotomus spinidens</i>	0	0	1	20,54	1	28,6	4	88,95	6	138,09
<i>Leptoscarus vaigiensis</i>	3	93	9	254,78	5	156,03	1	32,78	18	536,59
<i>Scarus tricolor</i>	0	0	0	0	0	0	1	19,1	1	19,1
<i>Parascorpaena mossambica</i>	0	0	1	25,19	0	0	0	0	1	25,19
<i>Scorpaenopsis gibbosa</i>	0	0	1	8,51	0	0	0	0	1	8,51
<i>Siganus sutor</i>	2	59,31	15	222,12	8	118,28	5	81,01	30	480,72
<i>Hippocampus camelopardalis</i>	0	0	6	29,01	0	0	0	0	6	29,01
<i>Hippocampus histrix</i>	0	0	0	0	1	2,67	0	0	1	2,67
<i>Hippocampus Kuda</i>	0	0	1	9,48	0	0	0	0	1	9,48
<i>Syngnathoides biaculeatus</i>	1	13,37	0	0	7	61,83	6	45,79	14	120,99
<i>Saurida gracilis</i>	0	0	0	0	1	24,24	0	0	1	24,24
<i>Pelates quadrilineatus</i>	4	23,82	1	12,76	0	0	1	34,04	6	70,62
<i>Arothron immaculatus</i>	1	18,2	0	0	0	0	0	0	1	18,2
<i>Ablabys binotatus</i>	0	0	0	0	0	0	3	74,42	3	74,42
TOTAL	16	231,14	105	1497,1	76	1305,7	59	818,98	256	3852,9

Table III - List of species obtained station II. N - number of individuals, B - biomass (g).

Station III (Table IV) was characterized by the presence of 13 species that were not present at the other stations. The species were: *Foa brachygramma*, *Nemipterus bipunctatus*, *Amblygobius sphynx*, *Bothus pantherinus*, *Pseudorhombus arsius*, *Cynoglossus durbanensis*, *Amblygobius albimaculatus*, *Vanderhostia delagoae*, *Parapercis xanthosoma*, *Papilloculiceps longiceps*, *Dascyllus trimaculatus*, *Epinephelus guaza* and *Solea bleekeri*.

	Saco da Inhaca								Ind/sp	Biom/sp
	10.7.93 G		17.7.93 O		25.7.93		31.7.93 O			
	N	B	N	B	N	B	N	B		
<i>Apogon nigrifinnis</i>	5	69,06	0	0	4	55,31	0	0	9	124,37
<i>Foa brachygramma</i>	16	32,8	11	18,71	24	33,71	13	24,17	64	109,39
<i>Petroscirtes breviceps</i>	3	23,06	3	17,14	1	10,74	0	0	7	50,94
<i>Bothus paratherinus</i>	1	0,63	0	0	0	0	0	0	1	0,63
<i>Pseudorhombus arsius</i>	1	96	0	0	0	0	0	0	1	96
<i>Aeoliscus punctulatus</i>	0	0	3	11,41	0	0	0	0	3	11,41
<i>Chaetodon auriga</i>	0	0	0	0	3	22,41	0	0	3	22,41
<i>Cynoglossus durbanensis</i>	1	27,71	0	0	0	0	0	0	1	27,71
<i>Amblygobius albimaculatus</i>	0	0	0	0	1	31,28	0	0	1	31,28
<i>Amblygobius sphynx</i>	2	145,93	0	0	0	0	1	16,53	3	162,46
<i>Vanderhorstia delagoae</i>	1	-	0	0	0	0	0	0	1	-
<i>Pterorhynchus flavomaculatus</i>	0	0	0	0	1	23,94	0	0	1	23,94
<i>Chellio inermes</i>	0	0	0	0	0	0	1	86,74	1	86,74
<i>Pteragogus flagellifer</i>	0	0	0	0	3	37,07	0	0	3	37,07
<i>Stethojulis interrupta</i>	1	3,52	1	2,33	3	6,52	3	11,93	8	24,3
<i>Stethojulis strigiventer</i>	1	3,44	0	0	0	0	0	0	1	3,44
<i>Lethrinus lentjan</i>	11	69,59	2	10,57	2	5,35	7	23,6	22	109,11
<i>Lethrinus nebulosus</i>	0	0	1	12,62	0	0	2	15,77	3	28,39
<i>Lethrinus variegatus</i>	1	7,01	0	0	3	13,6	6	11,77	10	32,38
<i>Lutjanus fulvivlamma</i>	2	25,78	0	0	0	0	1	22,7	3	48,48
<i>Paramonocanthus barnardi</i>	1	6,44	0	0	1	9,56	0	0	2	16
<i>Parapercis xanthozona</i>	1	19,6	0	0	0	0	0	0	1	19,6
<i>Parupeneus indicus</i>	0	0	0	0	1	2,96	0	0	1	2,96
<i>Nemipterus bipuntatus</i>	13	-	0	0	0	0	0	0	13	-
<i>Papilloculiceps longiceps</i>	1	98	0	0	0	0	0	0	1	98
<i>Platycephalus indicus</i>	2	328,6	1	57,48	0	0	0	0	3	386,08
<i>Sorsogona prionata</i>	6	75,75	2	106,33	3	80,34	5	86,05	16	348,47
<i>Plotosus lineatus</i>	12	2,2	0	0	0	0	0	0	12	2,2
<i>Dascyllus trimaculatus</i>	0	0	0	0	0	0	1	5,97	1	5,97
<i>Calotomus spinidens</i>	1	-	0	0	0	0	3	35,55	4	35,55
<i>Leptoscarus vaigiensis</i>	6	1,29	2	1,27	1	2,16	5	72,81	14	77,53
<i>Scarus tricolor</i>	1	4,98	2	2,77	4	12,5	0	0	7	20,25
<i>Dendrochirus brachypterus</i>	0	0	0	0	2	7,94	0	0	2	7,94
<i>Parascorpaena mossambica</i>	9	103,03	2	22,74	0	0	3	18,98	14	144,75
<i>Epinephelus guaza</i>	1	56,39	0	0	0	0	0	0	1	56,39
<i>Siganus sutor</i>	9	86,15	2	22,74	0	0	5	57,26	16	166,15
<i>Solea bleekeri</i>	1	21,23	0	0	0	0	0	0	1	21,23
<i>Crenidens crenidens</i>	2	25,76	1	12,47	0	0	0	0	3	38,23
<i>Hippocampus camelopardalis</i>	0	0	1	1,96	0	0	0	0	1	1,96
<i>Syngnathoides biaculeatus</i>	2	5,99	1	5,12	0	0	0	0	3	11,11
<i>Saurida gracilis</i>	4	36,36	1	10,12	0	0	2	33,77	7	80,25
<i>Ablabys binotatus</i>	0	0	0	0	0	0	1	7,97	1	7,97
TOTAL	118	1376,3	36	315,78	57	355,39	59	531,6	270	2579,04

Table IV- List of species obtained at station III. N - number of individuals, B - biomass (g).

The results of the influence of the moon phases on the abundance and distribution of the fishes indicated that during full moon the individuals were less abundant when compared with the numbers obtained during the new moon.

Cluster analysis and analysis of factorial correspondence of the sixteen samples, based in the number of individuals of the 26 more abundant species, showed that the

structure of the fish community was different at the three areas where the station were located and also during the day and the night (Fig. 2).

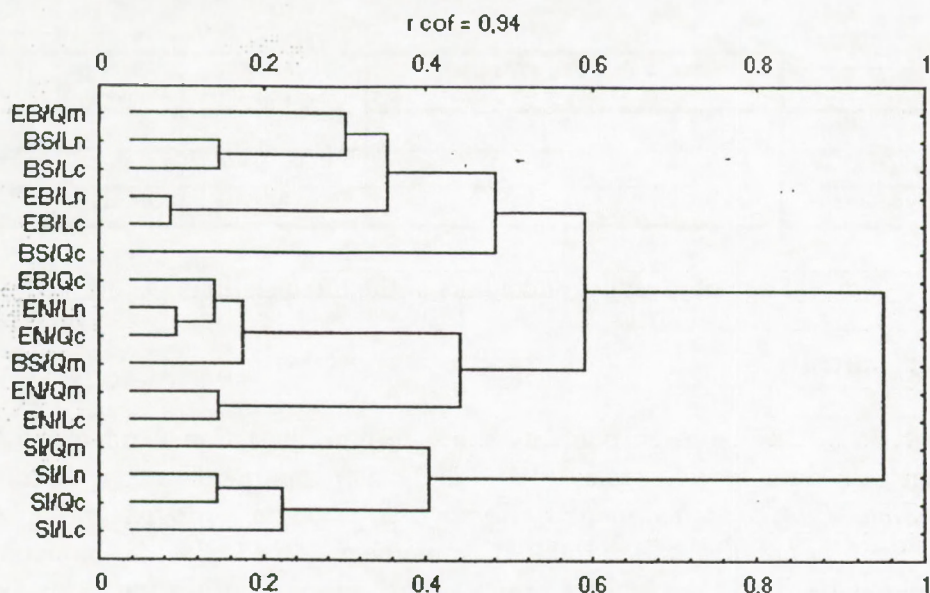


Figure 2. Cluster analysis of the different fish samples collected at Ilha da Inhaca. (BM - Estação de Biologia Marinha (day); EN - Estação de Biologia Marinha (night); IP - Banco da Sangala; SM - Saco; Qm - third quarter of the moon; Ln - new moon; Qc - first quarter of the moon; Lc - full moon)

Table V summarizes the values obtained for the number of species and abundance (in number and biomass) of the individuals obtained in each of the stations as well as the diversity and evenness indices (in number and weight).

	Est. Biologia		Sangala	Saco
	Day	Night		
N. of species	25	32	35	42
N. individuals	229	531	255	267
Biomass (g)	2247,4	5545,86	3740,7	2573,8
Diversity (H'n)	2,42	2,51	2,66	3,01
Diversity (H'w)	2,43	2,47	2,83	3,08
Evenness (En)	1,34	1,49	1,85	1,71
Evenness (Ew)	0,65	0,67	0,67	0,69

Table V - Values of Diversity, Evenness, biomass and number of species and individuals by Station

As shown in table VI the number of young fishes (total length being less than half of the adult's total length) represented almost 50 % of the total catch.

	Estação de Biologia Marinha(I)		Banco de Sangala (II)	Saco da Inhaca (III)	Total
	Day	Night			
Adults (%)	65.1	42.96	56.64	45.42	50.15
Juvenils (%)	34.9	57.04	43.36	54.58	49.85

Table VI - Percent age of juveniles and adults at the three stations

Stomach contents

The analysis of 387 stomach contents show that in all station carnivore fishes are dominant as number of species (16). The most important are: *Parascorpaena mossambica*, *Platycephalus indicus*, *Sorsogona prionata*, *Apogon cooki*, *Apogon nigripinnis*, *Foa brachygramma* (60,9 %) in number and (53,2%) in biomass (table VII). Station III shows the highest values where carnivore fishes represent 79,9% in number and 83,3 % in biomass, perhaps because in this station only a few numbers of omnivores were present and the herbivores were juveniles.

Herbivores are represented with 6 species, the most important being *Leptoscarus vaigiensis* and *Siganus sutor* and Omnivorous with 3 species (Table VII).

	Estação de Biologia (I)						Sangala (II)			Saco (III)			Total (#)		
	Day			Night											
	sp	%N	%B	sp	%N	%B	sp	%N	%B	sp	%N	%B	sp	%N	%B
Carnivorous	16	62,9	43,6	21	58,4	46,7	27	45,1	50	42	79,6	83,2	48	60,9	53,2
Herbivorous	6	14,4	37,7	6	25,4	45,1	5	23	31	6	18,1	13,8	8	21,3	35,3
Omnivorous	3	23,1	18,7	3	16,6	8,2	3	31,9	19	3	2,2	2,9	7	17,7	11,4
<i>L. vaigiensis/</i> <i>Herbivorous</i>	-	27,3	69	-	13,3	52	-	30,5	44,9	-	28,6	21,7	-	21,4	51
<i>S. sutor/</i> <i>Herbivorous</i>	-	27,3	6,5	-	70,4	41,1	-	50,8	40,3	-	32,6	46,6	-	53,6	36,2
<i>P. barnardi/</i> <i>Omnivorous</i>	-	96,2	90,9	-	97,7	97,8	-	97,6	94	-	33,3	21,7	-	95,6	91,5

Table VII - Number of species (sp) of each trophic category and percentage in number (% N) and biomass (% W) for all sampling areas and for the most important species.

DISCUSSION

The results show a great difference between Station III (Saco) and the other stations. In this sampled area - thirteen species - have not been collected in the other stations. These species were already referred in another chapter, the most important being *Foa brachygramma*. The species that are common to all sampling areas, have in Station

III, values of abundance and biomass remarkably different, specially *Paramonocanthus barnardi*, *Sorsogona prionata*, *Prarascorpaena mossambica*, *Lethrinus lentjan*, *Saurida gracilis*, *Aeoliscus punctulatus* and *Syngnathoides biaculeatus*.

Some species are abundant in Station I and II but were not found in Station III: *Pelates quadrilineatus*, *Novaculichthys macrolepidopus* and *Chrysptera annulata*.

There are other differences that clearly distinguish the ichthyological population of Station III from the others. At Station III we found a great proportion of juveniles and there is a species (*Plotosus lineatus*) whose individuals are only juveniles, while in the other stations they are only adults. We found also a greater number of benthic fishes than in the other stations: *Bothus pantherinus*, *Pseudorhombus arsius*, *Cynoglossus durbanensis*, *Papilloculiceps longiceps*, *Platycephalus indicus*, *Sorsogona prionata*, *Solea bleekeri*.

We can notice the almost absence of the omnivorous species and the presence of a few numbers of herbivorous when compared with the other stations. The carnivorous that exist in this area feed on a great variety of preys. These differences can be explained by the fact that at Station III we have an association of seagrass *Thalassia hemprichii* / *Halodule wrightii* that is different from the association we find in the other stations. This kind of association is different from the association *Thalassodendro ciliatum* / *Cymodocea serrulata*, because their leaves are less exuberant and less dense. The area covered by the first association is also smaller than the area covered by the second one and between these seagrass beds we find many voids. These facts may explain the existence of a greater number of exclusive species, mainly benthic fishes and a few numbers of herbivorous at Station III.

We can suggest other possible facts that may cause the structural difference of the ichthyological populations between this station and the others. The proximity of two other ecosystems, a vast mangrove that is practically close to the seagrass beds, and a small barrier of corals.

At low tide the water that had been warmed over the platform of the Saco is pushed offshore towards Ponta de Torres where we find the corals, at high tide the offshore water will cover the area of the Saco and a cold stream is formed. The fishes can use these streams in its movements in order to find a better place to feed or to breed.

Station II (Banco da Sangala) is not very different from Station I but there are some characteristics that distinguish them apart. In this station the Apogonidae is not very representative, only the specie *Apogon nigripinnis* (2 individuals) occur; on the contrary this family is well represented in the other stations, being the most abundant in the Station III. At Station II there are also less known species, such as *Antennarius pictus*, *Arothron immaculatus*, *Hippocampus histrix* and *Hippocampus kuda*.

At Station I we carried out night sampling using trawls and we found that during the night the abundance and diversity of species are greater than during the day.

FISHES OF THE SEAGRASS BEDS OF THE INHACA ISLAND (MOZAMBIQUE) - DYNAMIC, FEEDING HABITS AND SEXUAL DEVELOPMENT OF THREE SPECIES

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Two sampling areas were chosen in order to study the feeding habits of three species of the fish fauna associated with seagrass beds of *Thalassodendro ciliatum* / *Cymodocea serrulata* at Inhaca island (Mozambique). These stations were all located in areas of high densities of seagrass and submitted to exploitation by local population. The thirty-six samples show that the three species studied (*Apogon nigripinnis*, *Leptoscarus vaigiensis* and *Siganus sutor*) the last two are herbivorous and *Apogon nigripinnis* is carnivorous. Males and females *Apogon nigripinnis* are mature between October and March, *Siganus sutor* between September and February, and *Leptoscarus vaigiensis* we have found mature individuals along almost all the year.

Material and methods

Material was collected during the realisation of twelve samplings operations carried out in June 1993 till July 1994 in two stations located in areas of *Thalassodendro ciliatum* / *Cymodocea serrulata* association (fig 1). Sampling was performed during daylight by means of a beam trawl net (rectangular mouth of 50x150 cm and 1 cm mesh lenght) towed during 10 minutes at a velocity of 1.5 knots. At station I sampling was carried out also during the night. The material was obtained at high tide at the first quarter of the moon phases in a total of thirth six samples.

Individuals of *Apogon nigripinnis*, *Leptoscarus vaigiensis* and *Siganus sutor* were measured to the nearest milimeter (total length), and weighted (total weight). The weight of stomach contents were also determined. The stomach content was preserved in 10 % formalin for further analysis.

Results

The thirty six samples supplied 5922 individuals representing 66 species from 30 families. From these we used to our study 486 *Apogon nigripinnis*, 83 *Leptoscarus vaigiensis* and 1232 *Siganus sutor*

Apogon nigripinnis

At Station II (fig 2) this specie was only caught in March an April, that can be related with the hatching period. Its clear that this specie is more abundant at the seagrass during night.

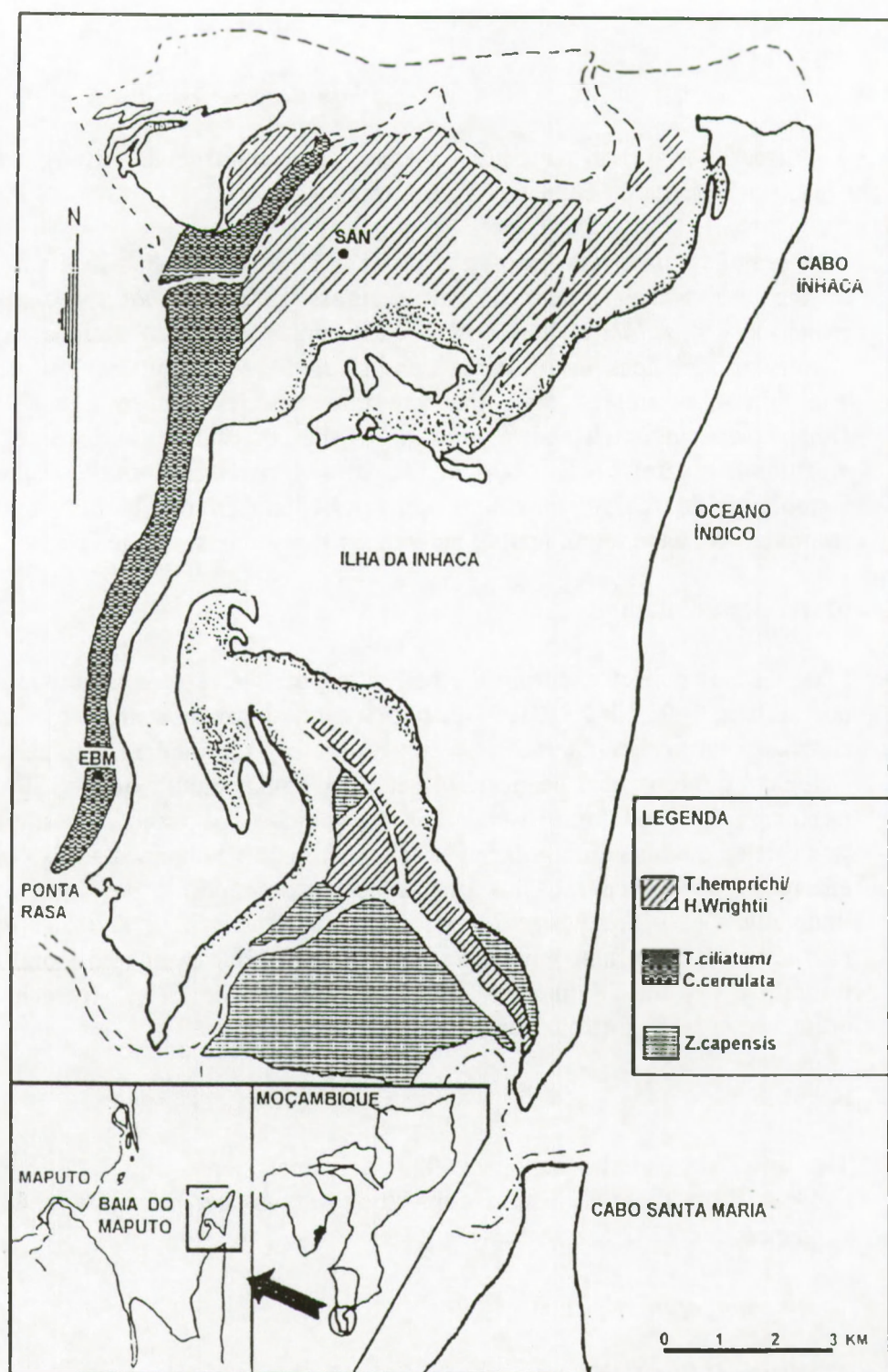


Fig 1 - Sampling areas.:

EBM - Estação de Biologia Marinha - Station I

SAN - Banco da Sangala - Station II

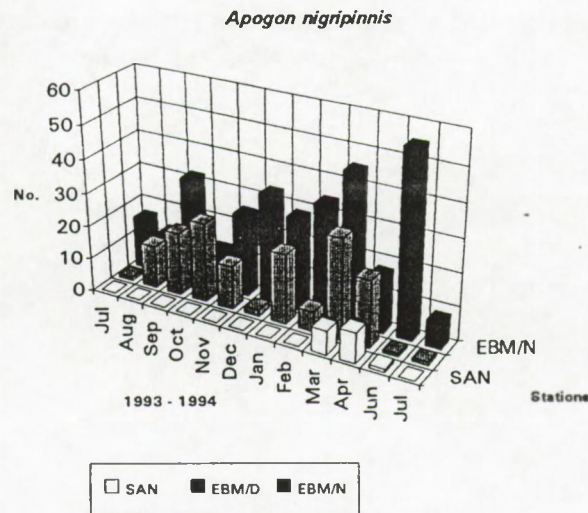


Fig 2 - Distribution number (n°) of *Apogon nigripinnis* along the 12 months

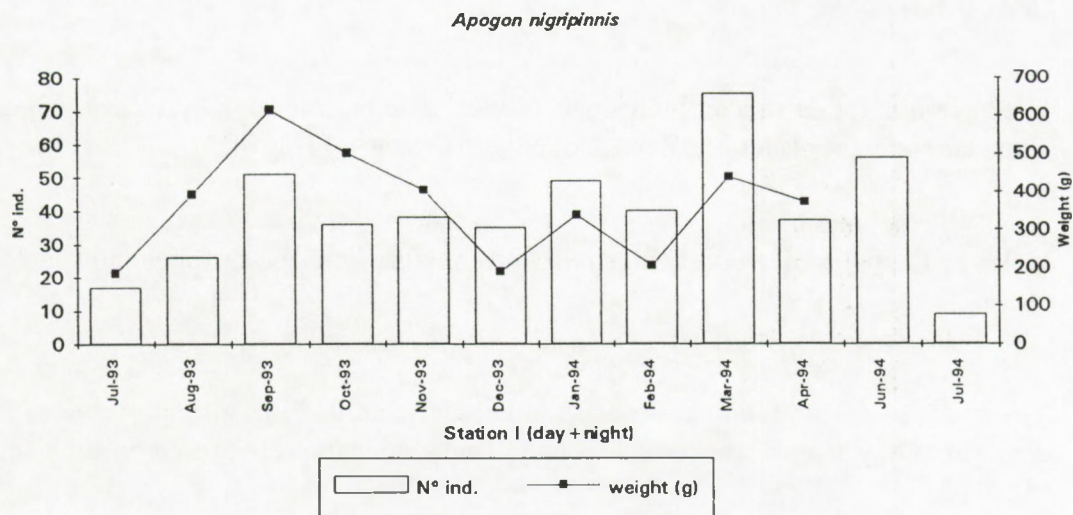


Fig. 3 - Distribution in number and biomass (g) of *Apogon nigripinnis* along the 12 months

At Station I the abundance of *Apogon nigripinnis* is more or less constant with a small peak at March 1994 resulting from the increasing number of young fishes (that explains the low weight of the catch).

September 1993 presented the higher total weight due to the presence of big individual of this specie.

We can verify that at July the number of *Apogon nigripinnis* at the seagrass beds is very low (fig. 3)

Stomach contents

Apogon nigripinnis presented a carnivorous diet (mostly crustaceans) and seems to be more active at night with a vacuity index about 55 %, during the daylight period the vacuity index is 71.23 %

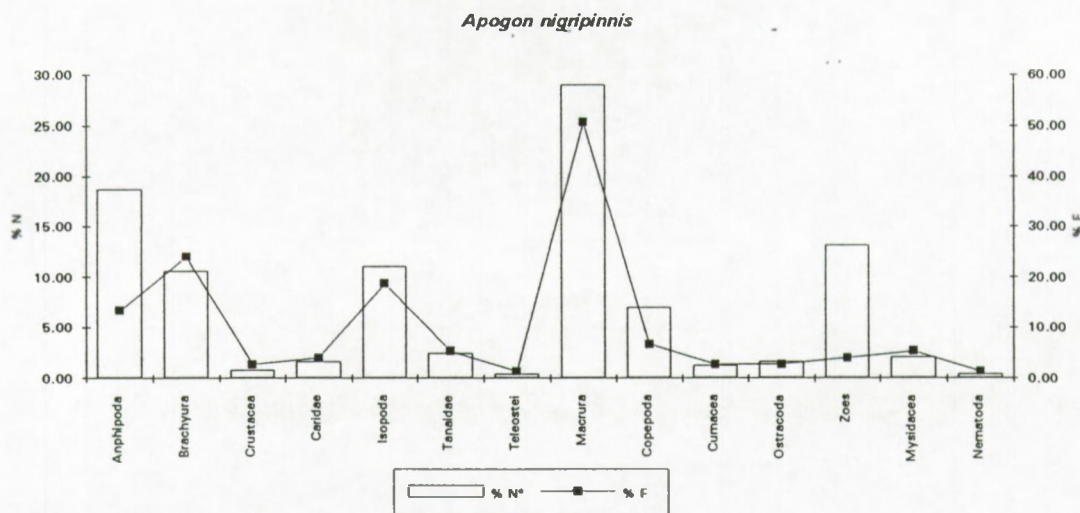


Fig 4 - Diet of *Apogon nigripinnis*

We have found that smaller individuals prefer little crustacean (Mysidacea, Isopoda, Tanaidae) and zooplankton (Zoes, Copepoda, Cumacea) (Fig. 4)

Sexual maturation

Males and females of *Apogon nigripinnis* are mature between October and March

Leptoscarus vaigiensis

This species was not found at Station I in February but its distribution is more or less constant at day samples, nevertheless only few individuals were present in each catch (fig 5)

The catch at night is more abundant but also more irregular (fig 6).

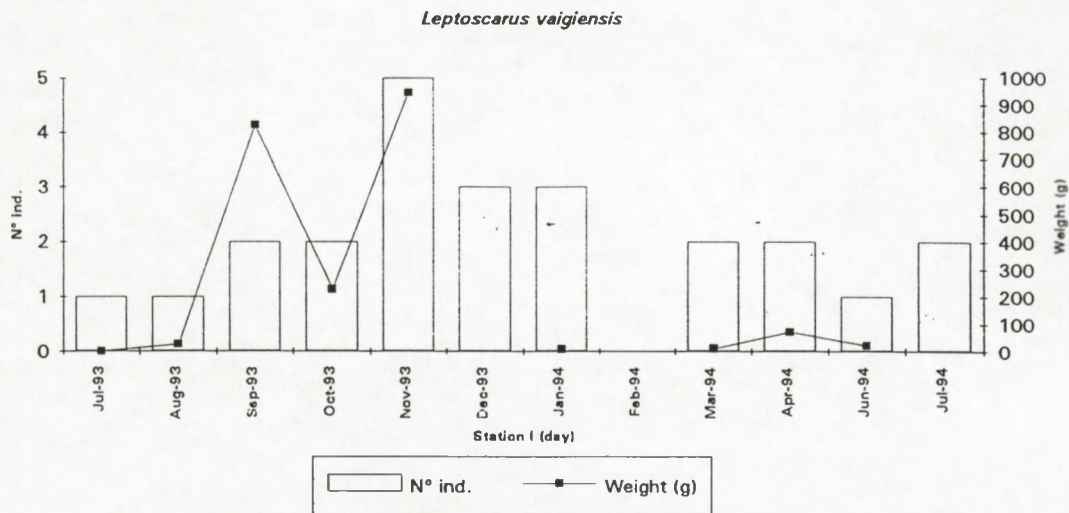


Fig 5 - Distribution in number and biomass (g) of *Leptoscarus vaigiensis* along the 12 months at Station I (daylight samples)

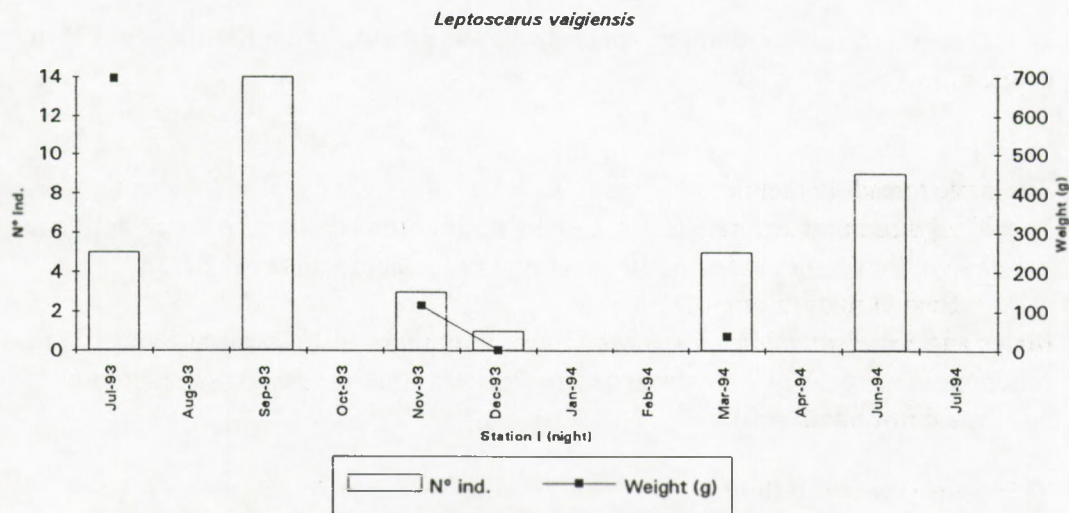


Fig 6 - Distribution in number and biomass (g) of *Leptoscarus vaigiensis* along the 12 months at Station I (night samples)

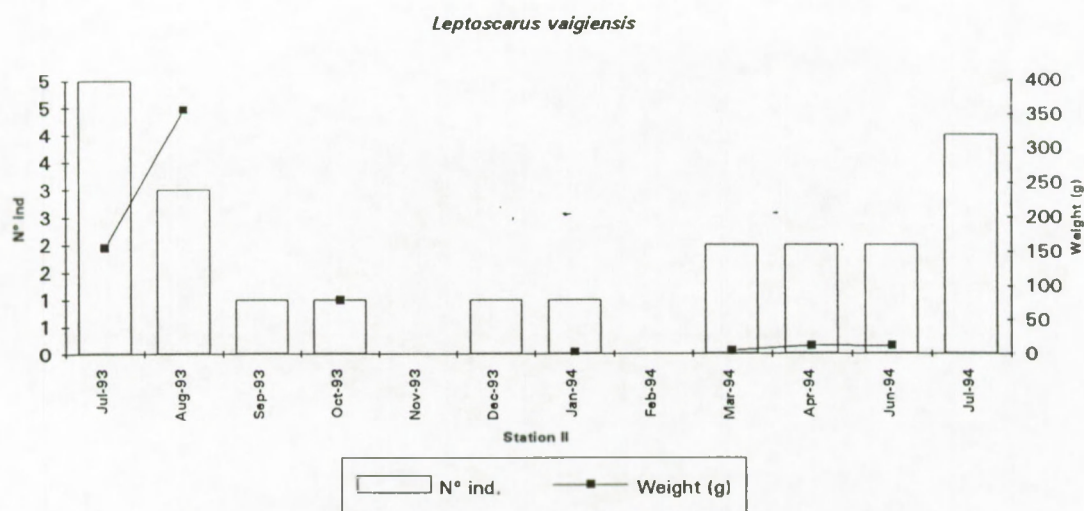


Fig 7 - Distribution in number and biomass (g) of *Leptoscarus vaigiensis* along the 12 months at Station II

Is interesting to remark that this species was absent at the two Stations, in February (Figs. 4,5,6)

Stomach contents

Leptoscarus vaigiensis presented a herbivorous diet and is more active during the day with a vacuity index of 40 % at night the vacuity index is 82.35 %

The diet of *Leptoscarus vaigiensis* is composed by seagrass and we find also others items like Algae, Hydrozoa and Porifera, that are seagrass epibiontes and are consumed not intentionally

Sexual maturation

Mature individuals of *Leptoscarus vaigiensis* were found almost along all the year.

Siganus sutor

Siganus sutor is the most important specie in number and biomass (figs 8,9,10)

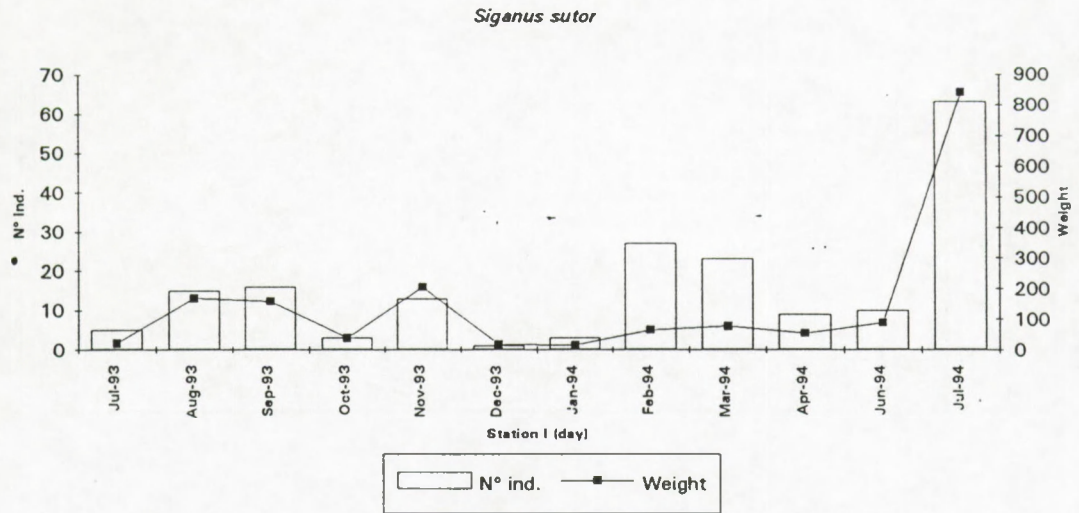


Fig 8 - Distribution in number and biomass (g) of *Siganus sutor* along the 12 months at Station I (day samples)

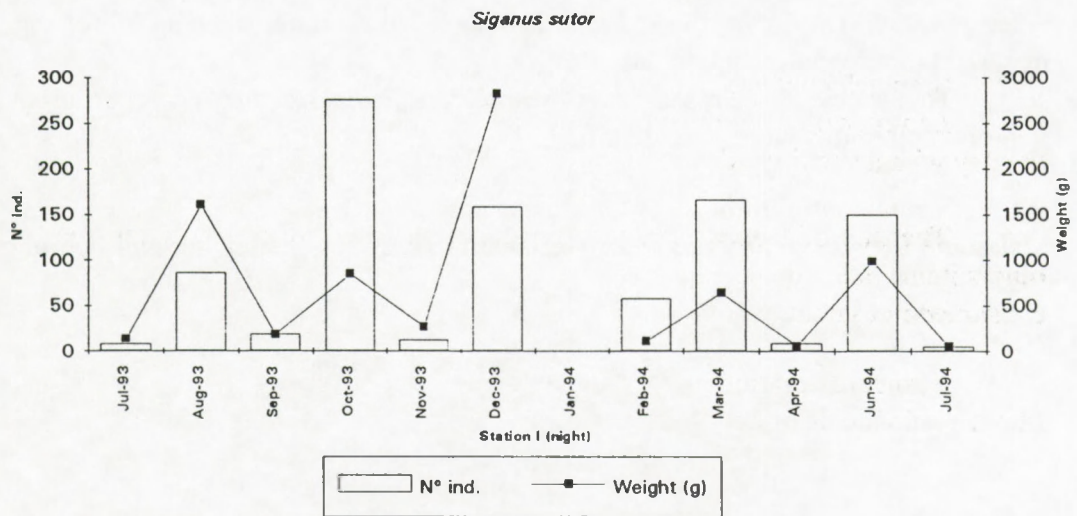


Fig 9 - Distribution in number and biomass (g) of *Siganus sutor* along the 12 months at Station I (night samples)

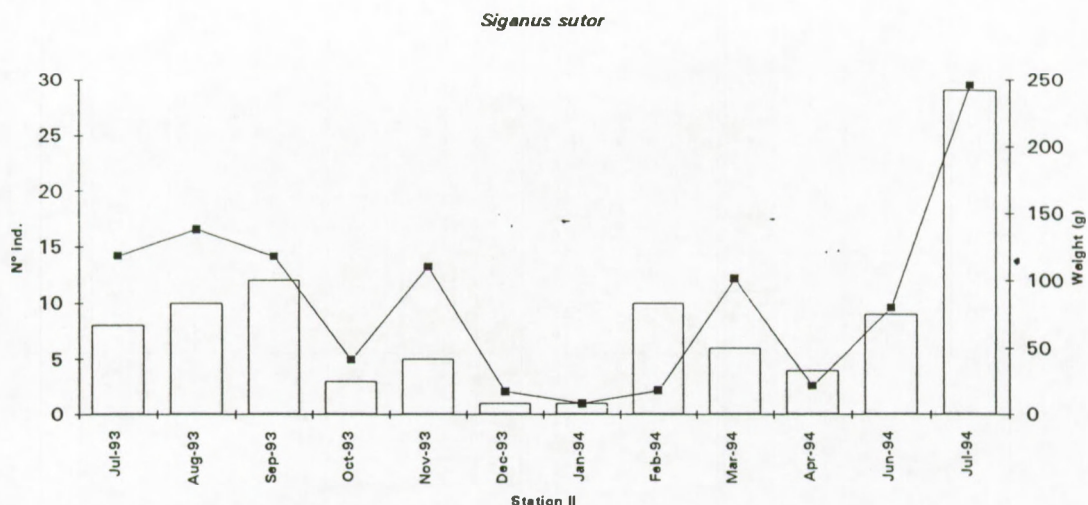


Fig 10 - Distribution in number and biomass (g) of *Siganus sutor* along the 12 months at Station II

Stomach contents

Siganus sutor presented a herbivorous diet eating at daylight time (vacuity index 14.06 %). At night, the stomach is empty, but the intestine was full of digestion material (vacuity index 93.44 %)

This specie also eat seagrass (*Cymodocea*, *Thalassia* and *Syringodium*) and seagrass epibiontes were also identified.

Sexual maturation

Males and females of *Siganus sutor* were mature between September and February.

MANGROVE FISHES FROM INHACA ISLAND (MOZAMBIQUE)

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Two sampling areas were chosen in order to study the fish fauna associated with mangrove at the Saco da Inhaca. The feeding habits and sexual development of *Ambassis natalensis* was observed.

Those sampling sites were all located in areas submitted to commercial exploitation by local population.

Material and methods

From September 1994 till February 1994 sampling was performed every month with baited traps but as this method was not efficient we started to use beam trawl nets since March 1994 to July 1995 in two stations located at Saco da Inhaca (Fig. 1).

Sampling was performed during daylight time at high tide with "tapa esteiros" with 45 m length and 0.5 cm mesh aperture.

The collected individuals were identified and measured to the nearest millimetre (total length), and weighted (total weight). The weight of the stomach contents of *Ambassis natalensis* were also determined. The stomach content was preserved in formaline (10 %) for further analysis.

Results

The baited traps sampling supplied 48 individuals (total weight 425.5 g) representing 12 species from 10 families (Table I). Gobiidae was the best represented familie, with 3 species.

The four samples made with de net supplied 1882 individuals (total weight 8967 (g) representing 35 species from 23 families (table II). Gobiidae was also the best represented familie, with 4 species.

Ambassis natalensis is the most abundant species representing 48 % of the total catch, and 16 % of the total weight.

Liza macrolepis is the most important presence in biomass with 38 % of the total catch weight and the second species in number, representing 15 % of the total catch.

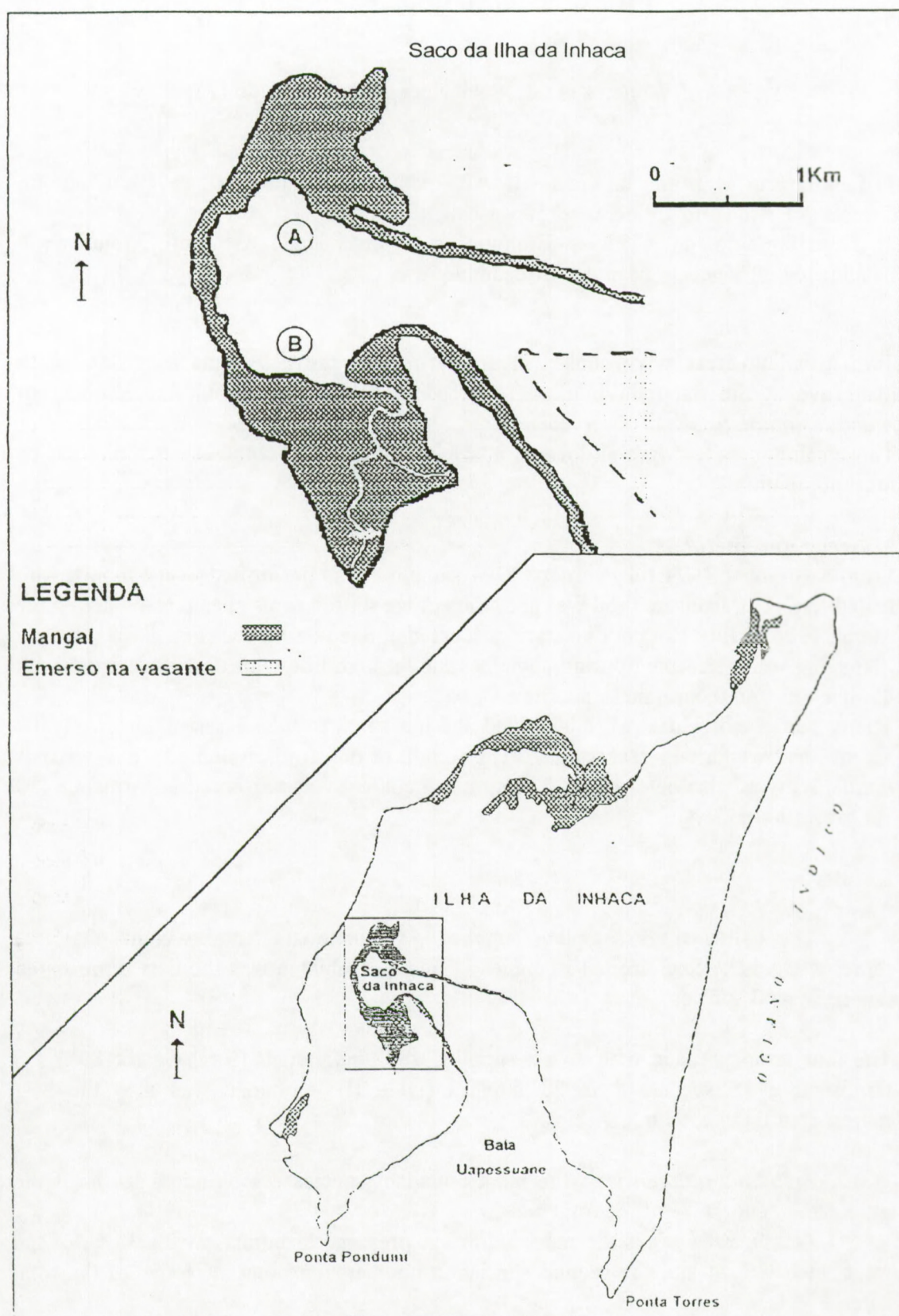


Fig 1 - Sampling areas - Saco da Inhaca

Table I

Month	9	9	10	10	11	11	12	12	1	1	Total	Total
Fishes at Mangrove Saco	N°	Wg	N°	Wg	N°	Wg	N°	Wg	N°	Wg	N°	W g
<i>Platycephalus indicus</i>							2	120			2	120
<i>Ambassis natalensis</i>	14	17	6	5.5			4	4	5	7.5	29	34
<i>Terapon jarbua</i>							3	13			3	12.5
<i>Apogon savayensis</i>	1	2									1	2
<i>Lethrinus rubrioperculatus</i>	2	6.5									2	6.5
<i>Sillago sihama</i>					1	26					1	26
<i>Liza macrolepis</i>					2	203					2	203
<i>Oligolepis keiensis</i>									2	2	2	2
<i>Amoya signatus</i>					1	1.5					1	1.5
<i>Yongeichthys nebulosus</i>			1	2	1	3					2	5
<i>Pseudorhombus arsius</i>									2	12	2	11.5
<i>Arothron immaculatus</i>					1	1.5					1	1.5
N° indi.	17		7		6		9		9		48	
N° species	3		2		5		3		3			
Total Weight (g)		26		7.5		235		137		21		425.5
Total species 12												

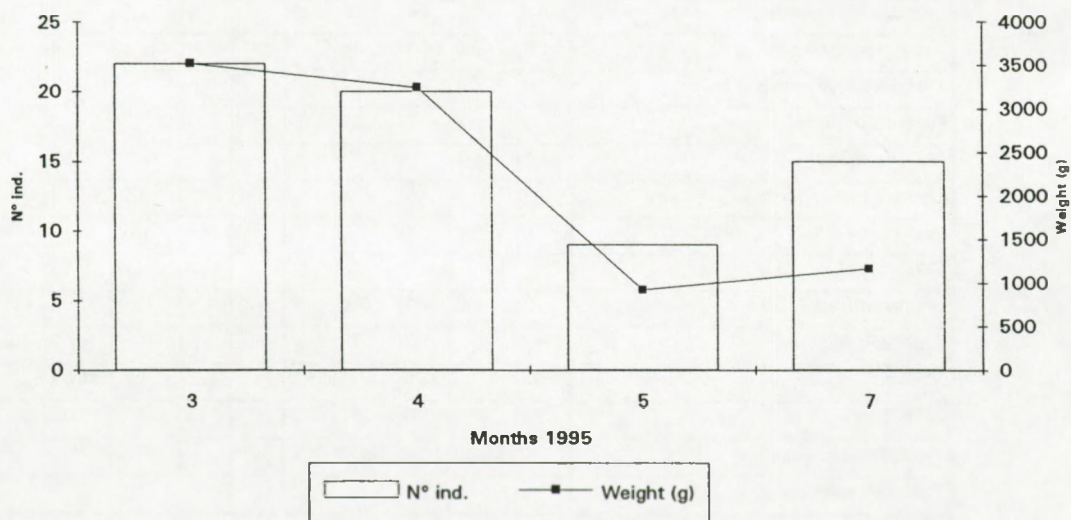


Fig. 2 - Distribution in number and biomass (g) of the total catch with the net during four months.

Table II

Month	3	3	4	4	5	5	7	7	Total	Total
Fishes at Mangrove Saco	N°	Wg	N°	Wg	N°	Wg	N°	Wg	N°	W g
<i>Ariosoma scheelei</i>	1	2							1	2
<i>Pisodonophis cancrivorus</i>			1	108					1	108
<i>Stolephorus holodon</i>			3	6					3	6
<i>Vinciguerria attenuata</i>			1	1					1	1
<i>Synodus variegatus</i>							1	1.5	1	1.5
<i>Hypoatherina temminckii</i>	7	20	39	94			1	3.5	47	117.5
<i>Fistularia commersonii</i>							1	2.5	1	2.5
<i>Platycephalus indicus</i>	5	301	9	569	1	25	1	40.1	16	935.1
<i>Ambassis natalensis</i>	254	406	302	684	108	183	238	188	902	1460
<i>Terapon jarbua</i>	107	513	91	423			1	9.5	199	945.5
<i>Pelates quadrilineatus</i>					2	21			2	21
<i>Apogon savayensis</i>	5	4							5	4
<i>Pomadasys commersonnii</i>			1	8					1	8
<i>Plectorhinchus gaterinus</i>							3	1.5	3	1.5
<i>Rhabdosargus thorpei</i>	1	14							1	14
<i>Acanthopagrus berba</i>					1	45			1	45
<i>Lethrinus rubrioperculatus</i>	1	4							1	4
<i>Gerres acinaces</i>	47	86	59	137			7	14	113	237
<i>Gerres filamentosus</i>	1	12			1	5.5			2	17.5
<i>Sillago sihama</i>	21	81	27	140	17	249	18	202	83	671.5
<i>Caranx sem</i>	1	4	5	25	1	11			7	40
<i>Caranx papuensis</i>	1	30							1	30
<i>Scomberoides commersonnianus</i>							1	7.5	1	7.5
<i>Liza macrolepis</i>	132	1741	93	826	26	385	39	532	290	3484
<i>Valamugil cunnesius</i>			11	171			4	131	15	302
<i>Oligolepis keiensis</i>	43	22	28	12	2	2	6	3.5	79	39.5
<i>Amoya signatus</i>	23	23	41	38					64	61
<i>Yongeichthys nebulosus</i>	9	54	4	24					13	78
<i>Fusigobius longispinus</i>	1	2	1	2					2	4
<i>Eleotris fusca</i>	1	1							1	1
<i>Eleotris melanosoma</i>	1	4							1	4
<i>Pseudorhombus arsius</i>	4	198					2	8	6	206
<i>Solea bleekeri</i>			9	68			3	24	12	92
<i>Arothron immaculatus</i>	3	2.5	1	0.5					4	3
<i>Arothron hispidus</i>			2	12					2	12
N° indi.	669		728		159		326		1882	
N° species	22		20		9		15		35	
Total Weight (g)		3523		3241		926		1168		8967
Total 35 species										

Sexual maturation

Males and females of *Ambassis natalensis* are mature in March, in April some of them have layed eggs already

Somach contents

Ambassis natalensis presented a carnivorous diet essentially composed by zooplankton and with a small vacuity index at daylight time (20.31 %)

